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BOTANICAL CHECKLISTS

Orchids of the Principality of Asturias (Northwestern Spain)

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Abstract. In this study we present a review of the orchid family in the Principality of Asturias, Northwestern Spain. The study area covers 10,000 km^2 for which we have compiled and curated up to 9,197 records coming from several sources: fieldwork, herbaria, specialized publications, gray-literature, citizen science platforms, Global Biodiversity Information Facility (GBIF), and social media. The territory comprises 52 confirmed species and 13 hybrids, with 16 other plausibly present species being discussed and another 6 explicitly dismissed. *Gymnadenia densiflora* (Wahlenb.) A. Dietr. and all nothotaxa, except those in *Serapias*, represent novelties for the area. For each of the 52 species, we provide a brief description of their habitat, altitudinal range and flowering period. Additionally, we present a statistical exploration of the main drivers of orchids' ecology and distribution in the territory. Our review demonstrates how the Principality of Asturias, despite its marginal geographic position away from major diversification centers, and the scarcity of detailed floristic studies and, in particular, of those specifically focused on orchids, qualifies as a significantly orchid-rich region within the European context, even when judged by the demanding standards of the rich Iberian flora. The role of citizen science, particularly triggered by these cherished plants, has been and will continue to be crucial in perfecting our knowledge of Asturian orchids.
Keywords: Atlantic flora, Cantabrian Mixed Forests, Cantabrian Mountains, checklist, citizen science, herbarium, Orchidaceae.

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Introduction

Orchids are botany's poster children. Their privileged status rests, on the one hand, in their profound scientific interest, spurred by Charles Darwin himself (Darwin, 1862; Arditti *et al*., 2012) and grounded on the interconnected evolutionary processes responsible for their huge diversity (Givnish *et al*., 2015; Baguette *et al*., 2020; Pérez-Escobar *et al*., 2024), their unique ways of pollination and dispersal, the dependency of their tiny seedlings on fungal partners, including instances of full mycoheterotrophic parasitism (Ogura-Tsujita *et al*., 2009), and the growing rarity of most of the few assessed species (Cribb *et al*., 2003; Vogt-Schilb *et al*., 2015; Vitt *et al*., 2023). On the other hand, the odd looks of their flowers —a veritable showcase of shapes, colors, textures, arrangements and sizes— provide an instant cure for even the most severe cases of plant blindness (Colon *et al*., 2020), an effect compounded by the growing public awareness of their intricate, often unbelievably deceptive and almost admirably and even eerily cunning sexual lives (Karremans, 2023). Biology aside, the word orchid evokes in many minds a seductive mix of exotic locations, adventurous quests and sheer luxury, not to mention the notorious cases of feud and treachery, even beyond the grave (Orlean, 1998; Dressler, 2004; Cribb, 2005).

Blessed with such unusual levels of public appreciation compared to most other plants, and as this very paper will support, orchids are disproportionately heeded in citizen science initiatives, as well as, more generally, among amateur botanists (Marcenò *et al.*, 2021), and therefore poised to be the key to lure new generations of dedicated naturalists into wider, 'less glamorous' expanses of field botany. An endeavor traditionally under-pursued in Spain despite the incomparable riches of the country and despite how an efficient recognition of plants in the field (Gómez, 2007), by literally exposing it to the light, conveys vast amounts of ecological information. The occasionally abstruse and dull intricacies of plant nomenclature and typification, notoriously involving baffling name

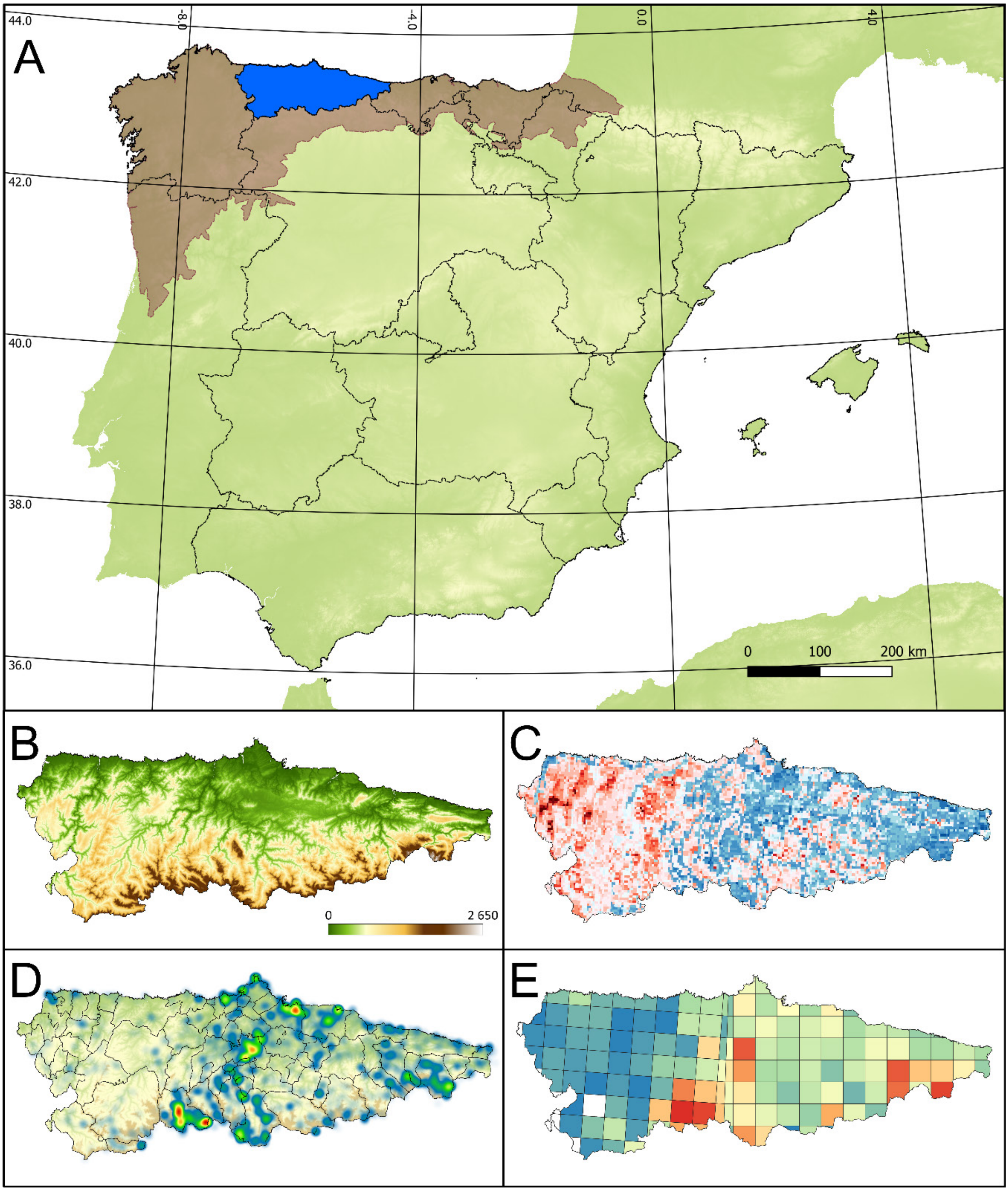

Figure 1. General features of orchids in the Principality of Asturias. A, Location within the Iberian Peninsula (●) and the Cantabrian Mixed Forests ecoregion (●); B, hypsometric map; C, map of soil pH, with blue colors indicating basic soils (●) against the acid soils (●); D, heatmap of the geolocalized records for the orchid family in Asturias; E, species richness of the Orchidaceae family in Asturias by 10×10 km UTM grid: warmer colors indicate a greater diversity of species, while uncolored squares indicate absence of records. Only records of the 52 species confirmed to occur in the region were used to produce maps D and E.

changes but whose mastery is necessary for any serious botanist (Knapp *et al*., 2004), become more palatable —so our hope goes— when using the cherished orchids as excipient. In this vein, this article prelude of a future, comprehensive field guide aims at providing an updated, critically discussed, nomenclaturally conscientious, duly documented and ecologically informed catalogue of the orchids of Asturias, a northern Spanish territory boasting of its admittedly sizable biodiversity but where botany is increasingly underrepresented in an already modest, if enthusiastic, community of naturalists.

Materials and Methods

Study area

The Principality of Asturias, in the northwestern corner of the Iberian Peninsula (Figure 1A), covers around 10,000 km^2 of very rugged terrain. It is by far the steepest province of Spain, with an average inclination of almost 30° and more than 80 % of its territory above 20° (Goerlich, 2022). Elevation varies greatly from the sea level to 2,650 m asl, temperature regimes accordingly varying from very mild, almost subtropical conditions in the coast with yearly average temperatures above 14°C, to periglacial in the highest areas, including a few still permanent snowfields (Gonzalez Trueba *et al*., 2008). Asturias can be succinctly but still accurately described as the northern, maritime slope, deeply carved by a dense drainage network all down to the sea (Figure 1B), of the highest sector of the Cantabrian Mountains. Its climate being thus characterized, as well as by its oceanity (i.e. small daily and yearly differences in temperature), by a generalized slope effect, with rather abundant rainfall all year round (above 1,000 mm almost everywhere, exceeding 2,000 mm in the rainiest areas) and, typically, with low direct solar irradiation, especially in summer, when maritime winds driven by the Azores High, forced to climb through said mountains, provoke frequent spells of long-lasting and dense cloud cover. As a result, the average direct solar radiation measured during the summer in the Asturian capital, Oviedo, is about half that registered in the city of León, on the other side of the mountains (Sancho Ávila *et al*., 2012).

The complex orography allows for the appearance of certain areas mimicking the Mediterranean, summer-drought prone climate prevalent in the rest of the peninsula (Felicísimo, 1994). Lithologically, Paleozoic rocks predominate, being more ancient, acidic siliceous rocks (quartzites, sandstones, slates) more abundant towards the west and not that old Carboniferous limestones increasingly widespread towards the east, but with high levels of fine-grained intermixing (Figure 1C) as a result of the faults and folds associated with a complex Variscan tectonic feature (“Asturian Arc”), re-exposed during the Tertiary by the Alpine uplift and subsequent erosion (Farias Arquer & Pedreira Rodríguez, 2021). Owing to all this kaleidoscopic variety of climates and lithologies, both nowadays and throughout the Quaternary climate oscillations, the current flora (as eloquently expressed by the orchids themselves, focus of this paper) is a pretty diverse assemblage dominated by widespread denizens of the Atlantic and Middle-European temperate deciduous forests biome (many of which realized their large current post-glacial ranges from refugia located around here) but enriched with a vast array of ancient and recent Iberian endemics, Tertiary subtropical relicts and quite a few Arctic-Alpine and Mediterranean lineages (González-García *et al*., 2024a).

Human transformation of the landscape has been substantial, but not as massive as in other western European regions as a consequence of the combination of the craggy terrain (preventing full-fledged mechanized agriculture) and the humid climate (promoting rapid plant growth and thus, through an efficient retention by roots and a steady supply of organic matter, having precluded, even after millennia with fire as the preferred tool in land management, as widespread and irreversible a soil loss as in truly Mediterranean mountain areas) (González-Álvarez, 2019). Most of the territory is exploited through forestry (with non-native species like *Eucalyptus globulus* Labill. predominating in the lowlands) and extensive cattle rearing (more intensive dairy farming mostly restricted to some areas of the northwestern lowlands). However, especially along the far less populated mountainous southern border, relatively large stands of seminatural forests and scrublands —significantly harboring some of the few remaining western European populations of wolves and brown bears— remain, increasingly so due to the ongoing abandonment of many rural areas. In contrast, the scarce large flat areas (the emerged ancient shore platform or “rasa” along the coast, the central Tertiary Basin and the floodplains of the main rivers), in which comparatively rare habitats like swamps and open wetlands were concentrated and where most of the around 1 million Asturian people dwell, are under growing pressure by their attractiveness to industrial and urban sprawl, their suitability for mechanized agricultural practices and their exposure to alien invasive species (Lázaro-Lobo *et al.*, 2024).

Data collection

After years of mostly casual data gathering, in 2021 we initiated a systematic and ongoing search and centralization of Asturian orchid records to provide solid documentary foundations for a field guide. The present paper, which presents and briefly summarizes all records registered before November 30, 2024, in an illustrated but tersely annotated checklist, can be interpreted as a streamlined blueprint for the future book. As sources of data, we used:

1) Fieldwork across all the territory, especially (for reasons sketched below) in areas rich in limestones (e.g. Picos de Europa National Park, Somiedo Natural Park), both casual and directed to find new populations or corroborate old records. Whenever sensible and documentarily convenient (as is the case with regional novelties), dried specimens were prepared and deposited in the herbarium of the Atlantic Botanic Garden (JBAG by its standard international acronym).

2) A consultation of the Asturian orchid materials kept in the following herbaria: BC (Institut Botànic de Barcelona), COFC (University of Córdoba), FCO (University of Oviedo—complete *in situ* revision), JACA (Pyrenean Institute of Ecology), JBAG (Atlantic Botanic Garden of Gijón—complete *in situ* revision), LEB (University of León), MA (Royal Botanic Garden, Madrid-complete online revision), SEV (University of Sevilla), and UPOS (Pablo de Olavide University).

3) Specialized publications (books, field guides, papers) and *websites* (SIVIM, Anthos, Asturnatura), but also *gray-literature* (online blogs, newspapers).

4) Citizen Science: we also made use of platforms like iNaturalist (www.inaturalist.org) and Observation (observation.org), both through direct consultation and through the creation of some specific projects (https://www.inaturalist.org/projects/orquideas-de-asturias) maintained by the Vegetation and Biodiversity Laboratory of the University of Oviedo and by the Scientific Team of the Atlantic Botanical Garden of Gijón/Xixón, encouraging users to submit their records to these platforms. Since early 2024,

records from a third platform, Biodiversidad Virtual (www.biodiversidadvirtual.org), have been migrated into Observation, enabling their easy incorporation into our database. For "shaded" observations, we personally contacted every observator and asked for the accurate coordinates.

5) GBIF (Global Biodiversity Information Facility, www.gbif.org): since most of the previously mentioned sources end up in this repository, the amount of new information obtained from GBIF was modest, but not negligible.

6) Social media: we compiled information from Instagram, Facebook and other social networks. We contacted many people who shared their observations there, with many of whom we have stayed in contact ever since, obtaining new records. Word of mouth enabled many other people to become interested in the topic, increasing both the quality and quantity of information obtained from this source.

We must clarify that some records could fit more than one category, e.g. the authors have collected some herbarium specimens during this project (author's observations) but also previously (herbaria) and our data have widely contributed to our iNaturalist and Observation projects, representing 38.11% and 0.87% of the respective totals (account as author's observations and not citizen science data), 52.49% in the latter case if we consider the observations of collaborators actively involved in this project. When possible, we recorded not only the species observation and coordinates, but also the elevation, habitat, date of record and phenology. All records were thoroughly reviewed, especially when referring to the rarer species or when their associated geographic information was at odds with all previous, well-established knowledge. We are also aware that some observations can be duplicated, e.g., Anthos takes part of its data from SIVIM and various herbaria; however, we have attempted to minimize duplicates. Also, misidentified records in Citizen Science and Social Media platforms were explicitly corrected as a form of "payment" to the selfless work by basic data providers, as well as a way to improve and encourage future advances in the public knowledge of these plants. Misidentified herbarium specimens from FCO, JBAG and MA were corrected as well. A comprehensive checklist of the species in the territory, along with their distribution, is available in Appendix 1 and Appendix 2, respectively. Additionally, all information gathered, along with the source for each record, is available in Zenodo (Gonzalez-Garcia et al., 2025). A single cautionary restriction concerns the geographic coordinates, which have been deliberately truncated to prevent easy damage to these plants, particularly appealing to the general public for their bizarrely showy flowers, and very sensitive to careless collecting during the flowering season.

All the species and hybrids occurring in the territory, and most of both plausible and doubtful taxa, have been illustrated throughout this work. Yet, although most of the photographs were taken in other territories, we made sure that they belonged to the correct taxon. When this latter case, locality is highlighted with an asterisk (*). Authorship of photographs is indicated by using the name abbreviation in the case of this paper's authors and the complete name otherwise. For relevant novelties, photographs were always taken within the study area (i.e., Principality of Asturias).

Biogeographic spectrum

In order to explore how orchids express the biogeographic make-up of the Asturian flora sketched when describing our study area, we established a very simple set of chorotypes and categorized our species into them after comparing general plots of their ranges (mainly through GBIF) with the explicit diagnoses offered by, for instance, Tison *et al*. (2014) and the BSBI Atlas of 2020 (Stroth *et al*., 2020): 'European' (EUR) includes species more or less widely distributed across European middle latitudes, in the biome of the deciduous broadleaf forests, even if some can extend southwards into the Mediterranean or eastwards into Siberia, and even all around the northern hemisphere; 'Mediterranean' (MED) gathers species whose range hardly, if at all, exceeds a longer or shorter stretch of the Mediterranean basin, including the Iberian Peninsula (i.e., regions whose ancient lowland forests were dominated by sclerophyllous evergreen trees); 'Mediterranean-Atlantic' (MED-ATL) corresponds to cold-sensitive species mainly distributed throughout the Mediterranean region but which —often associated with coastal, warmer areas— reach pretty high latitudes along western mainland Europe and the British Isles; 'Alpine' (ALP), to those species with obvious association with European mountains; 'Endemic' (END), lastly, is an admittedly hodgepodge category assembling species whose range is limited to the Iberian Peninsula or, at most, the neighboring areas of Morocco and France.

Ecology and Phenology

For the following analyses we excluded the records of (i) hybrid taxa, (ii) genus-level identifications and (iii) species whose presence in the territory is still uncertain and rather improbable. However, in the latter case, we kept some of the records by assigning them to the species having been most likely confounded: those records of *Epipactis kleinii* were assigned to *E. atrorubens*, those of *E. tremolsii* to *E. helleborine*, *Ophrys holosericea* to *O. scolopax* and *Orchis olbiensis* to *O. mascula*. Thus, out of the original 9197 records we kept 9082 (98.75%). As a general exploration of the main drivers of orchids' ecology and distribution in the territory, we took all georeferenced records (N=6862, 74.61%) and excluded those with coordinates uncertainty above 1 km, while keeping those with "non-measured" accuracy since most of them correspond to our own observations or to precise personal communications. The final dataset comprises 6379 records (69.36%). However, to avoid oversampling effects, we retained only one observation per species and square kilometer, resulting in a final number of 3254 records (35.38%).

We performed a Principal Component Analysis (PCA) with R version 4.1.3 (R Core Team, 2024), extracting environmental variables from different sources: bioclimatic variables (bio 1 to bio 19) from CHELSA v2.1 (Karger *et al*., 2017), soil variables (weight percentage of the sand particles, weight percentage of the silt particles, weight percentage of the clay particles, cation exchange capacity of soil, volumetric percentage of coarse fragments, soil organic carbon content) from SoilGrids (Poggio *et al*., 2021), soil pH from Hájek *et al.*, (2021), elevation and terrain roughness from EarthEnv (Amatulli *et al*., 2018) and global human modification index from Kennedy *et al*., 2019. Aspect, hillshade and slope were obtained using the digital elevation model (DEM) from EarthEnv and QGIS v3.82.2. PCA was reduced to the first two principal components, with an explained variation of 48.94% and 17.87%, respectively. From them, we selected the variables that contributed the most to each axis (i.e., those with a contribution higher than 0.2 or lower than -0.2), tested their correlations, and retained only the uncorrelated ones (i.e., with a correlation between -0.7 and 0.7). As a result, we kept elevation, bio2 (mean diurnal air temperature range), bio16 (mean monthly precipitation amount of the wettest quarter) and bio18 (mean monthly precipitation amount of the warmest quarter). These variables, along with soil pH, were used to represent the environmental space for each species.

Additionally, we elaborated a bloom calendar for all the species inhabiting the study area. Only observations for which we had a recorded date and the express certainty of anthesis (either full or in coexistence with some already withered, fruiting flowers) were used. In some specific cases, when the flowering date was found on the first or last days of the month, we were less strict and considered the previous or following month, respectively, within the species flowering period. A few aberrant, obviously outlying records (such as one of *Platanthera bifolia* flowering in November in Gozón) were not considered when drawing the calendar but were represented as isolated atypical events.

Results and Discussion

Representativity of the dataset and regional geographic trends

From the start of this project until November 30, 2024, we have assembled 9,197 records of orchids for the Principality of Asturias. However, 8 records that were originally referenced from Asturias actually belonged to other provinces, and the other 23 records had to be removed because they were too vague or unreliable, leaving a final number of 9166 records (99.7%). Of these, 32.81% came from the authors' and active collaborators' observations, 30.27% from citizen science platforms, 17.07% from specialized webography, 7.46% from personal communications, 4.85% from bibliography, 4.44% from herbaria, 1.98% from social media and 1.12% from unspecialized webography. These records belonged to the 52 species and 13 hybrids confirmed to occur in the region, as well as to 6 species whose presence in the region is implausible or, when credible, still unconvincingly supported by material or photographic proof. Additionally, we consider it plausible that at least 16 species that occur in the surrounding territories can be found in the Principality of Asturias (see section "Species to be looked for").

The distribution of both species and records was found to be uneven across the territory, with consistently higher values in Central and Eastern Asturias (Figure 1D). The striking shortage of occurrences in Western Asturias could be attributed, given the low human population density and fewer occasional visitors potentially contributing to citizen science initiatives, to a less intensive surveying effort. However, since an active group of naturalists working in the area, who have achieved an excellent coverage of many other taxonomic groups, do pay attention to orchids, it can be confidently concluded that this scarcity is a genuine phenomenon, most likely linked to the predominantly acid soils. Nevertheless, in greater or lesser degree, this family of vascular plants is distributed throughout the territory, with a clear pattern of increasing diversity eastwards and southwards (Figure 1E), with only eight UTM squares (seven of which, in the border with Galicia, hardly include any Asturian territory) and one municipality (San Tirso de Abres) with no occurrences. The richest UTM square was 29TQH27 with up to 40 species, followed by 29TQH37 (both in Somiedo Natural Park) and 30TUN58 (Picos de Europa National Park) with 33 species, suggestive of real hotspots insofar as they are congruent with the message conveyed by other taxonomic groups (Nagy, 2006; Alonso Felpete *et al*., 2011; Jiménez-Alfaro *et al*., 2013), and fully expectable given the outstanding diversity shown by those areas in terms of elevation, lithology and topography (Moreno *et al*., 2010), as well as their proximity and functional ecological connections with less oceanic areas across the Cantabrian mountains (Peredo *et al*., 2009). The next richest square (30TTP60, with 28 species) is so close to the Asturian capital, Oviedo, that an illusion caused by an increased surveying effort could well be suspected; however, since this high species richness is not at all found in other peri-urban areas (e.g., Gijón, Avilés) with significant peaks in the number of records (Figure 1D), the existence of a genuine hotspot around Oviedo looks very real.

On the other hand, several UTM squares had fewer than 5 species recorded: 7 with 4 species, 8 with 3 species, 11 with 2 species, and 10 with just 1 species (Figure 1E). At municipality level, Somiedo (46 species), Cabrales (36), Quirós (35), Cangas de Onís (32) and Lena (31) head the list. In contrast, the records within the borders of 18 out of the 78 Asturian municipalities correspond to 5 or less orchid species. About the species, 10 species occur in more than 50 of the 149 UTM squares that are partially or completely held in Asturias. Of these species, only two surpass the 100 squares: *Orchis mascula* (117) and *Dactylorhiza maculata* (105); followed by the clearly man-favoured *Serapias lingua* (90), *Ophrys apifera* (84) and *Spiranthes spiralis* (64). In contrast, 16 species occur in 10 squares or less, with *Anacamptis champagneuxii*, *Gymandenia densiflora*, *Ophrys speculum*, and *Orchis spitzelii* being the rarest, having only one confirmed population in the entire territory.

Species novelties

Since the onset of the project, whose first results are summarized in this paper, three species never seen in Asturias (*Gymnadenia densiflora*, *Ophrys speculum*, and *Orchis spitzelii*) have been

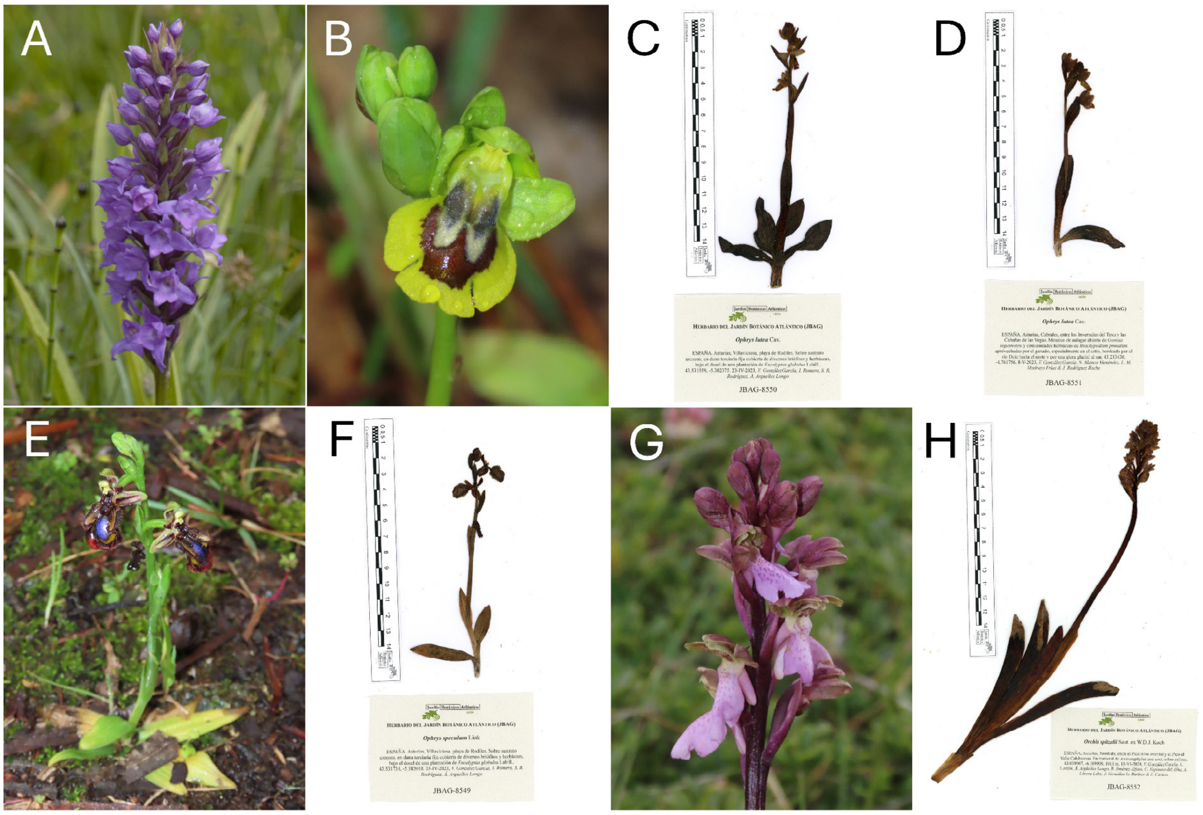

Figure 2. A, *Gymnadenia densiflora* (Lena, 05-VII-2023. David Martín Cisneros); B, *Ophrys lutea* (Villaviciosa, 23-IV-2023. VGG); C, *Ophrys lutea* (Villaviciosa, 23-IV-2023. JBAG-8550); D, *Ophrys lutea* (Cabrales, 8-V-2023. JBAG-8551); E, *Ophrys speculum* (Villaviciosa, 23-IV-2023. VGG); F, *Ophrys speculum* (Villaviciosa, 23-IV-2023. JBAG-8549); G, *Orchis spitzelii* (Somiedo, 13-VI-2024. VGG); H, *Orchis spitzelii* (Somiedo, 13-VI-2024. JBAG-8552).

discovered. Additionally, unpublished records of a fourth species (*Ophrys lutea*) were confirmed in the same location and found anew elsewhere.

Gymnadenia densiflora (Wahlenb.) A. Dietr.: 30TTN6364. Lena, mountain pastures of La Cubilla; 1500 m asl, flooded meadow on limestones. David Martín Cisneros & Gilberto S. Jardón, 05-VII-2023 (photograph, Figure 2A). In the same locality, upon reviewing the records, we found other orchids, such as *Dactylorhiza fuchsii*, *D. incarnata*, and *Gymnadenia conopsea*, as well as many other species typical of alkaline fens, including *Carex echinata* Murray and *Equisetum variegatum* Schleich. ex F.Weber & D.Mohr, *Eriophorum latifolium* Hoppe, *Mentha longifolia* (L.) L., *Parnassia palustris* L., *Pinguicula grandiflora* Lam., *Selaginella selaginoides* (L.) P.Beauv. ex Schrank & Mart. and *Swertia perennis* L. This taxon was originally described as *Orchis conopsea* var. *densiflora* Wahlenb., which is why, in *Flora iberica*, it is merely mentioned as an unimportant variety of *G. conopsea* (Aedo, 2005a). However, *G. densiflora* had been previously recorded for the Iberian Peninsula (Hermosilla, 1999), although misidentified in the first place as a hybrid between *G. conopsea* and *Anacamptis pyramidalis* (L.) Rich. (Hermosilla & Sabando, 1998). Benito Ayuso (2017) greatly improved our knowledge by reporting this species for several provinces (Girona, Guadalajara, Huesca, León, La Rioja, Soria, Teruel and Álava), and clarified its diagnosis against *G. conopsea*, more related to *G. odoratissima* (L.) Rich. (Marhold *et al.*, 2005; Benito Ayuso 2017). Although the validity of the alleged morphological differences between *G. conopsea* and *G. densiflora* has proven to be quite controversial, recent phylogenetic studies support the status of *G. densiflora* as a distinct species, closely related to the sister genus *Nigritella* (Bateman *et al.*, 2003; Stark *et al.*, 2011; Piñeiro Fernández *et al.*, 2019). The closest populations to the Asturian one would be those in the bordering province of León (Leonese Eastern Mountains) (Diez Santos, 2022); where, in comparison with the situation observed in the Asturian locality, grazing pressure by cattle is far less intense, enabling the co-occurrence of more sensitive species (e.g. *Epipactis palustris*).

Ophrys lutea Cav.: it was collected for the first time in the municipality of Villaviciosa (30TUP0722) in 2007 (FCO-030270), but its discoverer then, Herminio Nava, suspecting that its very local occurrence in such an anthropized and touristic locality could be the result of an ephemeral human introduction, refrained from including the species in the regional checklist of vascular plants (Fernández Prieto *et al.*, 2014). However, in 2023 we rediscovered this same population (Figure 2B, C) and found a new one in Picos de Europa National Park (30TUN5686; Figure 2D) (González-García *et al.*, 2024b), confirming beyond any reasonable doubt the native status of the species in Asturias.

Ophrys speculum Link, nom. cons.: found for the first time in Asturias in 2023, in Villaviciosa municipality (30TUP0722; Figure 2E, F), sharing space with several other orchid species

(González-García *et al.*, 2024b), including the already mentioned *Ophrys lutea*.

Orchis spitzelii Saut. ex W.D.J. Koch, saltem s.l.: found for the first time in Asturias in 2024, very localized in an *Arctostaphylos uva-ursi* (L.) Spreng. scrub above the treeline in Somiedo (29TQH3569; Figure 4G, H). Despite showing some characteristics (namely the relatively short spur) of the southern morphotype widespread in Spain and generally admitted as a separate species under the name *O. cazorlensis* Lacaita, Asturian plants are in our view sufficiently similar to the true Central European *O. spitzelii* (especially in the pretty deeply coloured labellum, its margins rolled inwards) as to be preferably labelled under that name (González-García *et al*., 2024c). Anyway, the relevance of this naming dilemma is lessened by the fact that such apparent geographic transitions point at the convenience of adopting a subspecific treatment for this set of morphotypes.

Hybrids novelties

Besides the species just discussed, the finding of several previously unrecorded hybrids in the Principality of Asturias represents a positive result of our survey. The newest version of the regional catalogue of vascular plants (Fernández Prieto *et al*., 2014) includes only three hybrids: *Serapias ×alfredii* Briq. (syn. *Serapias ×rainei* E.G.Camus; *Serapias cordigera* L. × *Serapias parviflora* Parl; Figure 3O), *Serapias × ambigua* Rouy (*Serapias lingua* L. × *Serapias cordigera;* Figure 3N) and *Serapias ×todaroi* Tineo (*Serapias lingua* × *Serapias parviflora*; Figure 3P). Afterwards, the intergeneric ×*Gymnigritella pyrenaica* E. Hermos. & Sabando, a hybrid between *N. gabasiana* and *G. conopsea*, was convincingly cited (Moreno Moral et al., 2020). However, due to the lack of any herbarium or photographic voucher, we have excluded this name from the first version of the checklist, in accordance with our criteria. However, during the course of this project we have found several novel nothotaxa: ×*Dactylodenia heinzeliana* (Reichardt) Garay & H.R. Sweet, *Dactylorhiza ×delamainii* (G. Keller ex T. Stephenson) Soó, *Dactylorhiza insularis* × *Dactylorhiza sambucina*, *Dactylorhiza ×kerneriorum* (Soó) Soó, *Ophrys ×fonsaudiensis* Soca, *Ophrys ×fraresiana* M.R. Lowe, Piera & M.B. Crespo, *Ophrys ×minuticauda* Duffort, *Orchis ×penzigiana* A.Camus and *Orchis ×loreziana* Brügger. Additionally, we have been communicated about the presence of another hybrid: *Dactylorhiza ×guillaumeae* Chr. Bernard, which would be the hybrid between *D. incarnata* and *D. sambucina*. This nothotaxon would be present in Somiedo Natural Park, specifically in Saliencia lakescape. Since both putative parental species thrive all around, often in close proximity, the presence of the hybrid seems likely. However, we are forced to maintain this nothotaxon out of this version of this checklist due to the lack of tangible evidence supporting its presence in the territory.

×***Dactylodenia heinzeliana*** (Reichardt) Garay & H.R. Sweet (*Dactylorhiza fuchsii* (Druce) Soó × *Gymnadenia conopsea* (L.) R.Br.): 30TTN7465. Lena, Payares mountain pass, La Calera; 1250 m asl, mountain meadow on limestones, with the presence of some shrubs, such as *Ulex gallii* Planch. and *Erica vagans* L. VGG & AAL, 30-VI-2024 (JBAG 8553; Figure 3A, B). Two plants found growing with numerous other orchids: *Dactylorhiza fuchsii*, *D. maculata*, *D. viridis*, *G. conopsea*, *Himantoglossum hircinum*, *Listera ovata*, *Ophrys apifera*, *O. insectifera* and *Orchis anthropophora*. Both plants presented features intermediate between both parental species, with a general *Dactylorhiza*-like aspect, including modestly-spotted leaves, but *Gymnadenia*-scented and thin-spurred flowers.

Dactylorhiza* × *delamainii (G. Keller ex T. Stephenson) Soó (*Dactylorhiza elata* (Poir.) Soó × *Dactylorhiza maculata* (L.) Soó): 29TPJ7511. Boal, road from Boal to Penouta; 575 m asl, roadside, in a wet meadow, co-occurring with both parental species. Gilberto S. Jardón, 28-V-2024 (photograph, Figure 3C). Several plants, all of which present characteristics intermediate to those of both parental species, namely the combination of thin spurs (closer to *D. maculata*) and hollow stems (diagnostic of *D. elata*). We kept this name despite that it was initially conceived just to name the hybrid whose parent was *Dactylorhiza sesquipedalis* (Willd.) M. Laínz., which would be the one occurring in the territory, if accepted as a taxonomic entity.

Dactylorhiza ×hjertsonii P.P. Ferrer, J.L. Lozano, R. Roselló, Feliu & Peña-Riv. (*Dactylorhiza elata* (Poir.) Soó × *Dactylorhiza fuchsii* (Druce) Soó) 30TTN6293. Morcín, La Carbayosa; 560 m asl; roadside, wet grassland next to limestones where water seeps, co-occurring with both parental species and also with *Orchis mascula* and *Platanthera bifolia*. Jorge Rodriguez Pérez & Elena Bravo Chaparro, 01-VI-2023 (photograph, Figure 3D). The thin spur, long middle lobe of the lip, spotted leaves (typical of *D. fuchsii*) and the dense, long inflorescence and large size (proper to *D. elata*) neatly reveal the hybrid origin of those plants. 30TTN6193. Morcín, Vega Les Bobies; 900 m asl, in wet mountain meadow on limestones, on the verge of the road, accompanied by *Pinguicula grandiflora*, AAL & LCR, 04-VII-2024 (photograph; Figure 3E). Two plants co-occurring with *Gymnadenia conopsea, D. fuchsii* and *D. maculata*. *D. elata* was absent from this exact location, but was found in proximity, growing in a grazed alkaline fen among *Juncus* spp. and *Eriophorum latifolium*. Both plants seen in Morcín were morphologically closer to *D. elata,* but their slightly spotted leaves and the long and thin spurs of their flowers strongly suggested the involvement of *D. fuchsii*. In their general appearance, these plants were quite similar to the original material used to formally describe this hybrid (Ferrer-Gallego *et al*., 2018).

Dactylorhiza insularis (Sommier) Landwehr × ***Dactylorhiza sambucina*** (L.) Soó: 29TQH2471. Somiedo, Braña de Mumián; 1400 m asl, mountain pasture on limestone with scattered *Cytisus* spp. and *Genista hispanica* L. and the presence of both putative parental species, along with other orchids such as *Orchis anthropophora*, *O. mascula* and *Dactylorhiza cantabrica*. VGG & Nacho Blanco

Menéndez, 1-V-2023 (photograph, Figure 3F); pinkish tones on the lip. 29TQH2569. Somiedo, Llamardal; 1235 m asl, mountain pasture on limestones. Presence of both putative parental species VGG & Nacho Blanco Menéndez, 1-V-2023 (photograph, Figure 3G). Although further, ideally molecular and karyological verifications would be desirable, this is how we interpret the origin of these plants, which mostly resemble *D. insularis*, except for the sometimes pinkish color of the labellum, the high number of spots on it, and the thick spur reminiscent of *D. sambucina*. Since the pollinia of *D. insularis* seems to be atrophied and sterile, the most likely explanation for the origin of this hybrid, if confirmed as such, is the successful fertilization of *D. insularis* by pollinia from a nearby *D. sambucina*. In any case, the alluded presumed hybrids are clearly different from surrounding plants referable to *D. cantabrica* (Pardo Otero *et al.*, 2024), which is also a triploid hybrid stabilized by apomixis but, inversely to *D. insularis*, with two genomes of *D. sambucina* and one of *D. romana* s.l. We have not found any published name for this putative hybrid, even though it is mentioned in the description of *D. cantabrica* (Pedersen, 2006). However, until the above required evidence is amassed, we will refrain from formally describing and naming it.

Dactylorhiza* × *kerneriorum (Soó) Soó (*Dactylorhiza incarnata* (L.) Soó × *Dactylorhiza fuchsii* (Druce) Soó). 30TTN6264. Lena, mountain pastures of La Cubilla; 1550 m asl, stream in mountain meadow, on limestones, dominated by *Juncus* spp. and *Eriophorum latifolium*. VGG, AAL, Saúl Rodríguez Rodríguez, Nacho Blanco Menéndez, Ismael Romero, Antonio González Cuesta, 23-VI-2024 (photograph, Figure 3H). Two plants co-occurring with *D. incarnata,* which was the only species present at this specific location. A mixed population of *D. fuchsii* and *D. maculata* was seen 200 m east along a stream flowing at the contact zone between limestones and quartzites. Surprisingly, *D. incarnata,* or hybrids thereof, were absent from this second location. It is therefore hard to determine which of those species originated this hybrid. However, lips observed in hybrid plants seemed more similar to the ones present in *D. fuchsii*, as the middle lobe was consistently longer than the two lateral lobes and this plant was quite more abundant than *D. maculata.* Plants were also higher and more robust than the individuals of *D. incarnata* growing nearby, with slightly maculated leaves. Flowers were also bigger than those of *D. incarnata*, and spurs thin and long, closer in appearance to those of *D. fuchsii*.

Ophrys* ×*fonsaudiensis Soca (*Ophrys insectifera* L. × *Ophrys passionis* Sennen ex Devillers-Tersch. & Devillers). 29TQH2375. Somiedo, Pola de Somiedo; 725 m asl. Roadside. Mikel Tapia Arriada & Joseba Castillo Bunsuri, 07-VI-2013 (photograph, Figure 3I). 29TQH27. Somiedo, Peñavera. Tomás Emilio Díaz González, VII-1978 (photograph). We rule out the true *Ophrys sphegodes* Mill. as a parent, insofar as this species is quite rare in Somiedo and the hybrid lacks as characteristic a feature as the green pseudo-eyes. Also, the not so rare *Ophrys incubacea* is to be discarded, the hybrids lacking any trace of projecting "arms" and dense pilosity in their labella.

Ophrys* ×*fraresiana M.R. Lowe, Piera & M.B. Crespo (*Ophrys lupercalis* Devillers-Tersch. & Devillers × *Ophrys lutea* Cav.). 30TUP0722. Villaviciosa, Rodiles Beach; 5 m asl. Dune system, somewhat stabilized and overshadowed by a *Eucalyptus globulus* plantation. Ismael Romero & Nacho Blanco Menéndez. 14-IV-2024 (photograph, Figure 3J). Both parents were present in this locality along with a lot of other orchids (this particular spot holding no less than 25 % of Asturian orchid species). The distinction from *O. lutea* is often delicate, being the speculum extended towards the shortened lip lobules and the white-haired throat, the most telling indicators of a hybrid origin.

Ophrys* ×*minuticauda Duffort (*Ophrys apifera* Huds. × *Ophrys scolopax* Cav.). 30TUN5097 Cabrales, San Andrés de Carreña; 190 m asl. Roadside. Hugo Campillo Gancedo. 04-VII-2014 (photograph, Figure 3K). 29TQH2377. Somiedo, La Malva; 630 m asl. Roadside. Carlos Miñambres. 11-VI-2023 (photograph, observation.org/observation/276513351/). Although we are doubtful about the occurrence in Asturias of the genuine *O. scolopax* s. str., for the time being we are sticking with the already available nothospecific name, at least until our research about the *Ophrys scolopax* group in Asturias is concluded: as further discussed below, we hold that at least two different taxa have been merged in northwestern Spain under the name *Ophrys scolopax*, among which the one here provisionally labelled as "*Ophrys scolopax* type-B" is involved in the origin of both the hybrid plants recorded above.

Orchis* ×*loreziana Brügger (*Orchis mascula* (L.) L. × *Orchis pallens* L.). 30TTN6272. Quirós, Agüeria mountain pastures; 1300 m asl. Mountain meadow. Eduardo Fernández Pascual. 01-V-2023 (photograph, www.inaturalist.org/observations/159163322). 30TUN1972. Caso, Tarna mountain pass; 1520 m asl. Mountain shrub on limestones dominated by *Genista hispanica*, together with other basophilous species like *Glandora diffusa* (Lag.) D.C.Thomas, *Helianthemum nummularium* (L.) Mill., *Hippocrepis comosa* L. and *Teucrium pyrenaicum* L., Marcos Perille. 16-V-2023 (photograph, Figure 3L). The labellum of both hybrid plants looked closer to *O. pallens*, except for the pinkish tones reminiscent of *O. mascula*, especially in the plant from Caso, whose lip was completely tinted in pink, while the one from Quirós presented a discolored throat. In both cases the labellum was completely spotless. As easily appreciated in the photograph from Caso (www.inaturalist.org/observations/162104633), in which some individuals of *O. mascula* are visible alongside *O.* × *loreziana*, the hybrid is significantly larger than its pink-flowered parent.

Orchis* ×*penzigiana A. Camus (*Orchis mascula* (L.) L. × *Orchis provincialis* Balb. ex Lam. & DC.) 30TTN99. San Martín del Rey Aurelio, Faya de los Lobos. J. van Bodegom. 11-V-1976 (MA-01-706178, Figure 3M). The specimen was already interpreted through that

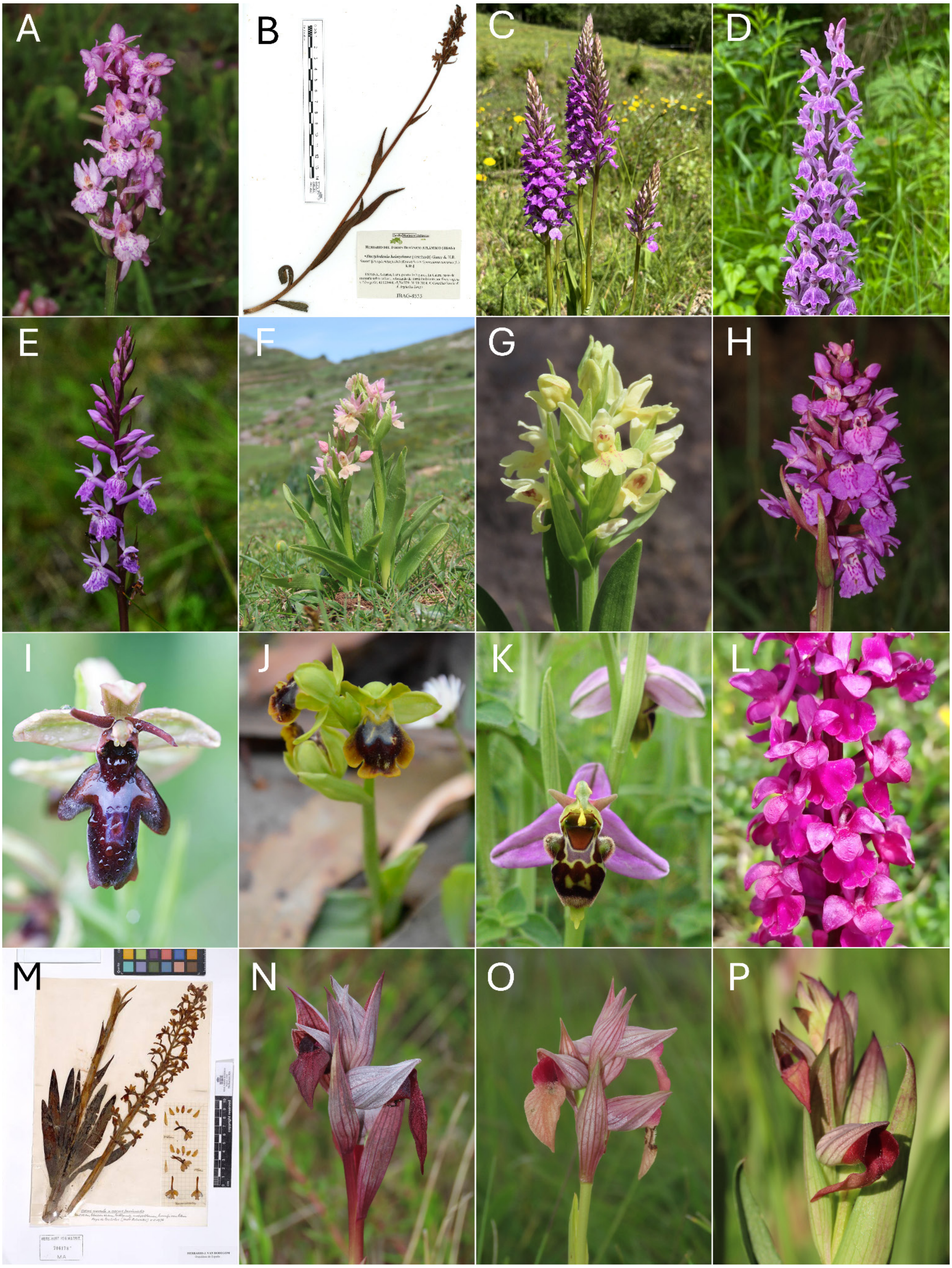

Figure 3. A, ×*Dactylodenia heinzeliana* (Lena, 30-VI-2024. VGG); B, ×*Dactylodenia heinzeliana* (Lena, 30-VI-2024. JBAG 8553); C, *Dactylorhiza* ×*delamainii* (Boal, 28-V-2024. Gilberto S. Jardón); D, *Dactylorhiza* ×*hjertsonii* (Morcín, 01-VI-2023. Jorge Rodriguez Pérez); E, *Dactylorhiza* ×*hjertsonii* (Morcín, 4-VII-2024. AAL); F, *Dactylorhiza insularis* × *Dactylorhiza sambucina* "pink form" (Somiedo, 01-V-2023. VGG); G, *Dactylorhiza insularis* × *Dactylorhiza sambucina* "yellow form" (Somiedo, 01-V-2023. VGG); H, *Dactylorhiza* ×*kerneriorum* (Lena, 23-VI-2024. VGG); I, *Ophrys* ×*fonsaudiensis* (Somiedo, 07-VI-2013. Mikel Tapia Arriada); J, *Ophrys* ×*fraresiana* (Villaviciosa, 14-IV-2024, Nacho Blanco Menéndez); K, *Ophrys* ×*minuticauda* (Cabrales, 04-VII-2014. Hugo Campillo Gancedo); L, *Orchis* ×*loreziana* (Caso, V-2023. Marcos Perille); M,. *Orchis* ×*penzigiana* (San Martín del Rey Aurelio, 11-V-1976. MA-01-00706178); N, *Serapias* ×*ambigua* (Gijón, 06-V-2024. VGG); O, *Serapias* ×*rainei* (Gijón, 06-V-2024. VGG); P, *Serapias* ×*todaroi* (Gijón, 11-IV-2024. VGG).

hybrid formula by his collector, correctly in our view: the dense inflorescence and pinkish coloration (as still perceivable in some flower pieces exquisitely displayed in the herbarium sheet), typical from *O. mascula*, appear combined with the geniculated lip typical from *O. provincialis*, the spur morphology being intermediate between both parental species. By limiting our attention to the shape and coloration of the labellum it would be hard to distinguish this plant from *O. langei*, but the dense inflorescence, the non-straight spur, the relatively early flowering date and the locality led us to confidently reject such possibility. With regard to the nothospecific name, we are aware of the reservations expressed by Bock & Tison (2012), who suggest, albeit vaguely and with no explicit support whatsoever, that A. Camus's name was coined for an intergeneric hybrid between *O. mascula* and a *Dactylorhiza*. However, we have checked Camus's protologue and found it in perfect agreement with the usual, here accepted interpretation. Furthermore, and despite the lack of any picture of this particular hybrid in that otherwise lavishly illustrated work, in the herbarium of the Muséum d'Histoire Naturelle de Paris we could find a specimen [P-01800646: "Herbier E. G. Camus / Bords de la route de la Spezia à Sestri Levante, entre le col de la Force et Pogliasca / Italie / 28 mai 1906 / Legit Paul Bergon / *Orchis mascula* × ... / vel × *provincialis* / × / E. G. Camus" (science.mnhn.fr/institution/mnhn/collection/p/item/p01800646)] which, insomuch as collected by one of the authors cited in the protologue and in a locality reasonably referable to the stated *locus classicus* ("environs de Gênes [Genoa]"), and more than certainly seen by A. Camus herself, represents a suitable lectotype: it resembles the Asturian specimen in every perceivable detail.

Species checklist

We present below the updated checklist of the 52 orchid species whose occurrence in the principality of Asturias is sufficiently attested. For each species we provide a brief summary of its chorotype, habitat, altitudinal range, flowering period and a selection of synonyms generally used in the past, as well as, when useful, some clarifying comments. The list of species is arranged alphabetically, except for the genus *Ophrys*, which is ordered according to the section the species belongs (i.e. *Ophrys*, *Pseudophrys* and *Euophrys*) and by morphological similarity, given the particularly challenging diagnostic difficulties inherent to this evolutionary dynamic genus. All species are illustrated following the same order. In cases where the existence of discrete variants is patent, be it as a consequence of intraspecific chromatic polymorphism as in *Dactylorhiza sambucina* or of still taxonomically unresolved morphological divergence as happens with *Ophrys scolopax*, more than one image is provided.

Anacamptis champagneuxii (Barnéoud) R.M. Bateman, Pridgeon & M.W.Chase. Syn. *Anacamptis morio* subsp. *champagneuxii* (Barnéoud) H.Kretzschmar, Eccarius & H.Dietr., *Herorchis champagneuxii* (Barnéoud) D.Tyteca & E.Klein, *Orchis morio* subsp. *champagneuxii* (Barnéoud) E.G.Camus & A.Camus. MED. Grasslands and hay meadows on basic soils. 300(600) m asl. III. As far as we now know, this species is very rare in the territory, although Díaz González & Vázquez (2009) suggested a wider spread across the region (Figure 4A).

Anacamptis morio (L.) R.M.Bateman, Pridgeon & M.W.Chase. Syn. *Herorchis morio* (L.) D.Tyteca & E.Klein, *Orchis morio* L. EUR. Grasslands, hay meadows and pastures, more rarely in shrublands and open forests; basic to slightly acid soils. (140)600-1230(1725) m asl. II-VI. (Figure 4B).

Anacamptis pyramidalis (L.) Rich. EUR. Grasslands, hay meadows, pastures and shrublands, less commonly in forest edges and clearings or even anthropogenic habitats such as roadsides, on basic soils. (15)160-710(1825) m asl. IV-VIII. (Figure 4C).

Cephalanthera longifolia (L.) Fritsch. EUR. Forests and woodlands, both deciduous and evergreen broadleaved, even coniferous. Also, on dune system forests and more rarely in grasslands and shrublands, on basic soils. (0)320-675(1450) m asl. IV-VI. Mixotrophic species that allegedly attracts its pollinators by how its flowers mimic those of C*istus salviifolius* L., a species relatively common in certain warm areas of Central and Eastern Asturian lowlands (Figure 4D).

Cephalanthera rubra (L.) Rich. EUR. Forests dominated by *Quercus rotundifolia* Lam. on limestones, more rarely on mixed deciduous forests or calcareous outcrops. 250(600) m asl. V-VI. Very rare in the territory, known with certainty from a few colonies inhabiting *Quercus rotundifolia* forests in Somiedo and Belmonte de Miranda. There is an incidental, unvouchered record from a deciduous wood near Covadonga, and its finding in the Cares and Deva gorges would not be unexpected. In this case, the alleged model mimicked by its deceptive, rewardless flowers is *Campanula* (Figure 4E).

Dactylorhiza cantabrica H.A.Pedersen. END. Grasslands and shrublands on limestones and, occasionally, quartzites. (500)1165–1390(1740) m asl. IV-VI. Species presumably originated through the hybridization between *D. insularis* and *D. sambucina.* Originally described from the Courel mountains (Galicia), it is actually widespread along the whole of the Cantabrian Mountains; specifically, both through personal findings and through the reassessment of ancient collections, we have already documented its occurrence in numerous localities along the mountains of southern Asturias, and we forecast that records will increase in the coming years. The details of its genetic makeup and evolutionary history, in connection with some intriguing variations (namely, the occasional pinkish hues), seem an interesting topic for further research (Pardo Otero *et al*., 2024). Its IUCN conservation status category at the Spanish level has been formally assessed and found to be "Vulnerable" (VU D1+2) (Moreno, 2008) (Figure 4F).

Dactylorhiza elata (Poir.) Soó. MED-ATL. Humid or even flooded terrains, growing in grasslands,

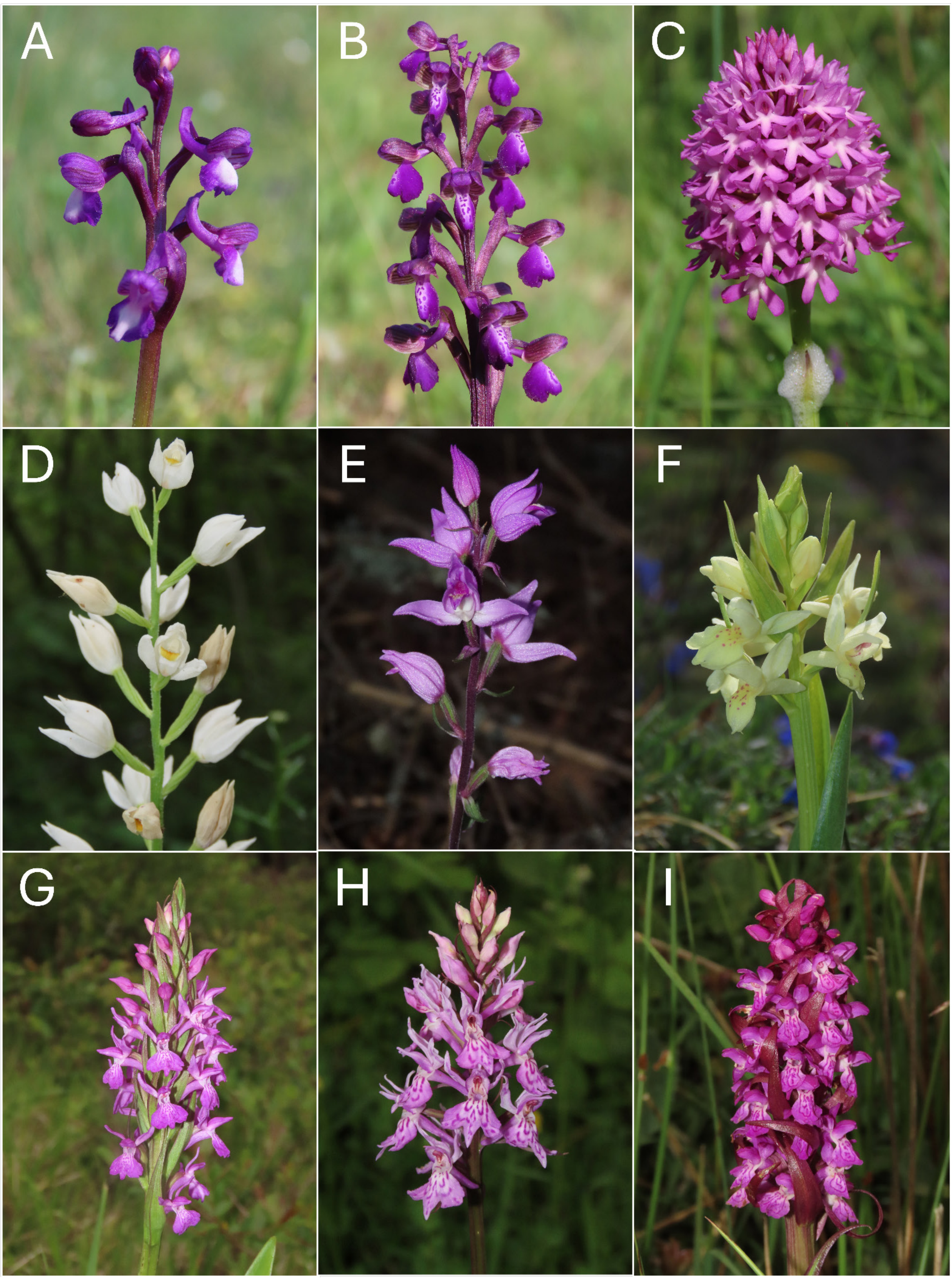

Figure 4. A, *Anacamptis champagneuxii* (León*, 16-IV-2024. VGG); B, *Anacamptis morio* (León*, 16-IV-2024. VGG); C, *Anacamptis pyramidalis* (Oviedo, 08-V-2022. VGG); D, *Cephalanthera longifolia* (Piloña, 13-V-2022. VGG); E, *Cephalanthera rubra* (Palencia*, 06-VII-2023. VGG); F, *Dactylorhiza cantabrica* (Somiedo, 01-V-2023. VGG); G, *Dactylorhiza elata* (Cantabria*, 11-V-2024. VGG); H, *Dactylorhiza fuchsii* (Lena, 23-VI-2024. VGG); I, *Dactylorhiza incarnata* (Lena, 23-VI-2024. VGG).

riparian forests or fens, more rarely in dune systems, marshes, shrublands or roadsides. (0)60-190(1595) m asl. IV-VII. Its considerable variability in terms of overall size, width of the spur and length of the bracts has inspired the proposition of a number of putative entities recognised at different levels through several nomenclatural combinations: *Dactylorhiza durandii* (Boiss. & Reut.) M.Laínz, *D. elata* subsp.

iberica (T.Stephenson) Kreutz, (recently renamed at species level by Kreutz (2024) as *D. asturiensis*) and *D. sesquipedalis* (Willd.) M.Laínz are among the most used. However, the variation found in the territory is continuous and lacks obvious geographical or ecological projection, so we refuse to admit the existence of even infraspecific entities, at least as far as the Asturian territory is concerned. Arguably, all this complex originated through hybridisation, made viable through allopolyploidy, between *D. incarnata* and *D. maculata* (Figure 4G).

Dactylorhiza fuchsii (Druce) Soó. Syn. *Dactylorhiza maculata* subsp. *fuchsii* (Druce) Hyl. EUR. Fringes of deciduous forests, especially of beech-dominated ones, generally in humid and cool places, also in mountain meadows on basic soils and more rarely in alkaline fens. (35)675–1200(1690) m asl. V-VIII. Although we are aware of the well-documented blurring of its limits with *D. maculata* in Central Europe, writing as we do from a corner of Atlantic Europe —*D. fuchsii*'s "*terra classica*" encompasses all of southern Britain and the whole of Ireland— we do not hesitate in granting *bona fide* species rank to this entity (Bateman, 2021), so well-defined over here, apart than by its ecology, by its wide, obtuse, very maculated basal leaves, its fusiform, long-stalked inflorescence and its idiosyncratically protruding middle lip lobe (Figure 4H).

Dactylorhiza incarnata (L.) Soó. EUR. Banks of mountain streams, alkaline fens and other flooded grasslands, shores of lakes and ponds, always on basic soils. V-VII. (1090)1400-1650(1900) m asl. Several records originally under this binomen turned out to actually correspond to *D. elata*, as expected from their low elevation (Figure 4I).

Dactylorhiza insularis (Sommier) Landwehr. MED. Grasslands, hay meadows and mountain pastures and shrublands, less frequently growing in forests; on basic soils. (670)1120–1400(1640) m asl. IV-VI. Allotriploid with apomictic reproduction and atrophied pollinia, product of the hybridization between *D. sambucina* and *D. sulphurea* s.l. (Figure 5A).

Dactylorhiza maculata (L.) Soó. EUR. Stream banks, bogs, fens, heathlands, shrublands, grasslands and meadows, mostly on acid soils and humid to flooded terrain. (0)320–1390(1800) m asl. IV-VIII. Fernández Prieto *et al.* (2014) admit at the subspecies level three traditionally recognised taxa: *D. maculata* subsp. *elodes* (Griseb.) Soó, *D. maculata* subsp. *ericetorum* (E.F.Linton) P.F.Hunt & Summerh. and *D. maculata* subsp. *maculata*. However, their differences are subtle, connected by transitions and associated with habitat in ways which make it difficult to rule out mere phenotypic effects and further research is needed (Taraška *et al*., 2023) (Figure 5B).

Dactylorhiza romana subsp. ***guimaraesii*** (E.G.Camus) H.A.Pedersen. MED. Acidophilous grasslands, heathlands and forest fringes, especially those dominated by *Quercus pyrenaica* Willd. (440)560–700 m asl. IV-VII. This species is rare in the territory, becoming somewhat more frequent in southern slopes around Picos de Europa. We adopt for once a subspecific treatment, both because there are good taxonomic reasons (obvious transitions between the morphotypes along the Mediterranean, from Portugal to the Caucasus) and because such procedure (given the fact that the basionym, judging by its protologue and the accompanying drawing, undoubtedly correspond to this taxon) exempts us from taking sides in the dilemma concerning the specific names most often assigned to this plant. *Dactylorhiza sulphurea* (Link) Franco would have priority, but some authors (Benito Ayuso, 2017) remain doubtful until the unlikely surfacing of a satisfactory lectotype, or the formalization of a suitable conserved type, as to whether the Portuguese plant originally studied by Brotero, and finally named by Link, was this or rather *D. insularis*, for the extreme scarcity of the technically validating diagnostic remark. In this last case, the correct name for the western representative of the *D. romana* complex would be *Dactylorhiza markusii* (Tineo) H.Baumann & Künkele; another problematic name coined for a Sicilian plant, in the same place where the yellow-flowered, short-spurred western typology and the typical *D. romana* enter into contact, and transitions appear. In fact, if the Sicilian plant is admitted as taxonomically fully synonymous with the Portuguese one, even in the subspecific rank one would be tempted to admit the priority of the combination *Dactylorhiza romana* subsp. *siciliensis* (Klinge) Soó over the one we have used. However, since Klinge's otherwise validly published subspecific name was created under an ostensibly illegitimate species name, it ends up being illegitimate itself, *guimaraesii* then becoming the first legitimate name in that rank (Figure 5C).

Dactylorhiza sambucina (L.) Soó. Syn. *Orchis sambucina* L. EUR. Hay meadows, mountain pastures and shrublands, more rarely in forests; on limestones or slates. (770)1330–1560(1790). IV-VII. Dimorphic species with a yellow (f. *sambucina*, Figure 5D) and a red form (f. *rubra*, Figure 5E). Occasionally in-between individuals, with brighter pinkish flowers (f. *zimmermanii*) can be found.

Dactylorhiza viridis (L.) R.M.Bateman, Pridgeon & M.W.Chase. Syn. *Coeloglossum viride* (L.) Hartm. EUR. Mountain pastures and shrublands, growing in cool, humid, even slightly flooded meadows and by streams; on limestone and slates. (1000)1525–1690(2045) m asl. V-VIII. (Figure 5F).

Epipactis atrorubens (Hoffm.) Besser. EUR. Mainly on sparsely vegetated karstified limestones, but also in mountain pastures and both deciduous and evergreen basophilous forests. (25)1250–1770(2150) m asl. V-IX. Plants from higher areas seem to flower only rarely, if they do at all (Figure 5G).

Epipactis helleborine (L.) Crantz. EUR. Both deciduous and evergreen basophilous forests, mostly those dominated by *Fagus sylvatica*, *Quercus ilex* or *Q. rotundifolia*. Less frequently in grasslands or megaphorbs (0)330-1180(1450) m asl. IV-VIII. By obtaining part of its nutrients from symbiotic fungi, this mixotrophic species can survive even in shady underwoods (Figure 5H).

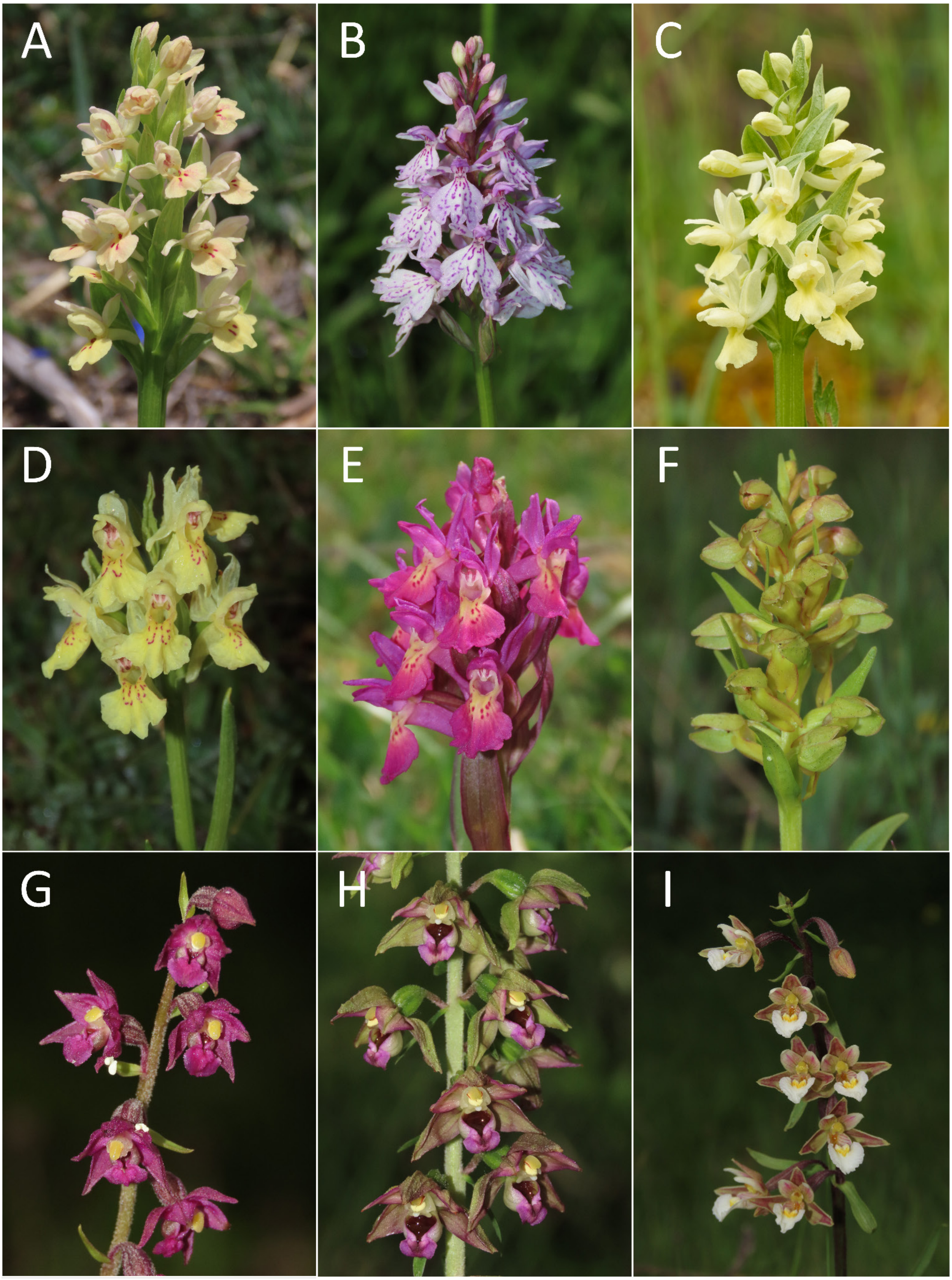

Figure 5A. *Dactylorhiza insularis* (Somiedo, 01-V-2023. VGG); B, *Dactylorhiza maculata* (Amieva, 25-V-2024. VGG); C, *Dactylorhiza romana* subsp. *guimaraesii* (Madrid*, 28-IV-2024. Víctor Molero Martín); D, *Dactylorhiza sambucina* f. *sambucina* (León*, 13-V-2023. VGG); E, *Dactylorhiza sambucina* f. *rubra* (Somiedo, 01-V-2023. VGG); F, *Dactylorhiza viridis* (Somiedo, 18-VI-2023. VGG); G, *Epipactis atrorubens* (Cabrales, 12-VII-2023. VGG); H, *Epipactis helleborine* (Huesca*, 08-VII-2024. VGG); I, *Epipactis palustris* (León*, 30-VI-2024. VGG).

Epipactis palustris (L.) Crantz. EUR. Alkaline fens and travertines, rarer (if still present) in interdunal wetlands. (0)480–810(1600) m asl. VI-VIII. Very uncommon, even more so after the disappearance of all known populations in the northern maritime areas as a consequence of urban, industrial or agricultural developments in the last centuries or decades. Although we have recently located two new populations in Quirós and Cabrales, the latter within the Picos de Europa National Park, both of them comprise very few individuals, with an area of occupancy of less than 25 m^2 and facing some of the threats mentioned above: this was particularly patent in the latter, which was directly grazed by horses. Given the almost irreversible destruction of most of its suitable habitat, intrinsically scarce in this hilly region, even in protected areas, it is unlikely that this severe rarity is an illusion caused by insufficient prospection. Despite proposals to grant it legal protection in response to these worrying trends (Fernández Prieto *et al.*, 2007), the species remains unprotected in Asturias (Figure 5I).

Gymnadenia conopsea (L.) R.Br. EUR. Grasslands and shrublands, more rarely in forest clearings, sparsely vegetated karstified limestones or alkaline fens; from dry to slightly flooded basic soils. (50)910–1470(1785) m asl. IV-VII. (Figure 6A).

Gymnadenia densiflora (Wahlenb.) A.Dietr. EUR. Flooded meadows on limestones. 1450–1550 m asl. VI-VII. One of the rarest species in Asturias, with a single population known so far. We hold as even probable, however, its presence in other alkaline wet mountain grasslands, since it seems to be rather common in the southern slopes of the Cantabrian Mountains. Differs from its congeners, among other characters, by the combination of a white throat and a lineal groove in its center. (Figure 6B).

Gymnadenia pyrenaica (Philippe) Giraudias. Syn. *G. odoratissima* subsp. *longicalcarata* C.E.Hermos. & Sabando, *G. odoratissima* auct., non (L.) Rich, saltem s. str. END. On limestone seeping banks and alkaline fens, frequently accompanied by *Carex lepidocarpa* Tausch and *Pinguicula grandiflora*; much rarer in shrublands or even forest clearings in cool areas (710)1120–1485(1530) m asl. VI-VIII. This species appeared categorized as "Vulnerable" in the Red List of Spanish vascular flora (Domínguez Lozano, 2000), later changed to "Least Concern" (Moreno, 2008) and finally "Data Deficient" (Moreno, 2010). Although records in Picos de Europa have been traditionally classified as *G. odoratissima,* some authors (Diez Santos, 2022; Kreutz, 2024) tend to separate those plants found at lower, sub-mediterranean locations on marshy meadows (*G. pyrenaica*) from those found in high mountain pastures (*G. odoratissima* s. str.). However, as this differentiation has not been clearly morphologically, ecologically or karyologically supported yet, we maintain the criteria of Benito Ayuso (2017), which agglutinates all Iberian populations under this name, discarding the presence of *G. odoratissima* s. str. in our territory. (Figure 6C).

Himantoglossum hircinum (L.) Spreng. MED-ATL. Grasslands, hay meadows and mountain pastures, on basic soils. Rarely growing in dune systems and roadsides. (0)1140–1595(1840) m asl. IV-VII. (Figure 6D).

Himantoglossum robertianum (Loisel.) P.Delforge. Syn. *Barlia robertiana* (Loisel.) Greuter. MED. Grasslands, shrublands, sparsely vegetated karstified limestones and dune systems, more rarely in forest fringes and roadsides; on basic soils. (0)50–540(1030) m asl. XII-VI. (Figure 6E).

Limodorum abortivum (L.) Sw. MED-ATL. Forests dominated by *Quercus ilex* or *Q. rotundifolia*, on limestones. (0)35–750(925) m asl. IV-VI. Mycoheterotrophic species, therefore able to grow in very shady places. Not as rare as once thought, but pretty uncommon nonetheless. Fernández-Prieto *et al*. (2007) proposed to protect this species at the regional level as "of special interest". (Figure 6F).

Listera ovata (L.) R.Br. Syn. *Neottia ovata* (L.) Hartm. EUR. Damp to flooded terrains, growing in forests, especially riparian, as well as in shrublands, grasslands, alkaline fens and seeping calcareous banks; on basic soils. Occasionally, in the understory of *Eucalyptus* plantations. (0)50–1300(1900) m asl. III-VII. (Figure 6G).

Neotinea maculata (Desf.) Stearn. MED-ATL. The true extent of this species' niche in the territory can only be guessed due to the extreme scarcity of records. We can presume that it grows in forest fringes, shrublands and dry grasslands. (600)700(1700) m asl. IV-V. As a consequence of its humble, inconspicuous appearance, this mostly autogamous species is easily overlooked in comparison with its bigger and more vibrant-colored relatives, and it might well be less rare than it currently seems, as suggested by Díaz González & Vázquez (2009). Figure 6H.

Neotinea ustulata (L.) R.M.Bateman, Pridgeon & M.W.Chase. Syn. *Orchis ustulata* L. EUR. Mainly mountain pastures and shrublands, occasionally in fringes of deciduous forests; on basic soils. (435)1260-1640(1890) m asl. V-VII. Figure 6I.

Neottia nidus-avis (L.) Rich. EUR. Mainly in basophilous forests dominated by *Fagus sylvatica*, *Corylus avellana*, *Quercus pyrenaica* or *Q. rotundifolia*, less frequently in mixed deciduous forests and fern communities close to forest fringes. (545)780-1300(1560) m asl. V-VI. Mycoheterotrophic species producing no chlorophyll, entirely reliant on the fungi that it parasitises. Figure 7A.

Nigritella gabasiana Teppner & E.Klein. Syn. *Gymnadenia gabasiana* (Teppner & E.Klein) Teppner & E.Klein. END(ALP). Mountain pastures and shrublands, on dry to humid but always basic soils. (1230)1500-1750(2035) m asl. VI-VIII. Only species in the territory whose labellum is directed upwards, since there is no resupination of the ovary during the flower development. Figure 7B.

Ophrys insectifera L. Section *Ophrys*. EUR. Mountain pastures, hay meadows, shrubland and forest fringes on basic soils; more rarely in roadsides and dune systems. (0)510-1215(1810) m asl. IV-VII. Pollinated by *Argogorytes mystaceus* and, occasionally by *A. fargei* and *A. combinata.* Figure 7C.

Ophrys apifera Huds. Section *Ophrys*. MED-ATL. Shrublands, fringes and clearings of both deciduous

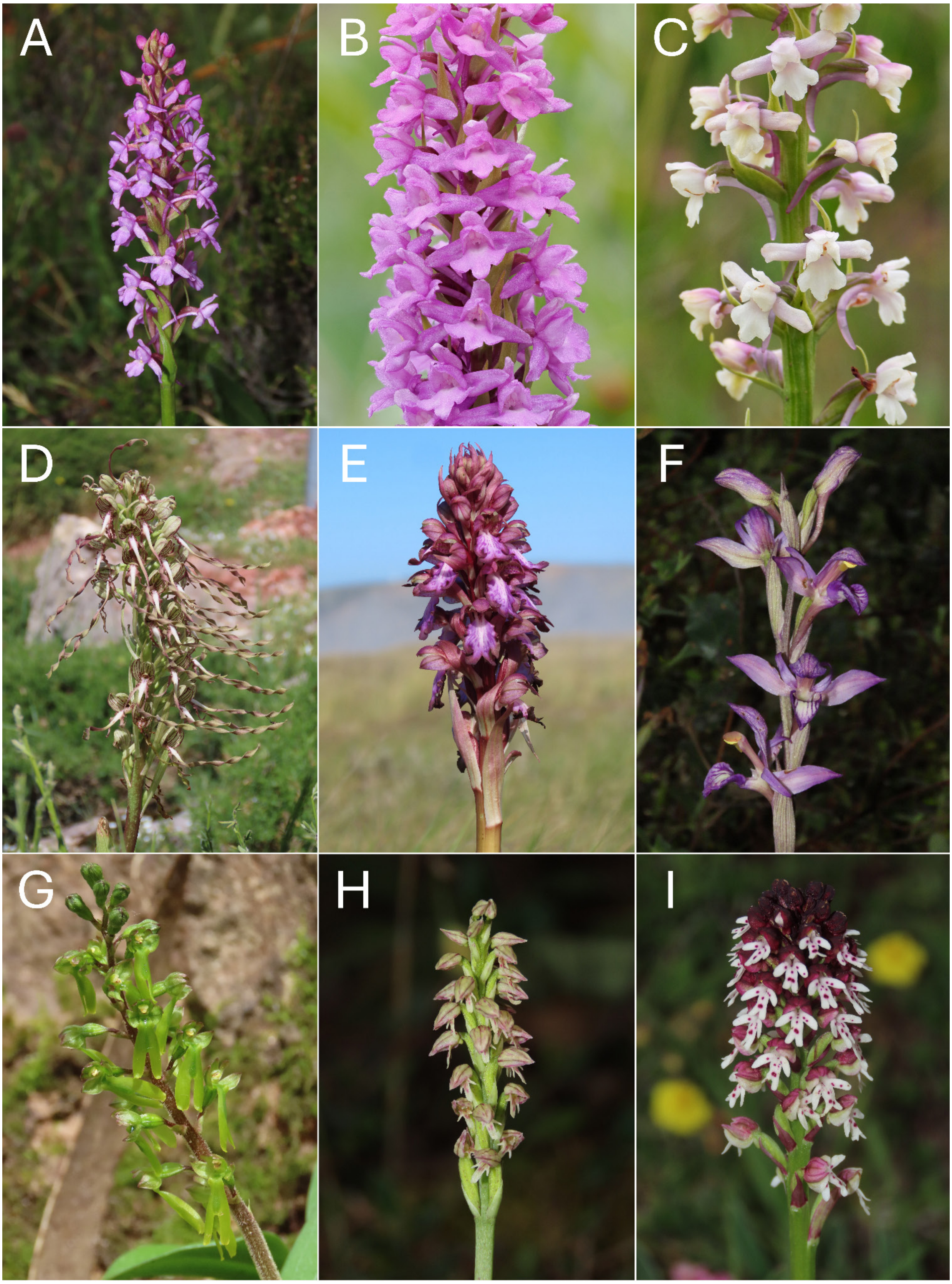

Figure 6. A, *Gymnadenia conopsea* (Somiedo, 18-VI-2023. VGG); B, *Gymnadenia densiflora* (Lena, 06-VII-2023. Gilberto S. Jardón); C, *Gymnadenia pyrenaica* (Álava*, 21-VI-2024. Álvaro Díaz Pastor); D *Himantoglossum hircinum* (Somiedo, 25-VI-2022. VGG); E, *Himantoglossum robertianum* (Gozón, 22-II-2022. VGG); F, *Limodorum abortivum* (Badajoz*, 28-IV-2024. VGG); G, *Listera ovata* (Gijón, 18-III-2022. VGG); H, *Neotinea maculata* (Madrid*, 20-IV-2024. VGG); I, *Neotinea ustulata* (Somiedo, 17-VI-2023. VGG).

and evergreen forests, grasslands, pastures, hay meadows and even almost bare limestone banks and dune systems. Also, in anthropogenic habitats. On dry to moist, basic to slightly acidic soils. (0)50-415(1600). IV-VII. Unlike the rest of *Ophrys*, this taxon relies on self-pollination to achieve reproductive success, with no apparent detrimental effects of selfing so far, even without polyploidy providing mutational buffer, thus being one of the most morphologically stable species within the genus and also one of the most widespread and best surveyed. The latter is explained by how its detection is facilitated by its tolerance to human activities: urban parks, garden lawns and brownfields rank high in its list of frequent habitats, perhaps by providing large areas of pollinator-impoverished but permanently open spaces where competition is relaxed and this species can persist despite the toll presumably exacted by selfing in its output of viable seeds (Figure 7D).

Ophrys scolopax Cav. Section *Ophrys*. MED. Grasslands, hay meadows and pastures, shrublands, both deciduous and evergreen forest fringes and clearings, even seeping or bare limestone banks and dune systems; on basic soils. (0)160–670(1235) m asl. IV-VII. Despite provisionally sticking to this binomen, we have reasons to believe that the true *O. scolopax* originally described by Cavanilles does not really occur in the region. In fact, we suggest that at least two different, possibly novel taxa, have so far been inadvertently concealed under this name. One of them, to which for now we will refer simply as Type-A (Figure 7E), with a smaller “cephalic area”, more muted colors and a wider labellum in dorso-ventral view, earlier flowering and found mainly in Eastern Asturias lowland and coast. Type-B (Figure 7F), on its part, flowers later in the season and for a longer period, something at least partially attributable to its inhabiting higher elevations throughout the region; it displays a bigger “cephalic area”, brighter colors and a more flattened labellum. Some of these Asturian *Ophrys* could fit in the recently described *Ophrys oceanica* Soca (2024), but further research is still needed. Their pollinators remain unassessed.

Ophrys speculum Link. Section *Ophrys*. Syn. *Ophrys ciliata* Biv. MED. Dune system fixed by *Eucalyptus* and *Pinus*. 0(100) m asl. IV-V. Pollinated by *Dasyscolia ciliata*. Only one population is known in the region (Figure 7G).

Ophrys lupercalis Devillers-Tersch. & Devillers. Section *Pseudophrys*. [*O. fusca* auct.]. MED. Dune systems, pockets of decalcification clays in calcareous cliffs and karstified slopes; on basic soils. (0)10–70(520) m asl. III-V. Pollinated by *Andrena nigroaenea*. Probably not as rare as suggested by its few records, in Asturias it appears to flower a bit later than in the neighbour Cantabria, where its blooming starts in late December or early January (Figure 7H).

Ophrys lutea Cav. Section *Pseudophrys*. MED-ATL. Dune systems, basophilous meadows and shrublands. 0–1050 m asl. IV-V. Pollinated by *Andrena cinerea*, *A. senecionis* and *A. humilis*, the latter having been observed by the authors in the two known populations in the territory (Figure 7I).

Ophrys incubacea Bianca. Syn. *Ophrys sphegodes* subsp. *atrata* (Rchb.f.) A.Bolòs. Section *Euophrys*. MED. Grasslands, pastures, shrublands and *Quercus rotundifolia* forests, occasionally on bare soil; on basic to slightly acid soils. (115)680–880(1400) m asl. IV-VI. Pollinated by *Andrena morio* (Figure 8A).

Ophrys passionis Sennen ex Devillers-Tersch. & Devillers. Syn. *Ophrys sphegodes* subsp. *passionis* (Sennen) Sanz & Nuet. Section *Euophrys*. MED-ATL. Grasslands, meadows, pastures and shrublands on basic soils. (290)670–1080(1425) m asl. III-VI. Pollinated by *Andrena pilipes*. In some populations, perhaps revealingly, some individuals were hard to assign to this taxon or rather to *O. incubacea*. Although both species share a concolor basal lip and blue-blackish pseudo-eyes, *O. passionis* tends to lack the dense pilosity and prominent “arms” and characteristic of *O. incubacea*; the latter ones, when present, tend to be notably smaller and lacking the speculum in their inner face (Figure 8B).

Ophrys sphegodes Mill. Section *Euophrys*. EUR. Grasslands, hay meadows and pastures, occasionally in shrublands, roadsides, gardens and brownfields; on basic soils. (70)170–335(1260) m asl. III-VI. Pollinated by *Andrena nigroaenea*, *A. thoracica, A. barbilabris, A. cineraria* and *A. limata*. It differs from its relatives by the lightest color of the basal field, when compared to the lip, and the green pseudo-eyes. Sepals and petals, non-ciliated, tend to be greenish in color, but we have found plants with white sepals too (Llanera municipality). Those individuals with a wide yellow lip border have been occasionally identified as *O. araneola* Rchb. (syn. *O. litigiosa* E.G.Camus, *O. sphegodes* subsp. *araneola* (Rchb.) M.Laínz), a species absent from our territory, and distinguishable through many other details from said individuals of *O. sphegodes* s.str. (Figure 8C).

Orchis anthropophora (L.) All. Syn. *Aceras anthropophorum* (L.) W.T.Aiton. MED-ATL. Shrublands, forest fringes, pastures and hay meadows on basic soils, occasionally on sparsely vegetated karstified limestones and dune systems. (0)675–1340(1810) m asl. V-VI. Distinctly dimorphic species whose labellum can be red or yellow (Figure 8D).

Orchis langei Lange ex K.Richt. Syn. *O. mascula* subsp. *laxifloriformis* Rivas Goday & B.Rodr.; *Orchis hispanica* A. Niesch. & C. Niesch. END. Shady slopes on the edge of *Quercus pyrenaica* stands, on slates and sandstones. 670(700) m asl. IV-VII. Judging by our current knowledge, one of the rarer species in Asturias. However, it might be slightly underreported as a consequence of the sometimes-delicate diagnosis vis-à-vis its widespread close relative *O. mascula*, from which it differs in having a geniculated labellum, inflorescences with fewer flowers and a barely curved upwards, often straight spur (Figure 8E).

Orchis mascula (L.) L. Syn. *Androrchis mascula* (L.) D.Tyteca & E.Klein. EUR. Both deciduous and evergreen forest and woodlands fringes, clearings and understory, shrublands, grasslands, hay meadows, pastures, roadsides and even dune systems and brownfields; on basic to slightly acid soils. (0)365–1220(2020). III-VI. The most widespread species in the region, highly variable in terms of morphology and colouration, all of which has led, as discussed in the following section, to widespread confusion and, in particular, to the wrong admission as members of the Asturian flora of other putative members of this otherwise still unsatisfactorily

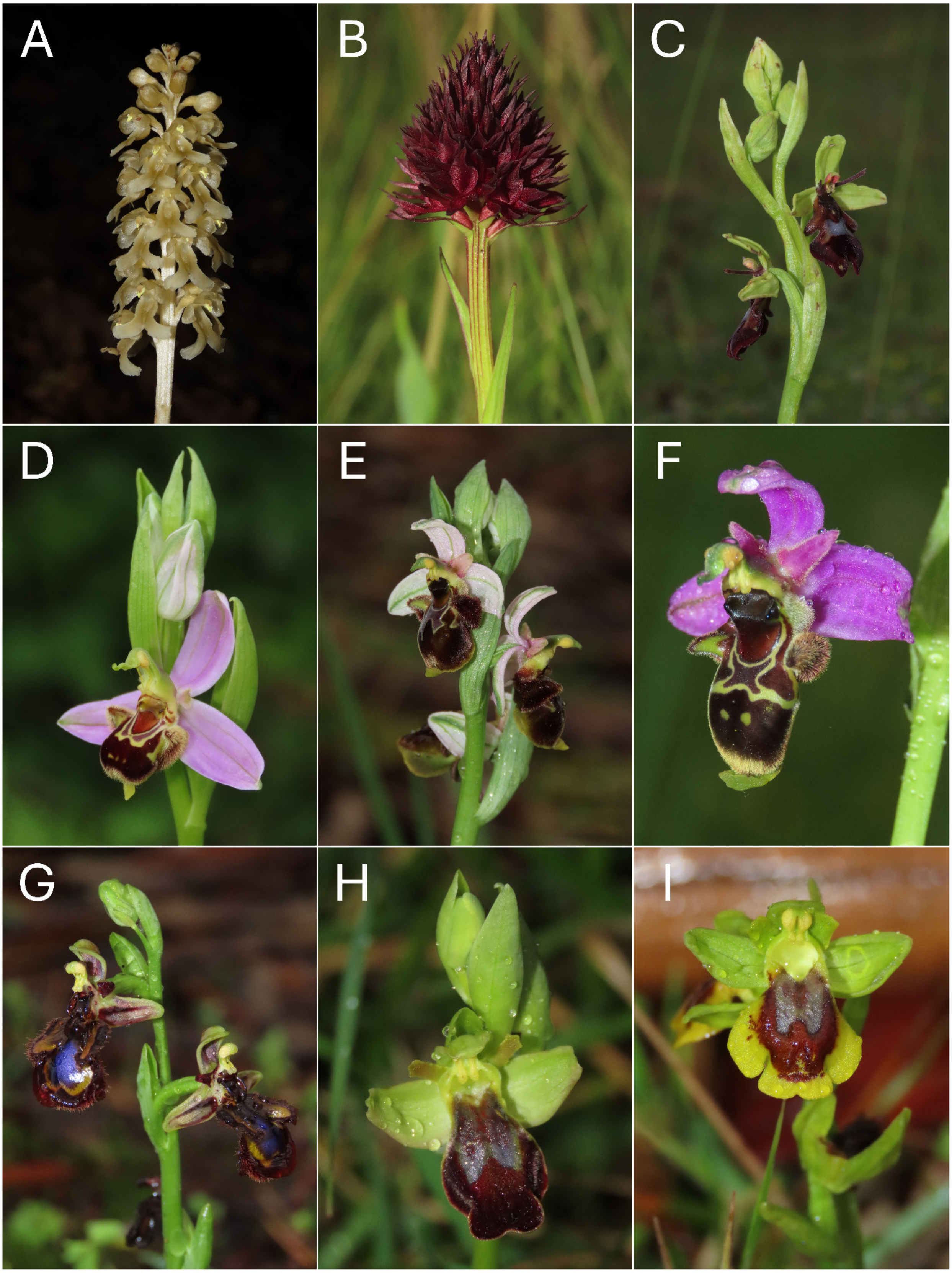

Figure 7. A, *Neottia nidus-avis* (León*, 10-VI-2023. VGG); B, *Nigritella gabasiana* (Huesca*, 09-VII-2024. VGG); C *Ophrys insectifera* (Somiedo, 17-VI-2023. VGG); D, *Ophrys apifera* (Lena, 18-V-2023. VGG); E *Ophrys scolopax* "Type-A" (Villaviciosa, 25-IV-2023. VGG); F, *Ophrys scolopax* "Type-B" (Somiedo, 03-VI-2023. VGG); G, *Ophrys speculum* (Villaviciosa, 23-IV-2023. VGG); H, *Ophrys lupercalis* (Cangas de Onís, 26-III-2024. VGG); I, *Ophrys lutea* (Villaviciosa, 23-IV-2023. VGG).

resolved group (e.g. *Orchis olbiensis* Reut. ex Gren.) (Figure 8F).

Orchis pallens L. ALP. Basophilous pastures and meadows, *Betula celtiberica* Rothm. & Vasc. forests understory or even on bare limestones. (400)1390-1640(1785) m asl. V-VI. (Figure 8G).

Orchis provincialis Balb. ex Lam. & DC. MED-ATL. Shrublands, pastures and meadows; on

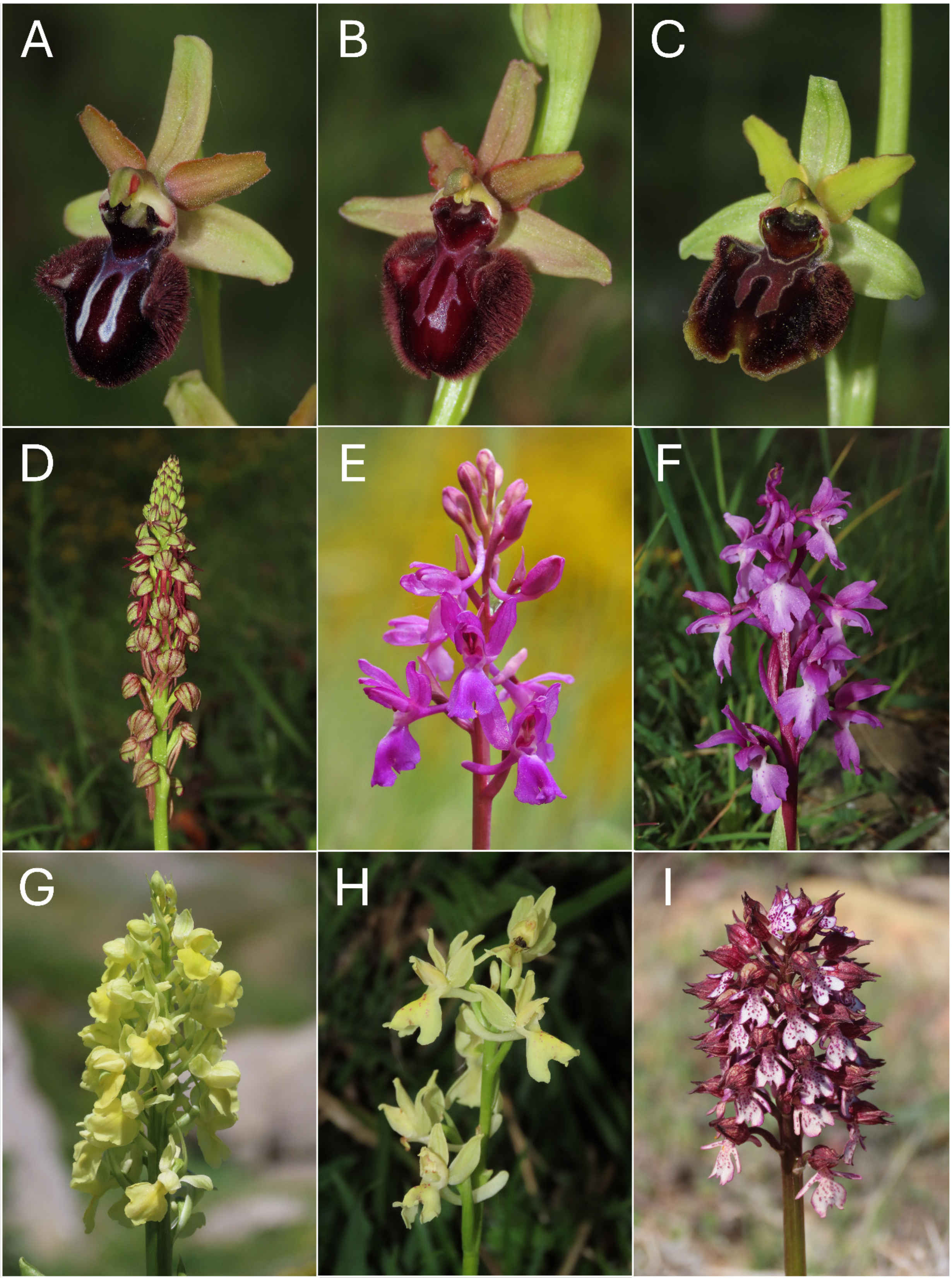

Figure 8. A, *Ophrys incubacea* (Madrid*, 20-IV-2024. VGG); B, *Ophrys passionis* (Oviedo, 07-IV-2024. VGG); C, *Ophrys sphegodes* (Oviedo, 26-III-2024. VGG); D, *Orchis anthropophora* (Somiedo, 04-V-2024. VGG); E, *Orchis langei* (Álava*, IV-2024. Álvaro Díaz Pastor); F, *Orchis mascula* (León*, 13-IV-2023. VGG); G, *Orchis pallens* (León*, 28-V-2022. VGG); H, *Orchis provincialis* (Cabrales, 08-V-2023. VGG); I, *Orchis purpurea* (Almería*, 14-IV-2024. VGG).

limestones or slates. (0)230–1150(1350) m asl. IV-VI. Its IUCN conservation status at the Spanish level has been formally assessed but found to be of “Least Concern” (Moreno *et al.*, 2019) (Figure 8H).

Orchis purpurea Huds. Basophilous grasslands and pastures. EUR. (290)450(1100) m asl. IV-V. One of the rarest orchids in the territory. The population from Monte Naranco (Oviedo municipality) might have disappeared, since it occurred close to a recently expanded limestone quarry (Figure 8I).

Orchis spitzelii Saut. ex W.D.J.Koch. EUR. *Arctostaphylos uva-ursi* and *Juniperus communis* subsp. *nana* (Baumg.) Syme shrublands on limestones. (1900)1910(1950) m asl. VI. So far known from a single Asturian locality, nonetheless we would expect its occurrence in other basophilous mountain shrublands dominated by bearberry, which we suspect favors the presence of fungi necessary for the establishment and development of this orchid. Its IUCN conservation status at the Spanish level has been formally assessed and found to be "Critically Endangered" (CR) (Moreno, 2008). However, as worrying as this assessment might seem, it did not consider the populations in the Cantabrian Mountains, where it can be locally abundant. Thus, we would expect its extinction risk to be downgraded in future assessments (Figure 9A).

Platanthera bifolia (L.) Rich. EUR. Shrublands, pastures and deciduous forests or even heathlands, mainly on basic soils but also, occasionally, on slightly acidic ones; on dry to humid terrains. (0)110–580(1390) m asl. V-VII. (Figure 9B). Although some authors raise doubts about the presence of *Platanthera bifolia* s. str. in the Iberian Peninsula and suggest applying the name *Platanthera fornicata* (Bab.) Buttler to these plants (Delforge, 2021), we have not found any substantial proof to support these evidences in Asturias. Morphological differences between these taxa and the Central European *Platanthera muelleri* A.Baum & H.Baum are slim; however, *P. bifolia* s. str., which bears smaller flowers, should be found in slightly to strongly acidic substrates, while *P. fornicata* or *P. muelleri*, characterised by their bigger flowers and closer resemblance to *P. chlorantha*, appear in neutral to alkaline substrates (Tyteca & Esposito, 2018). Further research should be done within this group in the Iberian Peninsula to effectively discern *P. bifolia* s. str. from *P. fornicata*.

Platanthera chlorantha (Custer) Rchb. EUR. Forests and pastures, occasionally in heathlands, on basic to slightly acid soils, on moist to humid terrains. (435)1010–1350(1630) m asl. V-VII. Figure 9C.

Pseudorchis albida (L.) Á.Löve & D.Löve. EUR. Basophilous mountain pastures and eutrophic *Fagus sylvatica* forests. (1200)1230–1650(1810) m asl. V-VII. As far as we know, this species is quite rare in the territory, but it might reveal itself to be more frequent if the comparative remoteness of the places it inhabits did not impose an insufficient survey. Figure 9D.

Serapias cordigera L. MED-ATL. Grasslands, hay meadows, pastures and garden lawns, occasionally growing in bogs, dune systems, brownfields or forest fringes; on basic to slightly acid soils, from moist to flooded terrain. (0)30–190(750) m asl. III-VIII. This species seems to have found a successful niche in the humid roadsides of Eastern Asturias, where almost continuous populations extend towards Cantabria and the Basque Country. Westwards, as soils become more acidic, the less basophilous *Dactylorhiza elata* tends to predominate in these synanthropic spaces. Figure 9E.

Serapias lingua L. MED-ATL. Grassland, hay meadows, pastures and garden lawns, occasionally in forest fringes, marshes, dune systems, roadsides and brownfields; on basic to slightly acid soils, from dry to moist terrain. (0)55–265(1120) m asl. III-VII. The co-occurrence of this species with its two other congeners is highly frequent, leading to the emergence of hybrids, especially with *S. cordigera*. In some locations, we have observed "hybrid swarms" displacing one or both parents, although it is still to be checked whether these hybrids manage to set seed—sexually or via apomixis—or their reproduction is exclusively clonal. Figure 9F.

Serapias parviflora Parl. MED-ATL. Grasslands, hay meadows, roadsides, brownfields and garden lawns, more rarely in dune systems and marshes. On slightly basic to slightly acid, dry to moist soils. 0–160(820) m asl. III-VII. As a curious aside, it was in Asturias, during Durieu's 1835 botanical journey, where this species was first recognised as new; but the name then provisionally coined ("*Serapias occultata*"; Gay, 1836) took too long to be validly published, so Parlatore's binomen holds priority. Figure 9G.

Spiranthes aestivalis (Poir.) Rich. MED-ATL. Oligotrophic wetlands on acid soils. (0)60–120(130). VI-VII. The actual status of this species in the region deserves a careful examination: we could only confirm two populations, the rest having seemingly vanished, perhaps along the same path followed by *Epipactis palustris* in alkaline wetlands. This species appears categorized as "Near Threatened" in the Spanish Red Atlas and Book of threatened vascular flora (Figure 9H).

Spiranthes spiralis (L.) Chevall. EUR. Mainly found on anthropogenic habitats, such as urban parks, garden lawns, roadsides and brownfields, but occurring in more natural habitats as well: forest clearings and fringes, grasslands and, occasionally, dune systems. Generally, on dry, basic to slightly acid soils. (0)30–250(1290) m asl. VIII-X. (Figure 9I).

Doubtful species

Although the vast majority of the records we gathered were already associated, directly or through obvious synonyms, to the names of species confirmed to occur in the territory, occasional taxonomic rectifications being thus unimportant in terms of inventory, a small fraction would correspond to species whose presence in Asturias is very unlikely, for biogeographical or ecological reasons elaborated as follows.

Anacamptis palustris (Jacq.) R.M.Bateman, Pridgeon & M.W.Chase***.*** There are a handful of Leonese records near the Asturian border, all of them coming from authors as demonstrably unreliable as Gandoger (1917) and Romero Rodríguez (1983), presumably found by Lacaita in Picos de Europa (Losa & Montserrat, 1953), data way too vague and

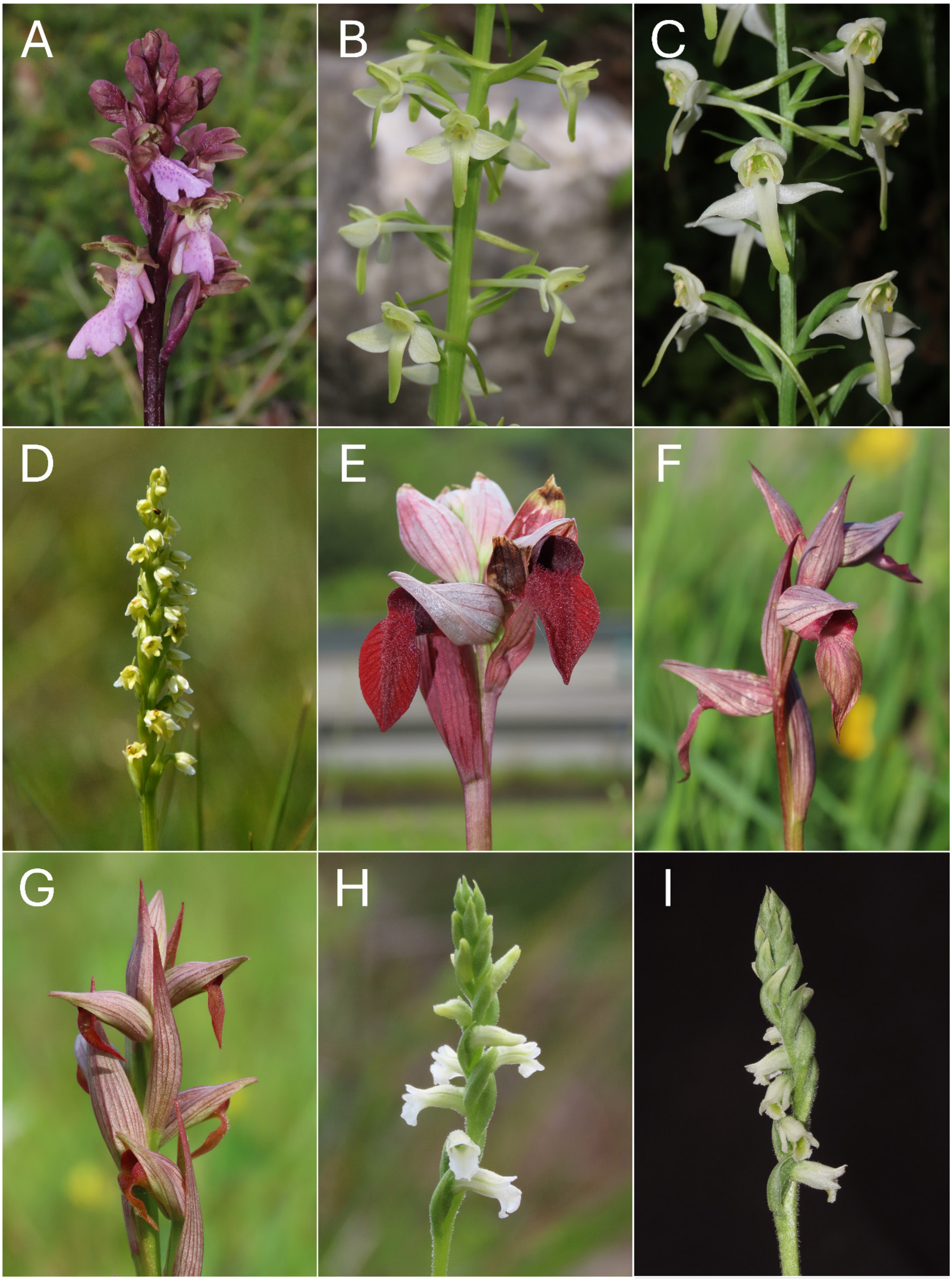

Figure 9. A, *Orchis spitzelii* (Somiedo, 13-VI-2024. VGG); B, *Platanthera bifolia* (Oviedo, 07-VI-2022. VGG); C, *Platanthera chlorantha* (Cabrales, 12-VII-2023. VGG); D, *Pseudorchis albida* (León*, 07-VII-2024. AAL); E, *Serapias cordigera* (Villaviciosa, 23-IV-2023. VGG); F, *Serapias lingua* (Gijón, 11-IV-2024. VGG); G, *Serapias parviflora* (Gijón, 20-V-2023. VGG); H, *Spiranthes aestivalis* (Cudillero, 20-VI-2022. VGG); I, *Spiranthes spiralis* (Oviedo, 29-VIII-2023. VGG).

unreliable as to seriously shatter our skepticism towards the occurrence of this species not just in Asturias but in the whole of northwestern Iberia. The nearest confirmed population is found in the south of the province of Valladolid and, as the rest of the not too numerous known Iberian populations, under a markedly Mediterranean climate and on the slightly saline soils of the Duero basin (Aedo, 2005b). Furthermore, reiterated old records of *Orchis palustris* or *O. laxiflora* subsp. *palustris* in León province should be ascribed to *D. elata* occurring in wet areas, as several prospections in suitable areas and old locations give clues of a possible case of misidentification.

Dactylorhiza majalis (Rchb.) P.F.Hunt & Summerh. This putative hybrid between *D. fuchsii* and *D. incarnata*, stabilized through allotetraploidy, was recorded for the first time by Laínz (1959), although he corrected himself later (Laínz, 1960), referring his previous records under this binomen to *D. incarnata* or the red morph of *D. sambucina*. Instructively, more recent misidentifications seem to have proliferated at the hand of Artificial Intelligence (AI), since citizen science platforms (e.g. PlantNet, Observation, iNaturalist) that use this technology to identify or, at least, suggest an identification seem to have difficulties discerning between this species and *D. elata*, which is actually present in the territory. For the moment, we cannot admit this species as a member of the Asturian flora. In the Iberian Peninsula, it is highly unlikely that it will be demonstrated to occur outside the Pyrenees and their foothills (Sánchez Pedraja, 2005).

Ophrys holosericea (Burm.f.) Greuter, a specimen collected in "La Florida" (municipality of Gijón, not Tineo as wrongly interpreted when databased by its curators) on 12 April 1913 by Cesáreo Martínez is kept under this name in the herbarium of the Royal Botanic Garden of Madrid (MA-01-00029585). The specimen was labelled by its collector as "*Ophrys arachnites*"—presumably with the illegitimate combination *Ophrys arachnites* (Scop.) Reichard in mind—and then revised as "*Ophrys fuciflora*" by Guinea (1953), its current determination surely deriving from the full synonymisation of *O. holosericea* and *O. fuciflora* in *Flora iberica* (Aldasoro & Sáez, 2005). Despite the taxonomic consistency of this sequence of synonyms, it is very doubtful that this specimen is actually referable to the species in question, not even confirmed as occurring in the Iberian Peninsula. Judging by the date and the locality (today turned into an urban area, any verification in the field being thus virtually useless), we are prone to conclude that *O. scolopax* s.l. (in particular, the group here provisionally labelled as Type A) is the best option until the original material can be revised.

Orchis olbiensis Reut. ex Gren. Despite the existence of pretty abundant and sometimes explicitly discussed and allegedly photographically supported reports (López Fernández *et al.,* 2017), we reject the existence of this species in Asturias, all of its records being referable to *O. mascula*, which displays a wide morphological and chromatic variation across the territory, especially in Somiedo, where *O. olbiensis* has been reported with more insistence. In particular, all those pale specimens ostensibly lack the real diagnostic features of *O. olbiensis*; namely, the numerous, very distinct purple dots all over the labellum, even in its lateral lobes, and the thin spur curved upwards and clearly longer than the labellum. As stated by Benito Ayuso (2017), relying solely on the pale flowers has caused many false attributions of *O. mascula* s. str. to *O. olbiensis*. Morphologically more defensible, though also wrong in our view, would be to attribute these admittedly somewhat atypical pale individuals to another alleged species of the *O. mascula* complex: namely *Orchis tenera* (Landwehr) Kreutz in Eurorchis 3: 98 (1991), whose mention in this Asturias-centered review would become nonetheless inescapable as a consequence of the erroneous mention by Galán Cela & Gamarra (2003) of an Asturian placename ("Luarca") as its type locality. Luarca is the type locality of an inconsequential form (f. *cordata*) of *Dactylorhiza elata* described in Landwehr's work (1977) right before *O. tenera*, whose true type locality is the Sierra de Alcaraz (Albacete), almost 700 km to the southeast. By comparison with *O. olbiensis*, this seems a weakly if at all differentiated entity, purportedly distinguished from *O. mascula* s. str. by its smaller flowers, displayed in delicate, laxer inflorescences and bearing a straight spur, features hardly reconcilable with the appearance of those problematic Asturian specimens. Since the nearest populations of plants undoubtedly assignable to *O. olbiensis*, already isolated themselves, are well to the east, around the border of the provinces of Burgos and Palencia, and since this taxon is strongly associated to frankly Mediterranean environments, its presence in Asturias seems, if not impossible, at least highly improbable.

Serapias olbia Verg. Another taxon described from the Mediterranean coasts in the surroundings of the ancient Greek outpost of Olbia (Hyères, Provence, France) and unduly reported as occurring in Asturias. In this case, however, the sources of such mistake are obscure. As far as we have been able to track, it all comes down to an unsubstantiated claim included in Delforge's renowned European guide at least since its edition of 2002. But since Delforge himself—and we cannot but agree—dismisses those ghostly Asturian records as a misinterpretation of spontaneous hybrids between *S. lingua* and *S. cordigera*, there is no incentive to dig deeper into this trifle: the species can be safely left off our checklist.

Serapias vomeracea (Burm.f.) Briq. Cited by Amparo Mora in the Floristic Catalogue of Picos de Europa National Park (Alonso Felpete *et al*., 2011). However, considering that the closest population is found in the province of Segovia, more than 200 km to the south and in a very different climatic context, when first adding the record to our database we were sure that it could not be admitted as it stood. However, we hesitated in attributing it to *S. cordigera* or to *S.* ×*ambigua*, both widespread in the region and with which—especially with the latter—*S. vomeracea* actually shares features like the hairiness of the lip and its color and shape. Carlón *et al.* (2024) revised the original specimen and concluded that this record should indeed be assigned to *S.* ×*ambigua*, both whose parents were recorded in the same publication from the very same locality.

Species to be looked for

Asturias is surrounded by territories with rather marked Mediterranean conditions, especially towards the south (as a consequence of the generalised rain shadow effect of the main Cantabrian ridge) but also for more local topographical causes, both to the east (in the basin of Liébana) and the west, where connections with areas rich in Mediterranean plants like Courel and El Bierzo are facilitated through the deep and sinuous (i.e., warm and isolated from maritime cloudiness) valley of the river Navia. In some of those bordering zones, unknowing to our still incomplete spatial coverage, some of the most genuine Mediterranean species that follow may already be present, awaiting discovery. The colonization of others, in the current global warming scenario, may well be underway (Fay, 2015; Cole & Waller, 2020). Long hidden or just arrived, attention must be paid to the following species, for some of which records do exist, albeit plainly wrong or far too vague and unattested to qualify as confirmation:

Anacamptis coriophora (L.) R.M.Bateman, Pridgeon & M.W.Chase. An unpublished specimen collected in the municipality of Morcín (FCO 033950, sub *Orchis coriophora* L.) could be confirmed to actually correspond to *Gymnadenia conopsea*. However, the presence of *A. coriophora* in Asturias is not to be completely dismissed, since the species occurs in the Leonese slopes of the Cantabrian Mountains as well as in the Galician province of Lugo. In any case, the habitat occupied by those Leonese and Galician populations (humid to damp, slightly acidic to basic grasslands, often accompanied by *A. morio*, *Dactylorhiza elata* and *Serapias lingua*), on top of being intrinsically rare in the Asturian territory, especially in those areas with a Mediterranean hue, has been particularly hit by overgrazing, all our searches in apparently favourable areas having been so far unsuccessful.

Anacamptis fragrans (Pollini) R.M.Bateman. This species, closely related to *A. coriophora*, has been found in La Hermida gorge (Cantabria) and in the province of León, especially in El Bierzo and around Boñar. *A. fragrans* seems to prefer drier and more basic soils than *A. coriophora*, the best chances to find it in Asturias thus lying in warm south-facing slopes of Peñamellera Baja or in the Cares gorge, where the presumably detrimental effect of excess summer precipitation and humidity are lessened (Figure 10A).

Anacamptis laxiflora (Lam.) R.M.Bateman, Pridgeon & M.W.Chase. Judging by the materials list sent to us, and despite the apparent omission of that particular record from the corresponding dataset in GBIF, the herbarium of the Pyrenean Institute of Ecology in Jaca preserves under this name a specimen combining a credible collector (Pedro Montserrat), an appropriate date (June 17th, 1969) and an apparently suitable habitat (landscape dominated by open meadows on Tertiary sedimentary terrains prone to water-logging). However, until we can revise the original material, we suggest assigning this occurrence to *Dactylorhiza elata* or *Orchis mascula,* both typical from humid meadows and common in the municipality where this specimen was collected. Additionally, even if the species once occurred in Asturias, it is regrettably highly likely that it has suffered here the same fate that has just fallen upon it in the neighbouring region of Cantabria, where the only well and recently documented populations in all of northwestern Spain were located (Aedo *et al*., 2005b), and where a phony protection has not prevented the complete destruction (through compaction, fertilization and frequent mowing in a context of intensive cattle farming) of the two known colonies, carefully monitored since 2000: in one of them, the plants were last seen in 2016; in the other, in 2019 (Durán Gómez *et al*., 2024).

Anacamptis papilionacea (L.) R.M.Bateman, Pridgeon & M.W.Chase. Although its strongholds lie in areas with truly Mediterranean climate, the southern slopes of Picos de Europa, the mountains around Riaño in León and the valley of Liébana in Cantabria, all close to the Asturian borders, are known to harbor quite a few colonies of this showy species, whose recent finding in the western coast of Cantabria (Durán Gómez *et al*., 2024) opens still a new unexpected way through which it might enter Asturias (Figure 10B).

Cephalanthera damasonium (Mill.) Druce. The well-attested presence of this species found in both temperate and Mediterranean areas, and most readily distinguishable from its congeners by its pale-yellow flowers, in basophilous steep forests from León and Cantabria, in the foothills of Picos de Europa and very close to the Asturian borders, makes us confident that, sooner or later, and most likely somewhere in the Cares gorge, it will reveal itself as a member of the Asturian flora (Figure 10C).

Dactylorhiza caramulensis (Verm.) D. Tyteca. This still insufficiently studied taxon probably derives from the (back) crossing between *D. elata* and *D. maculata*, though —as shown by the occurrence of pure stands, with none of the putative parental species present, in contrast with the occasional, ephemeral appearance of sterile hybrids like those indicated above— stabilized in a still undetermined way. Its *terra classica* encompasses mountain areas of northern Portugal showing, as a consequence of environmental similarity and effective dispersal connectivity, deep floristic resemblance with southwestern Asturias, where the presence of this presumed species —characterized by its robust size, its dense inflorescences and the long, relatively thin and down-curved spur of its flowers— seems thus very likely.

Epipactis bugacensis Robatsch. Reported originally as *E. rhodanensis* Gévaudan & Robatsch (apparently a mere posterior synonym, at least at species level) in a website (floressilvestrescantabricas.blogspot.com/2013/03/orquidaceas.html), where a photograph is claimed to have been taken in Beleño (Ponga municipality) on July 2013. Since this is the only putative Asturian record of the species and given the lack of response to our request to the author of the photograph for further details to explicitly rule out a possible mislabelling, we opt for keeping it off our catalogue. This notwithstanding, insofar as the species has been convincingly reported from not-too-distant riverine forests in León and Cantabria, its occurrence in montane Asturian forests dominated by *Alnus*, *Populus* or *Salix* would not come as a total surprise (Figure 10D).

Epipactis kleinii M.B.Crespo, M.R.Lowe & Piera. Although for the widespread confusion of this taxon with mere pale-colored individuals of *E. atrorubens* we remain unconvinced of the occurrence this species in Asturias, sufficiently sound proof might arise soon, especially in places —like the calcareous gorges of the rivers Cares and Deva, the species having been reliably recorded in sectors of the former pertaining to León and areas of the latter within Cantabria— whose orography and lithology mimic Mediterranean conditions (Figure 10E).

Epipactis leptochila (Godfery) Godfery. Two of the just four known Iberian populations —the others would be those reported from the Catalan Pyrenees by Alamany (2020), since according to Benito Ayuso (2017) the plants form the Maestrazgo correspond to the narrowly related but distinct *E. provincialis*— lie in basophilous beechwoods in northern León, pretty close to the Asturian border. Benito Ayuso (*loc. cit.*) carried out quick attempts to find the species in Asturias, whose lack of success should not too seriously discourage further searches: as a matter of fact, this author found one single individual in the original Leonese population, while we could see a number of them in the following years, suggesting the existence of considerable interannual fluctuations in the number of flowering plants and lessening the weight of evidence represented by those unfruitful, admittedly shallow Asturian pursuits (Figure 10F).

Epipactis microphylla (Ehrh.) Sw. Associated with forest habitats; this species is rare but well attested in León and Cantabria. We have studied some suggestive herbarium material collected in the municipality of Ribadedeva (FCO 033035), with small cauline leaves and hairy stem and ovaries reminiscent of *E. microphylla*; but the lack of basal leaves in the specimen imposes prudence and prevents us from confirming this species as present in Asturias. If it does actually occur within the Asturian borders, it should not take long to find indisputable proofs during further field surveys in such area that we have visited several times and found rich in *E. helleborine*, as well as in the Cares and Deva gorges in Picos de Europa (Figure 10G).

Epipactis tremolsii Pau. It has been more widely and openly reported in the region than the rest of the orchids discussed in this section (see, for instance, the explicit record by López Fernández & Fernández Prieto, 2020). Sometimes considered just as a subspecies of *E. helleborine* or even a phenotype or at most an ecotype (associated with drier and hotter places and characterized by more densely arranged and coriaceous leaves, with a marked undulated edge) of the widespread *E. helleborine*. In September 2024, in a steep, south-facing calcareous outcrop close to a path amidst a *Quercus rotundifolia* open forest located in the municipality of Peñamellera Baja, we found some individuals whose leaves and whose early flowering (the plants were already in fruit, whereas nearby typical *E. helleborine* were still flowering) were actually very suggestive of *E. tremolsii*. Our judgment of their true identity, and specifically of the nature of its links with those surrounding canonical *E. helleborine* —as well as, more importantly, the taxonomic reality of this putative species— is suspended until we can return and perform deeper studies on flowering, fully developed plants (Figure 10H).

Limodorum trabutianum Batt. Often considered a subspecies or even a mere aberrant form of *L. abortivum* (Delforge, 2018), whose ecological behavior shadowy places in dense *Quercus ilex* or *Q. rotundifolia* forests it mirrors. It can be recognized by the much shorter spur (less than 4 mm in length) and the non-articulated labellum, as well as by a much paler coloration throughout. Its occurrence in Asturias is quite plausible, as some populations in La Hermida gorge (Cantabria) are located less than 10 km away from the provincial border, with large expanses of suitable habitat all the way across said border.

Ophrys castellana Gren. & M.Philippe. Since this species of the section *Euophrys* well characterized by its pale, usually white sepals with a central green stripe and its ciliate petals, as well as by its hygrobasophilous ecological behavior and by an arguably specific pollinator (*Andrena schenckii*) is locally common in northeastern León (Hermosilla, 2018), its occurrence in the Asturian side of the Cantabrian mountains is not entirely impossible, albeit the by far most environmentally suitable area (namely, the south-facing calcareous slopes of Somiedo's valleys) is too far to the west from the known Leonese populations. Attention should be paid to avoid mistaking this species for white-sepaled individuals of *O. sphegodes,* like those occasionally found in central Asturias (Figure 10I).

Ophrys ficalhoana (J.A.Guim.) Wucherpf. Iberian-French endemic, widely distributed across the peninsula and recently found in Southern Galicia (Perille *et al.*, 2024). Locally abundant in the limestones of the southern watershed of the Cantabrian Mountains, it has not been found yet within the Asturian slope despite insistent searches in Picos de Europa, where there are many populations pretty close to the Asturian borders, especially in the valleys of Sajambre, Valdeón and Liébana (Figure 10J).

Ophrys kallaikia C.E.Hermos. Another member of the section *Euophrys*, recently described from sand dunes along the Galician coast, from where it is thought to be endemic. The white stigmatic cavity evokes *O. incubacea* and *O. passionis*, but it bears smaller flowers which, together with the frequent yellow margin of the labellum, explain its occasional misidentification with *O. araneola*. An apparently specific pollinator (*Andrena nitida* subsp. *hispaniola*) may have been tailoring, through iterative cycles of sexual isolation, the still subtle morphological

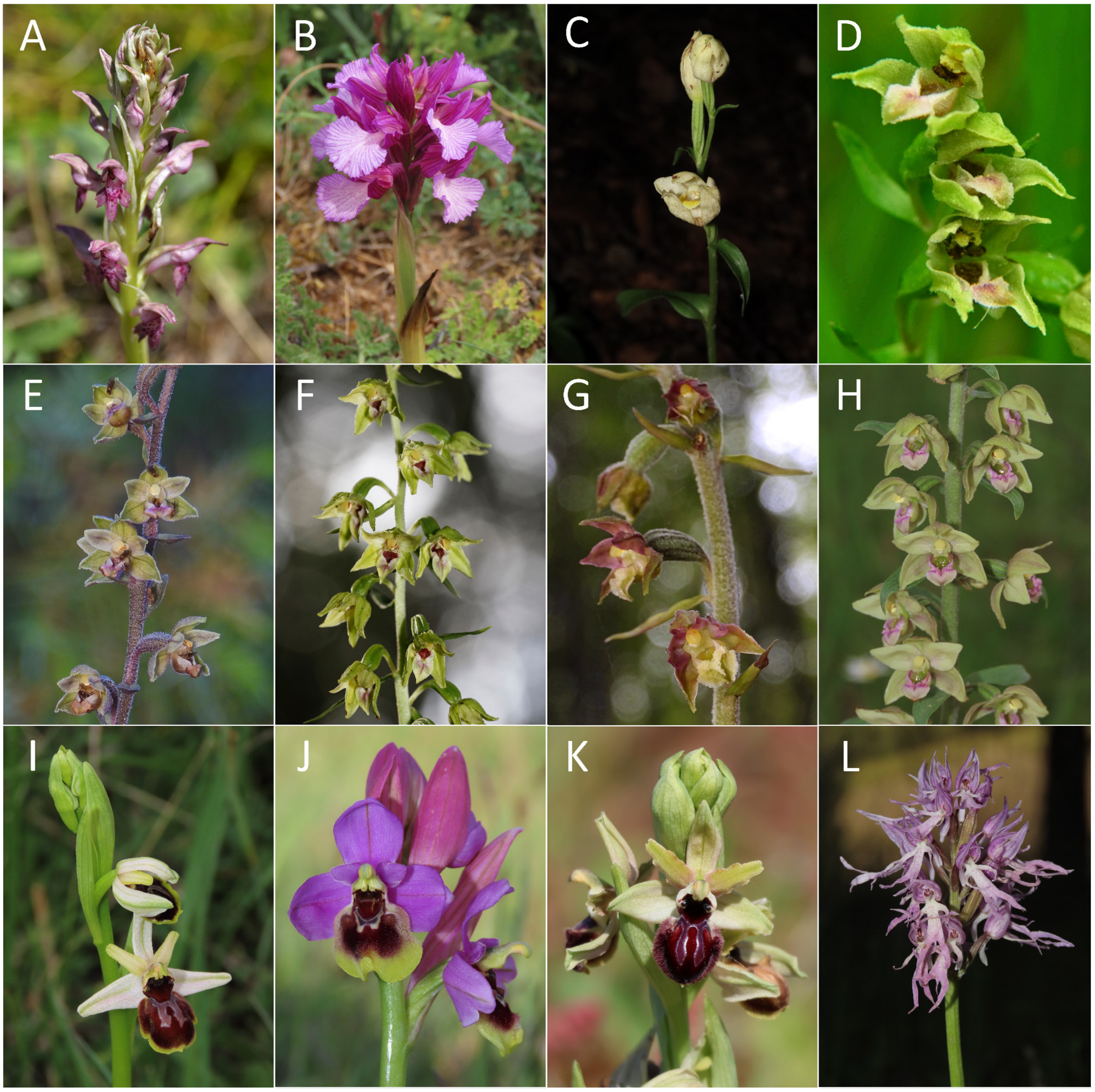

Figure 10. A, *Anacamptis fragrans* (León*, 09-V-2022. AAL); B, *Anacamptis papilionacea* (León*, 30-IV-2023. VGG); C, *Cephalanthera damasonium* (León*, 10-VI-2023. VGG); D, *Epipactis bugacensis* (Presumably Ponga, VII-2013. Andrés Asún); E, *Epipactis kleinii* (Teruel*, VII-2021. Álvaro Díaz Pastor); F, *Epipactis leptochila* (Germany*, 15-VI-2024. Michael Pollich); G, *Epipactis microphylla* (Navarra*, VII-2024. Álvaro Díaz Pastor); H, *Epipactis tremolsii* (Cáceres*, 27-04-2024. VGG); I, *Ophrys castellana* (León*, 12-V-2024. VGG); J, *Ophrys ficalhoana* (León*, 12-V-2024. VGG); K, *Ophrys kallaikia* (A Coruña*, 24-III-2024. Diego González Dopico); L, *Orchis italica* (Granada*, 12-IV-2024. VGG).

delineation of this taxon (Hermosilla, 2018). Though first searches have been unsuccessful, it might end up appearing in any of the remaining sand dunes systems of the Asturian western coast (the easternmost known populations of *O. kallaikia* lay less than 50 km away from the border between Asturias and Galicia). However, most of the Galician populations have suffered dramatic declines in number in recent years, mostly due to poor habitat management and consumption of the bulbs by wild boars (Marcos Perille, pers. comm.) (Figure 10K).

Orchis italica Poir. Preferring frankly Mediterranean climates, this species occurs and even abounds in certain areas of the bordering provinces of León (El Bierzo) and Lugo (Courel) (Cortizo Amaro & Sahuquillo Balbuena, 2006), where distance and topographical isolation from the ocean combine with calcareous lithology to generate pretty summer-dry climates. It is conceivable that any of the scarce limestone outcrops of south-western Asturias, where not that different conditions arise locally, harbors this species. A spontaneous individual, most likely unwittingly taken from the field along with other orchids during the gathering of living plants to stock the exhibition of natural forests, persisted for some years in the Atlantic Botanic Garden of Gijón (Figure 10L).

Species richness

The 52 species already confirmed as present in Asturias represent 41 % of those admitted as members of the Ibero-Balearic orchid flora by the current most complete review of the family in the Iberian territory (Benito Ayuso, 2017). The proportion increases significantly, to 52 %, when more taxonomically synthetic treatments like the one in *Flora iberica* (admitting only 90 species, 47 of which are already demonstrably known to inhabit Asturias) are considered. These apparently modest figures become more respectable as soon as one realizes that Asturias covers just 1.8 % of the Iberian territory and is, arguably, the only Iberian region lacking areas with a truly Mediterranean climate. Revealingly, this area-adjustment becomes unnecessary when comparisons are focused in other western European countries for which lists elaborated with similar taxonomic criteria are also available: the far better studied Britain —the number of British orchid records, estimated conservatively from the whole dataset of the last version of the BSBI Atlas (Stroth *et al*., 2020), is two orders of magnitude larger than that available for Asturias— even using as we have much more varied sources, holds only about 10 % more species than Asturias (58 vs. 52) for a surface 20 times bigger; whereas Portugal, 9 times bigger than Asturias, no less well surveyed —13000 orchid records only in Flora-On (2024)— and comprising a wide latitudinal strip with no shortage of calcareous and fully Mediterranean territories, is less rich with around 49 species.

This appreciable geographic concentration of species (easily strengthened if, as we expect, further surveying efforts provide proof of the occurrence of at least some of those up to 16 additional species whose presence in Asturias we esteem plausible) is still more remarkable when the focus is set on exceptional territories such as the municipality of Somiedo. In this case, substantial increases in the number of species are improbable, the survey coverage being already considerable thanks to the dedication of several naturalists; but our current knowledge suffices to establish an astonishing conclusion: being, for instance, 300 times smaller than Portugal, this outstanding area, for the reasons outlined in the general discussion on the geographic distribution of the Asturian orchid flora, harbors almost as many orchid species (46 vs. 49).

While being truly outstanding in a European context, this regional and local concentration of species richness is not unparalleled in Spain, even in the immediate surroundings of Asturias. Although accurate comparisons are complicated by the lack of consensus among authors, a common trend among orchid taxonomists (Pillon & Chase, 2007), it can be safely stated that both Cantabria and León hold more species of orchids than Asturias, about 62 (Durán, 2018) and 68 respectively. Remarkably, Cantabria attains that higher figure in spite of being half the size of Asturias, something attributable to it having a higher proportion of calcareous substrates and, more importantly, extensive areas where Mediterranean conditions are faithfully mimicked by orographic effects (Liébana) or even genuinely expressed (the extreme south, draining into the Ebro). The higher orchid richness of the province of León, on its part, might at first sight be explainable by its area, 50 % larger than Asturias; however, the complexity of its territory in lithological, topographical and climatic terms —vast areas of both temperate (mostly montane, but with pockets of milder lowlands, especially in the northeastern valleys) and genuine or orographically-induced Mediterranean climate— leads to local hotspots rivalling that of Somiedo: the so called “Montaña de Riaño”, in northeastern León, is home to all the 68 Leonese species in just 2,686 km^2 (Díez Santos, 2022).

In contrast, the province bordering Asturias to the west, Lugo, is considerably less rich with 35 species, 34 in Romero Buján (2008), plus the above discussed, recently described *Ophrys kallaikia*. Such difference cannot be explained in terms of land area (both territories are virtually equal) nor climate or topographical diversity. Lugo contains pretty high mountains and shows a stark gradient from very cloudy, rainy, cool, hyperoceanic conditions all year round in the northern maritime hills to nearly Mediterranean, with warm, sunny and dry summers, in the southern inlands). Again, the scarcity and scattered occurrence of basic substrates is the most likely cause for this relative paucity, as corroborated by the fact that the most celebrated provincial orchid hotspot (Courel) coincides with a rare cluster of limestone outcrops, and several species are associated with coastal sandy soils, containing lime under the form of fragments of the shells of dead marine animals. This situation can be extrapolated to the whole of Galicia (the autonomous region of which Lugo makes part), whose large size (thrice that of Asturias) does not translate into a particularly rich orchid flora, the total number of species barely exceeding 40.

The opposite pole in the Iberian orchid richness gradient is located in Navarre and Aragón, areas with an enormous topographical, lithological, with dominance of basic substrates, and climate diversity, comprising from high alpine mountains in the Pyrenees to extremely arid, low-altitude semideserts in the Ebro basin: up to 82 species have been recorded for Navarre (Robles *et al*., 2022: a figure attained, admittedly, by means of a very analytic treatment of *Epipactis* and *Ophrys*, but the number resulting from a more synthetic approach would be no less impressive for a territory equal in size to Asturias). Aragón, on its part, no less geographically diverse but almost five times larger, counts nearly 90 species (Muñoz, 2014).

Ecology and phenology

As a glance at Appendix 3 suffices to comprehend, PCA’s first component, explaining 48.94% of the total variance, is clearly interpretable as a mainly thermally driven gradient, going from the warm lowlands to the left (reasonably enough, the leftmost plotted centroids are those of *Serapias cordigera* and *S. parviflora*) to cold mountain areas to the right (*Nigritella gabasiana* and *Orchis spitzelii*, the latter represented by a single record, occupying the rightmost positions). The second component, accounting for 17.87% of the total variance, seems also grounded in thermal differences: namely, a gradient going from less oceanic, with bigger daily and yearly temperature differences (mediated by less cloud cover and, in expected correlation, less rainfall during the summer; i.e. more Mediterranean conditions) in the upper area of the diagram (the species with the uppermost centroids *Dactylorhiza romana* subsp. *guimaraesii*, *Ophrys passionis* and *Orchis purpurea*, judging by their general distributional areas, suit this interpretation) to more oceanic areas with cooler, cloudier, rainier summers in the lower parts of the diagram. In this case, there are reasons to suspect that the species are plotted there not for their intrinsic association with such conditions but because their few records happened to be fortuitously concentrated in northeastern Asturias, where those climatic characteristics are particularly patent. That said, the orchids currently known to occur in the territory occupy practically the entire environmental space of the region, indicating a possible niche redundancy in those species that have yet to be discovered (Appendix 4). As expected by the dramatic differences in the number of records among species, the centroid for the commonest species, *Orchis mascula*, appears almost in the very center of the plot. The considerable amplitude of the ecological niche of this species (Figure 11) reveals that this dominance, rather than indicating its specialization in a narrow set of conditions thus concomitantly dominant across the territory, is to be attributed to a generalist behavior.

Taking the ecological analysis beyond the overall factors revealed by PCA to finer on-the-ground delineation, most of the orchids occurring in the territory were found to prefer open and sunny spaces, such as secondary grasslands and shrublands, or azonal habitats like dune systems, peat bogs and fens, with just a handful (e.g. *Cephalanthera longifolia*, *Epipactis helleborine*, *Limodorum abortivum*) preferring shady forests. Traditional, not too intensive human activities (delayed summer mowing, extensive grazing) may thus have benefitted orchids to some extent (Paušič *et al*., 2017), since the proliferation of those open habitats derives mostly from agricultural practices (more on this in the section devoted to conservation issues). Even marginal spaces in urban green areas or roadways, paradoxically less disturbed and massively fertilized than many conventional modern rural landscapes, can act as refugia for some species that show preference for these anthropized habitats (Rewicz *et al*., 2017, Fekete *et al*., 2020), such as *Ophrys apifera*, *Serapias cordigera*, *S. lingua* and *Spiranthes spiralis*.

Remarkably, as already mentioned when discussing the geographic coverage of our data, most species have a clear preference for basic soils. This seems to be the rule in this family, at least in the Euro-Mediterranean area, except for rare cases like *Dactylorhiza maculata* or *Spiranthes aestivalis* (Figure 11). The drivers of this strong association between orchid diversity and basic soils—which explains, for instance, the noteworthy lack of contribution of soil pH to the retained first two principal components in our PCA—remain unknown: it may be an effect of how karstified limestone terrains hamper mechanized agriculture, how clayey soils derived from the dissolution of limestones experience variations in humidity benefitting the geophytic habit of orchids, or how leaching generates pH microgradients and boosts edaphic diversity; finally, it may stem from mere historical contingency (Chytrý *et al*., 2010). Let's make it clear that basicity by no means equals eutrophy: actually, the partnership with fungi that kick-started orchids' unique reproductive biology and explosive diversification (Waterman *et al*., 2011) is tightly linked to oligotrophic conditions. Their consequent high sensitivity to fertilization has contributed, as elaborated in the section 'Conservation', to aggravate the impact of modern agriculture on these plants.

Regarding elevation, we have found that the same species that grow at higher areas also encounter highly continental conditions (i.e., a large difference between day and night and winter and summer temperatures) such as *Dactylorhiza cantabrica*, *D. incarnata*, *D. sambucina* and *Neotinea ustulata* (Figure 11). However, on the one hand we have found that some of the species attaining higher altitudes may prefer or, at least, tolerate less continental areas with a milder climate, such as *Epipactis atrorubens*. On the other hand, species actually favored by continental conditions may find them in topographically exceptional areas even at lower elevations (e.g., *Dactylorhiza romana* subsp. *guimaraesii*, *Ophrys incubacea* or *Orchis purpurea*). Other species like *Ophrys lupercalis, O. lutea, O. speculum* and *Spiranthes aestivalis* show, as far as the Asturian territory is concerned, a strong association with oceanic, temperature-buffered conditions, the strength of this conclusion being nonetheless reduced by the scarcity of records and the knowledge of the ecology of those species gained in other geographic areas where they are less rare.

Moving on to precipitation, this is clearly not a limiting factor in our territory, with even the less rainy areas (lowland central and western Asturias) reaching total annual average values above 900 mm, some areas (Picos de Europa and southwestern mountain ranges) exceeding 2300 mm. Under these conditions, namely the lack of a severe and systematic summer drought, more neatly Mediterranean species such as *Dactylorhiza romana* subsp. *guimaraesii* and *Ophrys incubacea* become less competitive and see themselves restricted to grow preferably in the less rainy areas or in drought prone places (e.g., sandy or shallow soils, steep limestone slopes).

With this ecological information, in addition to the complete distribution for each species, we were able to classify them in different chorotypes. Therefore, around 50% of Asturian species could be classified in the 'European' chorotype, which agrees with the dominant temperate climate of the region. However, a non-insignificant number of species fit in the 'Mediterranean' (15%) category, where both common and rare species are found: *Anacampris champagneuxii* and *Ophrys speculum*, both clearly Mediterranean species, have one only well-known population in all territory, contrasting with the widely spread *Himantoglossum robertianum*. An in-between category would be 'Mediterranean-Atlantic' (25%), also hosting both common (e.g. *Ophrys apifera*, *Serapias lingua*) and uncommon species (e.g. *Neotinea maculata*, *Ophrys lutea*). Nevertheless, one of the most difficult categories to assign was the 'Alpine' one (4%), since several species from our territory are mostly or uniquely found in our mountains but, when these populations

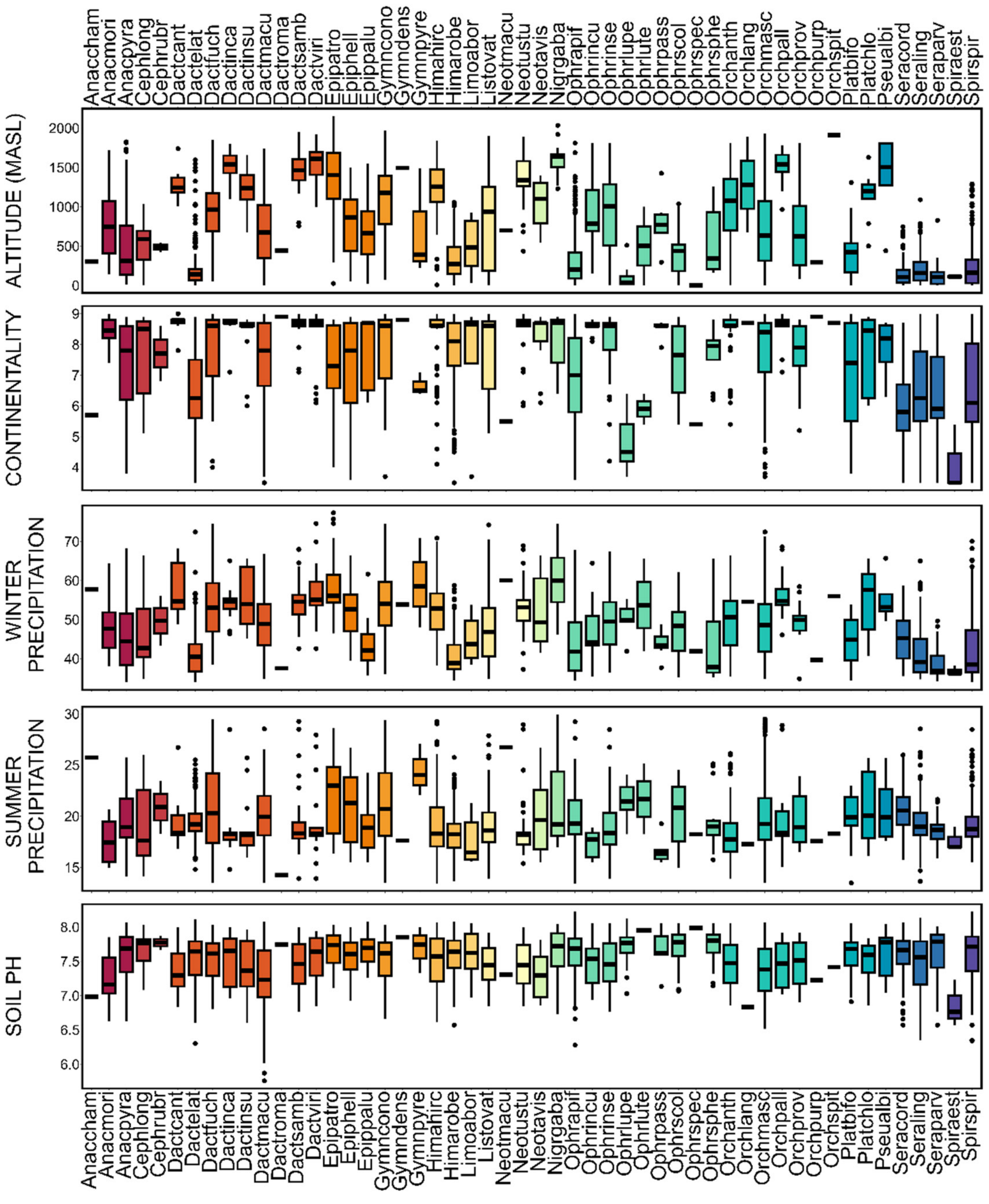

Figure 11. Boxplots representing the most important variables in the understanding of the ecology of the orchid family in the Principality of Asturias, extracted from PC1 and PC2, along with soil pH. Species are alphabetically ordered and coloured by genus.

are compared with the whole species distribution, only two of them seem to be truly linked to the alpine world: *Orchis pallens* and *Nigritella gabasiana*. This latter one fits also in the last category: 'Endemic' (7%), being the representative of its genuinely Alpine genus in the Cantabrian Mountains and most of the Pyrenees. Other two species from this category might be interpreted as vicariants of European lineages: *Gymnadenia pyrenaica*, of *G. odoratissima* in northern Iberia and SW France or alternatively, as the result of a stabilized hybridisation event between the latter and *G. conopsea*, perhaps through allotetraploidy as suggested by Trávníček *et al*. (2012); and *Orchis langei*, of *O. mascula* in montane Mediterranean oak and pine forests. The last species would be *Dactylorhiza cantabrica*, which seems to be a hybridogenous taxon deriving from the encounter of a Mediterranean (*D. romana* s.l.)

and a European (*D. sambucina*) lineage, apparently restricted to the Cantabrian mountains.

Concluding, and with regards to phenology, all Asturian orchids are geophytes spending part of the year below ground, undetectable to the human eye. The emergence of the leaves varies from species to species, as some of them present leaves since the autumn season (e.g. *Ophrys*), while others wait until spring or summer to display them (e.g. *Epipactis*). *Spiranthes spiralis*, uniquely, displays the leaves poised to flower next season besides the already flowering stem and not just under it, as it happens in *S. aestivalis*. The peak bloom takes place between late-spring and early-summer, being May and June, the months when more species, up to 42, can be observed flowering (Figure 12). Some species can skip flowering in years of unfavorable conditions or even, like *Limodorum abortivum* (Claessens & Kleynen, 2014), flower cleistogamously below ground. Only *Spiranthes spiralis* flowers in autumn, while no species has been recorded to flower in November, except for a single anomalous individual of *Plantanthera bifolia* that, as the observer could confirm to us, was in fact flowering during this month in Gozón municipality in the 1970s. *Himantoglossum robertianum* is the only species confirmed to flower in December, although only in coastal areas and in particularly warm winters.

Non-binding catalogs of threatened flora

At the general Spanish level, none of the species occurring in the territory was originally included in the Atlas and Red Book of the threatened vascular flora (Bañares *et al.,* 2004) or its later addenda (Bañares *et al*., 2006; 2009; 2010) until 2017 (Moreno *et al*., 2019), when *Orchis provincialis* and *Spiranthes aestivalis* were included. By contrast, in the Red List of Spanish vascular flora, one species did appear within its first publication (Domínguez Lozano, 2000): *Gymnadenia odoratissima* (surely alluding to the taxon by us admitted as *Gymnadenia pyrenaica*), while two more species were added in posterior updates: *Dactylorhiza cantabrica* and *Orchis spitzelii* (Moreno, 2008). Most of the Asturian species assessed at the European (Bilz *et al*., 2011) and World level (IUCN, 2024) fall under the category of “Least Concern” (LC), the exceptions being *Anacamptis morio*, “Near Threatened” (NT) in Europe and worldwide, *Dactylorhiza elata* NT in the world red list, LC in the European one, *Orchis spitzelii* NT at both levels, and *Spiranthes aestivalis* “Data Deficient” (DD) at both levels.

Legal protection and current conservation concerns

Despite the high diversity of species occurring in the territory and the rarity and well-documented recent demise of quite a few, none is included in the regional catalogue of threatened vascular plants (Anon., 1995). This implies the complete lack of specific protection for even those species which, known to occur in a single locality, face the most pressing risk of disappearance (e.g., *Gymnadenia densiflora*, *Ophrys speculum*, *Orchis spitzelii*). Admittedly, these species had not been recorded when said piece of legislation was published, but this is not the case with others, such as *Limodorum abortivum* and *Spiranthes aestivalis*, whose rarity was already well known back then. Fernández Prieto *et al.* (2007) made a proposal to update the catalogue which included those two orchids under the category ‘of special interest’ (‘de Interés Especial’ in Anon., 1995), along with *Epipactis palustris*, proposed as ‘in danger of extinction’ (‘en Peligro de Extinción’ in Anon., 1995) and, with no explicit category until more data could be retrieved, for *Dactylorhiza insularis*, *Dactylorhiza romana* subsp. *guimaraesii* and *Nigritella gabasiana*. This proposal, itself already outdated by now, was never translated into legislative changes despite the efforts of some officials, so a manifestly obsolete 30-year-old catalogue is all there is. Only *Orchis provincialis* and *Spiranthes aestivalis* would be the only legally protected Asturian orchid species by means of the Spanish List of Wild Species under Special Protection Regime (Anon., 2011).

Although at present we have no knowledge of any species extinction at regional level (unlike in Cantabria, where the above alluded cautionary extinction story of *Anacamptis laxiflora* could be documented, Durán Gómez *et al.,* 2024), we are aware of local population extinctions of some of the most sensitive species; especially those, like *Epipactis palustris* and *Spiranthes aestivalis*, inhabiting wetlands systems, as sketched when describing our study area, intrinsically rare in a mountainous area like Asturias and, on top of that, disproportionately affected by artificial draining, landfills, water diversions, etc. The profound transformation that some areas of Asturias have suffered in the last century, mostly due to a shift towards a more industrial-based economy to the detriment of more traditional land uses, has carved deep wounds in the landscape. Gijón, as an example, once harboured dunes, marshes and forests where orchids like *Epipactis palustris* or *Orchis provincialis* grew until recently. The only known population of *Listera ovata* in Gijón municipality grows in the surroundings of El Tragamón, one of the few remaining natural forests in the municipality and now conserved under the protection of the Atlantic Botanical Garden. Rodiles beach in Villaviciosa, and within the Ría de Villaviciosa Partial Nature Reserve, harbors around 25% of species of Asturian orchids, some of them with their only population there (*Ophrys speculum*) or representing exceptional cases for species which are quite more abundant at higher altitudes (*Himantoglossum hircinum*, *Ophrys insectifera*). However, this spot is far from being considered an ideal place for orchid—or other taxa—conservation, as the dune system is fully occupied by alien species (e.g., *Oenothera glazioviana* Micheli*, Stenotaphrum secundatum* (Walter) Kuntze) and it has been artificially stabilized by a plantation of *Eucalyptus globulus* and subjected to growing touristic pressure, leading to multiple direct and indirect disturbances, including the systematic collection of living specimens (we have witnessed the removal of several individuals of *Himantoglossum robertianum*) or the construction of new facilities, such as an oversized parking lot. These land-cover changes may be more pressing threats than even climate change (Vogt-Schilb *et al*., 2015).

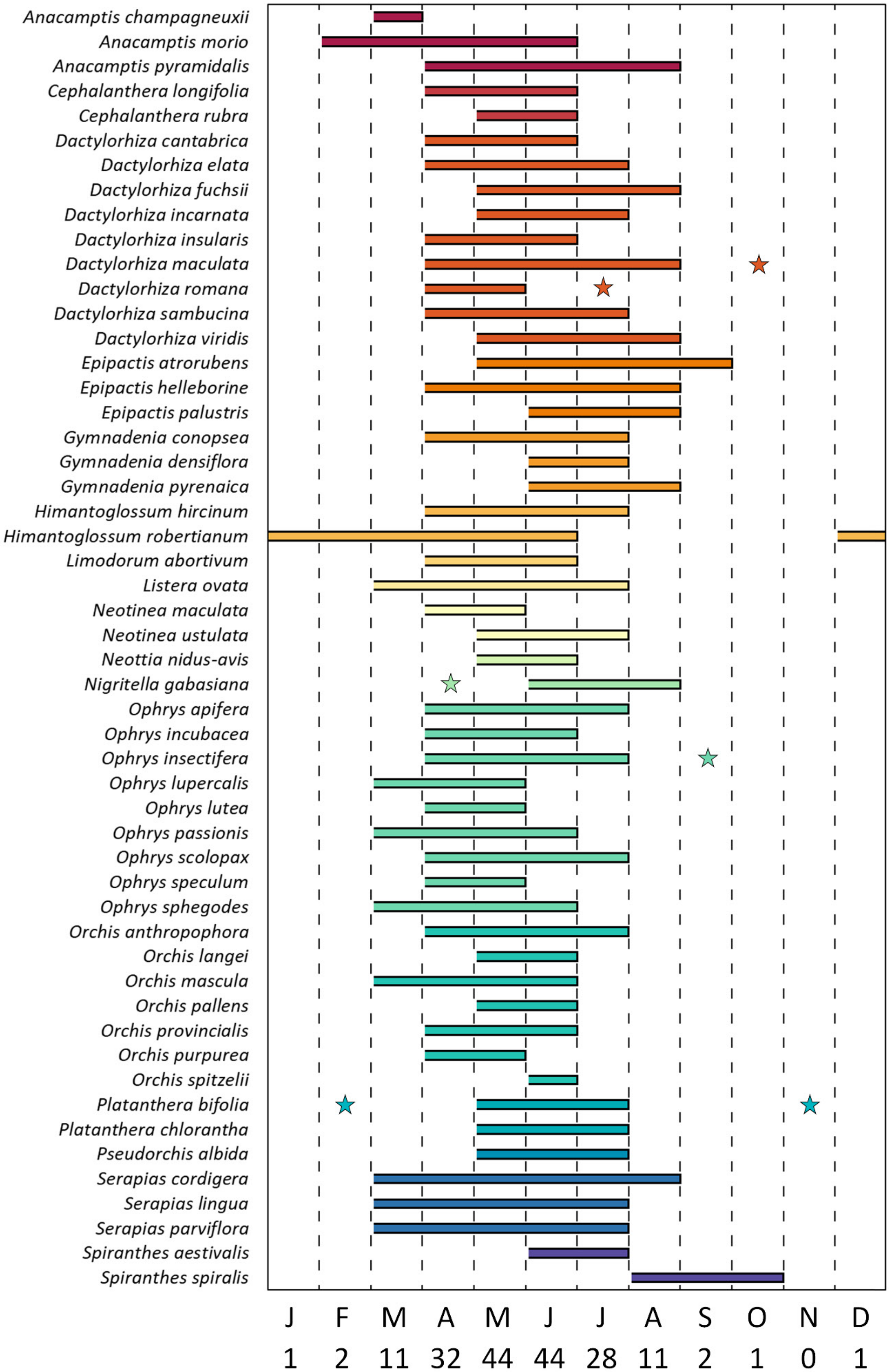

Figure 12. Bloom calendar or the Orchidaceae family in Asturias. Stars (★) indicate months when a species was recorded flowering out of its usual season (bars). Numbers below the graph represent the number of species that flower during that month (only dates in bars). Species are alphabetically ordered and coloured by genus.

The human role in orchids distribution is, however, somewhat ambivalent. Without human activities, nearly all the Asturian landscape would be covered by forests rather than the shrublands or grasslands inhabited by most orchids. The mosaic of different light regimes and disturbance frequencies created by traditional, mostly self-sufficient agrarian communities represented a substantial increase in opportunities for orchids in comparison with the primeval scattered pockets of rocky outcrops, wetlands or patchy clearings created by wild animals or storms, perhaps even to the extreme of providing suitable conditions for species which otherwise would not occur. But caution is in place before prescribing a full comeback of agriculture (specifically, in the Asturian case, of animal husbandry) as the solution to the recent demise of these plants and other organisms: current agricultural practices, to be minimally profitable, involve a highly unequal pressure on the landscape (i.e. a non-intermediate disturbance regime), the most accessible areas being intensively exploited (even when extensively managed during the summer, the number of heads is kept higher than ever before through the availability of imported fodder in winter), while those too abrupt or far from roadways are abandoned anyway. By contrast with old, more flora-friendly ways, the hay meadows traditionally supplying all said winter fodder are nowadays, even when not entirely replaced by cultures, mowed much more frequently, starting earlier in the season—mechanization overcoming the constraints imposed by the ancient labour-intensity; silage in plastic, the mandatory wait for the long, dry days of high summer to cure the hay, and preventing most species from setting seed. Therefore, and paradoxically enough, the new urban ecosystems are often better shelters for orchids, as well as for other kinds of plants and insects than the increasingly intensified (i.e., ploughed, fertilized, pesticide-sprayed, irrigated, drained, frequently mowed) current agrarian landscapes (Adamowski, 2006; Fernández-Pascual *et al*., 2025: Rewicz *et al*., 2015; 2017).

Conclusions

This research represents the most profound study to date of the family Orchidaceae in the Principality of Asturias. Most of the information published so far —not too abundant to begin with— is scattered in papers of general floristics, and the only serious attempts at a synthesis of Asturian orchids —on top of being very outdated (Díaz González & Fernández Prieto, 1981) or, when less so, referred to larger geographic areas (Díaz González *et al*., 2002)— lie in the realm of popular science, consequently tending to avoid open questions and lacking geographic detail, depth in the ecological analysis, comprehensive citation of previous information and rigorous critical discussion of taxonomic and nomenclatural issues. However, let it be clearly understood that our team has always been open to collaborate with other researchers or non-professional orchid-lovers rather than competing with them, and sharing our full data will be on the table for anyone genuinely and demonstrably interested and experienced in this topic.

Citizen science has played a key role in the build-up of data. Although online platforms such as iNaturalist and Observation promote a passive arrival of data, due in large part to the charm of this botanical family, we looked for a more active collaboration. Bringing the general public closer to this project through social media publications, informative talks and specialized workshops in the field has resulted in a greater arrival of observations, improving not only the amount but the quality of the data.

The uneven distribution of species and populations in the territory can be clearly attributed to the nature of the soil and its relationship with the orchids, rather than other environmental factors or the inequalities in sampling effort. Their presence in anthropogenic habitats is limited to a few species able to successfully overcome constraints such as a reduced number of pollinators and frequent mowing.

Given the fact that since the start of this project, 4 years ago, a significant number of taxa (4 species and 10 hybrids) have been discovered in the territory, the chances of finding even more in the coming years are quite high, with the eventual discovery of up to 16 additional species being plausible. However, even our current figures (52 confirmed species and 13 hybrids) suffice to present Asturias as a considerably orchid-rich territory, harboring almost half of Iberian orchids in less than 2 % of Iberian land area.

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Authorship contributions

VGG: Conceptualization, Methodology, Investigation, Data Curation, Writing, Review, Editing, Visualization, Supervision, Funding acquisition); AAL: Methodology, Investigation, Writing, Review, Editing); LCR (Investigation, Data Curation, Writing, Review, Editing).

Conflict of interest

None.

Data availability statement

Original dataset for creation of the manuscript can be accesed at https://doi.org/10.5281/zenodo.16365688.

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Supplementary material

Summary English. Orchids of the Principality of Asturias (Northwestern Spain).

Summary Spanish. Las orquídeas del Principado de Asturias.

Appendix 1. Checklist of the orchid family in the Principality of Asturias (northwestern Spain). Taxa are divided in four categories depending on if they have been cited in the territory and if their presence has been confirmed, is plausible or rather unlikely; and also, if their presence in the territory is possible but yet to be proven. Altitudinal range and flowering period are provided only for confirmed species, while chorotype is provided for all taxa, excepting those of hybrid origin. Taxa are alphabetically ordered within each category.

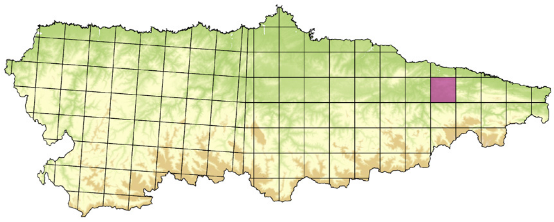
TAXON	ALTITUDINAL RANGE (M ASL)	CHOROTYPE	FLOWERING PERIOD
Confirmed presence in the territory			
Anacamptis champagneuxii (Barnéoud) R.M.Bateman, Pridgeon & M.W.Chase.	300(600)	MED	III
Anacamptis morio (L.) R.M.Bateman, Pridgeon & M.W.Chase.	(140)600-1230(1725)	EUR	II-VI
Anacamptis pyramidalis (L.) Rich.	(15)160-710(1825)	EUR	IV-VIII
Cephalanthera longifolia (L.) Fritsch.	(0)320-675(1450)	EUR	IV-VI
Cephalanthera rubra (L.)	250(600)	EUR	V-VI
×*Dactylodenia heinzeliana* (Reichardt) Garay & H.R. Sweet	-	-	-
Dactylorhiza cantabrica H.A.Pedersen	(500)1165-1390(1740)	END	IV-VI
Dactylorhiza ×*delamainii* (G. Keller ex T. Stephenson) Soó	-	-	-
Dactylorhiza elata (Poir.) Soó	(0)60-190(1595)	MED-ATL	IV-VII
Dactylorhiza fuchsii (Druce) Soó	(35)675-1200(1690)	EUR	V-VIII
Dactylorhiza ×*hjertsonii* P.P. Ferrer, J.L. Lozano, R. Roselló, Feliu & Peña-Riv.	-	-	-
Dactylorhiza incarnata (L.) Soó.	(1090)1400-1650(1900)	EUR	V-VII
Dactylorhiza insularis × *Dactylorhiza sambucina*	-	-	-
Dactylorhiza insularis (Sommier) Landwehr.	(670)1120-1400(1640)	MED	IV-VI
Dactylorhiza ×*kerneriorum* (Soó) Soó	-	-	-
Dactylorhiza maculata (L.) Soó.	(0)320-1390(1800)	EUR	IV-VIII
Dactylorhiza romana subsp. *guimaraesii* (E.G.Camus) H.A.Pedersen	(440)560-700	MED	IV-VII
Dactylorhiza sambucina (L.) Soó.	(770)1330-1560(1790)	EUR	IV-VII
Dactylorhiza viridis (L.) R.M.Bateman, Pridgeon & M.W.Chase	(1000)1525-1690(2045)	EUR	V-VIII
Epipactis atrorubens (Hoffm.) Besser	(25)1250-1770(2150)	EUR	V-IX
Epipactis helleborine (L.) Crantz.	(0)330-1180(1450)	EUR	IV-VIII
Epipactis palustris (L.) Crantz	(0)480-810(1600)	EUR	VI-VIII
Gymnadenia conopsea (L.) R.Br.	(50)910-1470(1785)	EUR	IV-VII
Gymnadenia densiflora (Wahlenb.) A.Dietr.	1450-1550	EUR	VI-VII
Gymnadenia pyrenaica (Philippe) Giraudias.	(710)1120-1485(1530)	END	VI-VIII
Himantoglossum hircinum (L.)	(0)1140-1595(1840)	MED-ATL	IV-VII
Himantoglossum robertianum (Loisel.) P.Delforge	(0)50-540(1030)	MED	XII-VI
Limodorum abortivum (L.) Sw.	(0)35-750(925)	MED-ATL	IV-VI
Listera ovata (L.) R.Br.	(0)50-1300(1900)	EUR	III-VII
Neotinea maculata (Desf.) Stearn.	(600)700(1700)	MED-ATL	IV-V
Neotinea ustulata (L.) R.M.Bateman, Pridgeon & M.W.Chase.	(435)1260-1640(1890)	EUR	V-VII
Neottia nidus-avis (L.) Rich.	(545)780-1300(1560)	EUR	V-VI
Nigritella gabasiana Teppner & E.Klein	(1230)1500-1750(2035)	END(ALP)	VI-VIII
Ophrys apifera Huds.	(0)50-415(1600)	MED-ATL	IV-VII
Ophrys ×*fonsaudiensis* Soca	-	-	-
Ophrys ×*fraresiana* M.R. Lowe, Piera & M.B. Crespo	-	-	-
Ophrys incubacea Bianca	(115)680-880(1400)	MED	IV-VI
Ophrys insectifera L.	(0)510-1215(1810)	EUR	IV-VII
Ophrys lupercalis Devillers-Tersch. & Devillers	(0)10-70(520)	MED	III-V

TAXON	ALTITUDINAL RANGE (M ASL)	CHOROTYPE	FLOWERING PERIOD
Ophrys lutea Cav.	0-1050	MED-ATL	IV-V
Ophrys ×minuticauda Duffort	-	-	-
Ophrys passionis Sennen ex Devillers-Tersch. & Devillers	(290)670-1080(1425)	MED-ATL	III-VI
Ophrys scolopax Cav.	(0)160-670(1235)	MED	IV-VII
Ophrys speculum Link	0(100)	MED	IV-V
Ophrys sphegodes Mill.	(70)170-335(1260)	EUR	III-VI
Orchis anthropophora (L.) All.	(0)675-1340(1810)	MED-ATL	V-VI
Orchis langei Lange ex K.Richt.	670(700)	END	IV-VII
Orchis ×loreziana Brügger	-	-	-
Orchis mascula (L.) L.	670(700)	EUR	IV-VII
Orchis pallens L.	(400)1390-1640(1785)	ALP	V-VI
Orchis ×penzigiana A. Camus	-	-	-
Orchis provincialis Balb. ex Lam. & DC.	(0)230-1150(1350)	MED-ATL	IV-VI
Orchis purpurea Huds.	(290)450(1100)	EUR	IV-V
Orchis spitzelii Saut. ex W.D.J.Koch	(1900)1910(1950)	EUR	VI
Platanthera bifolia (L.) Rich.	(0)110-580(1390)	EUR	V-VII
Platanthera chlorantha (Custer) Rchb.	(435)1010-1350(1630)	EUR	V-VII
Pseudorchis albida (L.) Á.Löve & D.Löve	(1200)1230-1650(1810)	EUR	V-VII
Serapias ×ambigua Rouy ex E.G.Camus	-	-	-
Serapias ×rainei E.G.Camus	-	-	-
Serapias ×todaroi Tineo	-	-	-
Serapias cordigera L.	(0)30-190(750)	MED-ATL	III-VIII
Serapias lingua L.	(0)55-265(1120)	MED-ATL	III-VII
Serapias parviflora Parl.	0-160(820)	MED-ATL	III-VII
Spiranthes aestivalis (Poir.) Rich.	(0)60-120(130)	MED-ATL	VI-VII
Spiranthes spiralis (L.) Chevall.	(0)30-250(1290)	EUR	VIII-X
Recorded and plausible but not enough supporting material provided			
Anacamptis coriophora (L.) R.M.Bateman, Pridgeon & M.W.Chase.	-	MED	-
Anacamptis laxiflora (Lam.) R.M.Bateman, Pridgeon & M.W.Chase.	-	MED-ATL	-
Dactylorhiza ×guillaumeae Chr. Bernard	-	-	-
×*Gymnigritella pyrenaica* E. Hermos. & Sabando	-	-	-
Epipactis bugacensis Robatsch	-	EUR	-
Epipactis kleinii M.B.Crespo & M.R.Lowe & Piera	-	MED	-
Epipactis microphylla (Ehrh.) Sw.	-	EUR	-
Epipactis tremolsii Pau	-	MED	-
	-		-
Recorded but doubtful			
Anacamptis palustris (Jacq.) R.M.Bateman, Pridgeon & M.W.Chase	-	MED	-
Dactylorhiza majalis (Rchb.) P.F.Hunt & Summerh.	-	EUR	-
Ophrys holosericea (Burm.f.) Greuter	-	MED-ATL	-
Orchis olbiensis Reut. ex Gren.	-	MED	-
Serapias olbia Verg.	-	MED	-
Unrecorded but plausible			
Anacamptis fragrans (Pollini) R.M.Bateman	-	MED	-
Anacamptis papilionacea (L.) R.M.Bateman, Pridgeon & M.W.Chase	-	MED	-

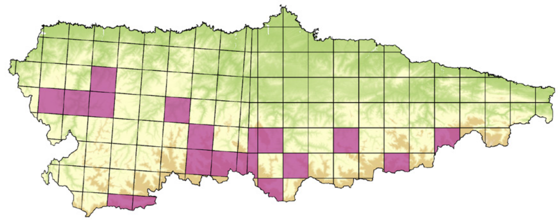
TAXON	ALTITUDINAL RANGE (M ASL)	CHOROTYPE	FLOWERING PERIOD
Cephalanthera damasonium (Mill.) Druce	-	EUR	-
Dactylorhiza caramulensis (Verm.) D.Tyteca	-	END	-
Epipactis leptochila (Godfery) Godfery	-	EUR	-
Limodorum trabutianum Batt.	-	MED-ATL	-
Ophrys castellana J. & P. Devillers-Terschuren	-	END	-
Ophrys ficalhoana (J.A.Guim.) Wucherpf.	-	END	-
Ophrys kallaikia C.E.Hermos.	-	END	-
Orchis italica Poir.	-	MED	-

Appendix 2. Distribution maps for the 52 species of orchid known to occur in the Principality of Asturias. Maps show all credible records accumulated from the early 1800's to 2024.

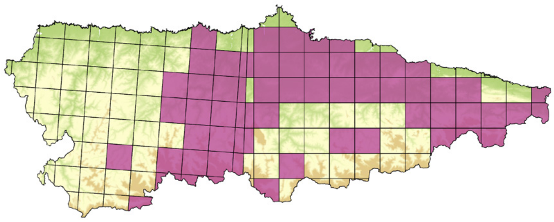
Anacamptis champagneuxii



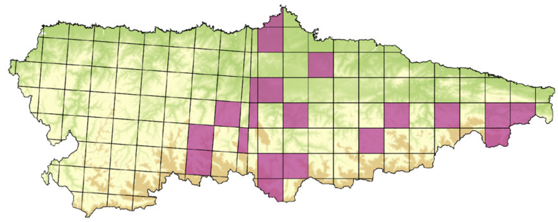
Anacamptis morio



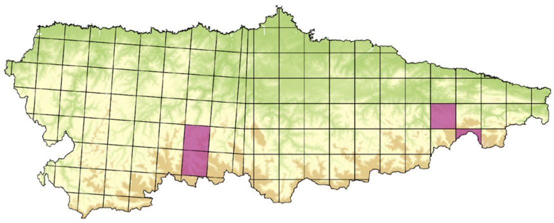
Anacamptis pyramidalis



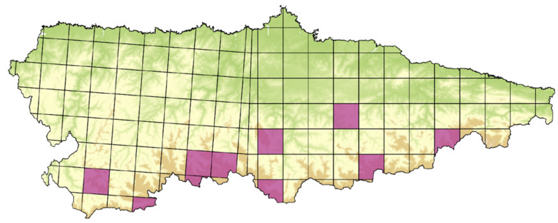
Cephalanthera longifolia



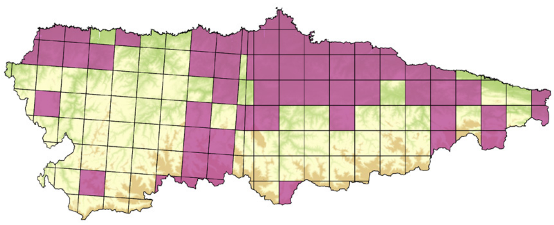
Cephalanthera rubra



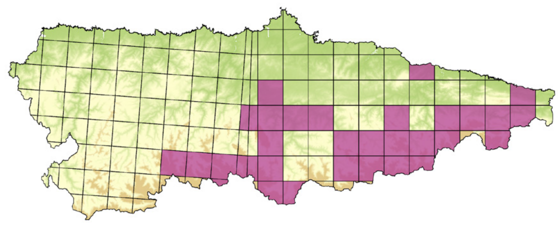
Dactylorhiza cantabrica



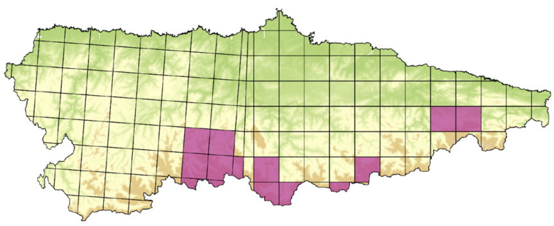
Dactylorhiza elata



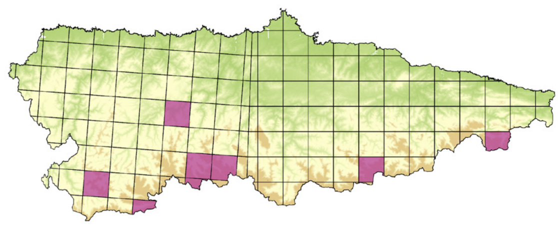
Dactylorhiza fuchsii



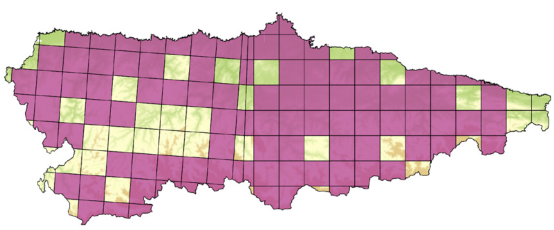
Dactylorhiza incarnata



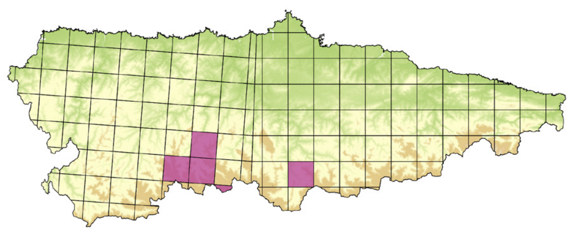
Dactylorhiza insularis



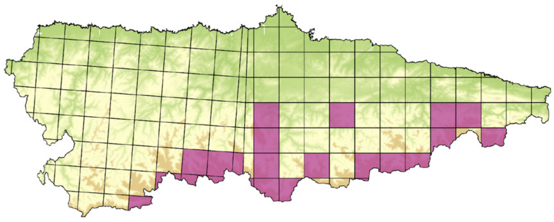
Dactylorhiza maculata



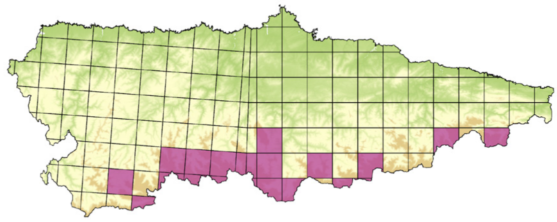
Dactylorhiza romana subsp. *guimaraesii*



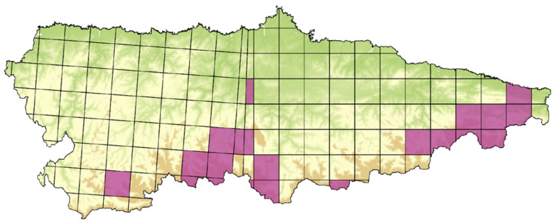
Dactylorhiza sambucina



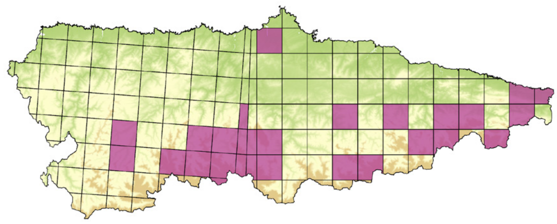
Dactylorhiza viridis



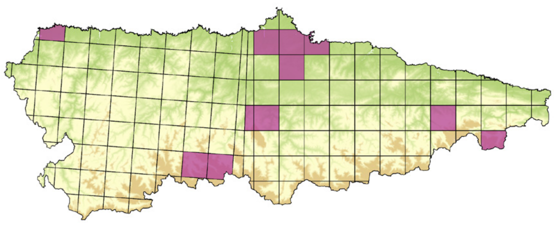
Epipactis atrorubens



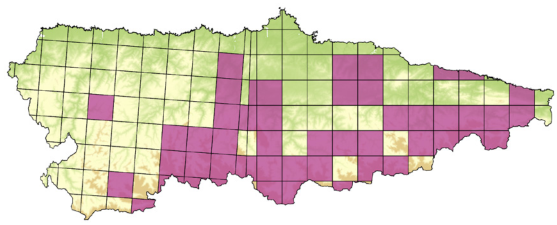
Epipactis helleborine



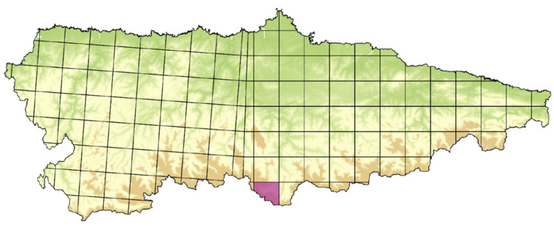
Epipactis palustris



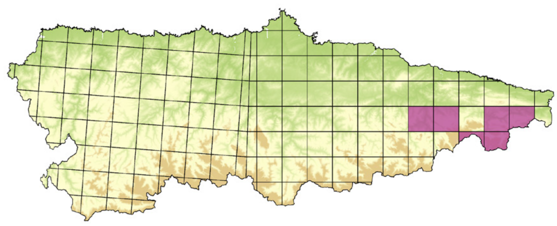
Gymnadenia conopsea



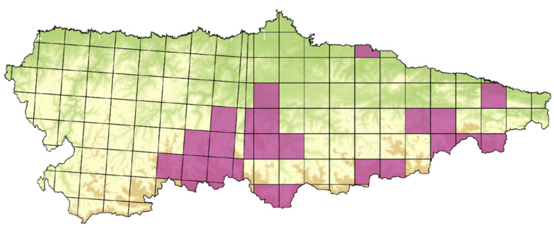
Gymnadenia densiflora



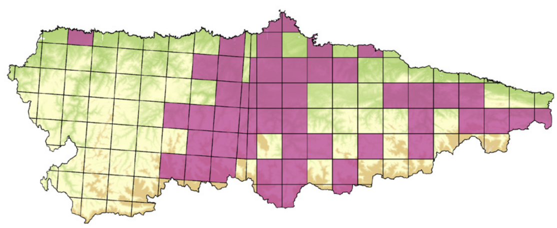
Gymnadenia pyrenaica



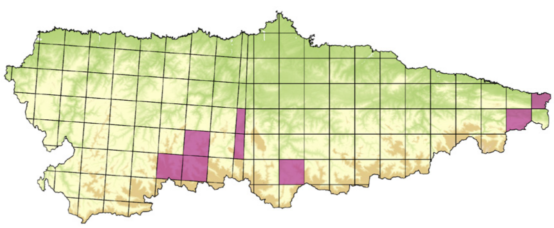
Himantoglossum hircinum



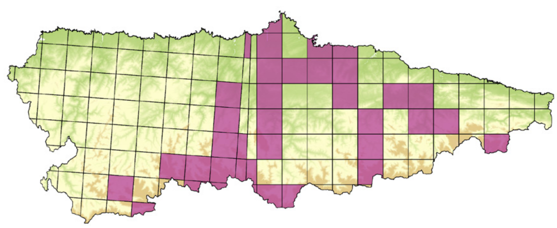
Himantoglossum robertianum



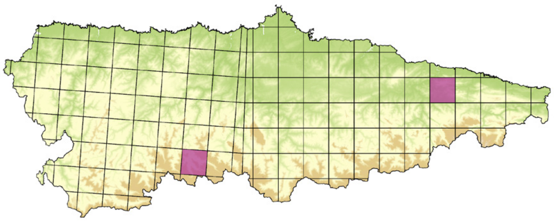
Limodorum abortivum



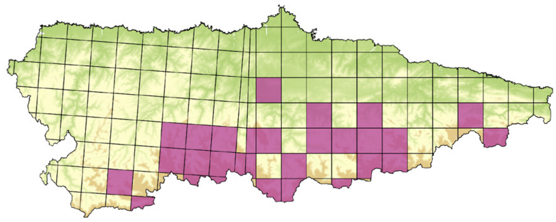
Listera ovata



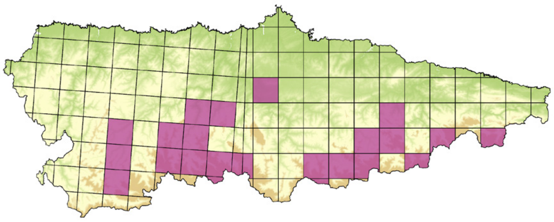
Neotinea maculata



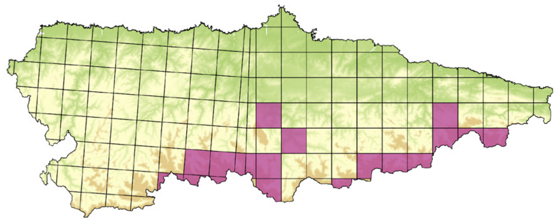
Neotinea ustulata



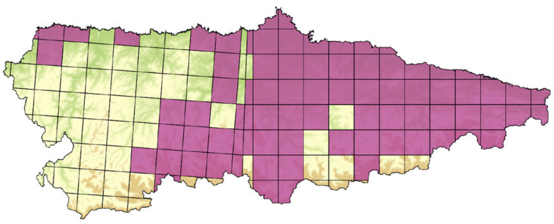
Neottia nidus-avis



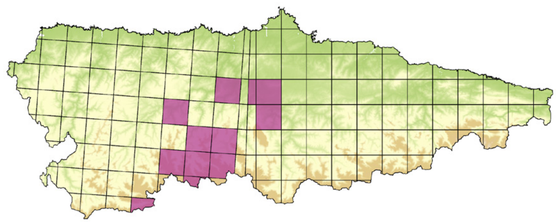
Nigritella gabasiana



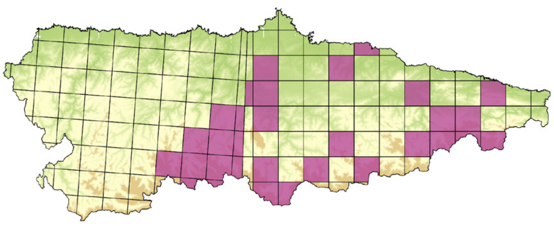
Ophrys apifera



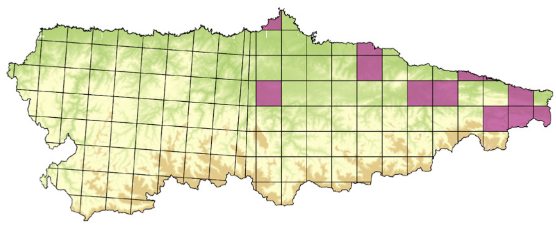
Ophrys incubacea



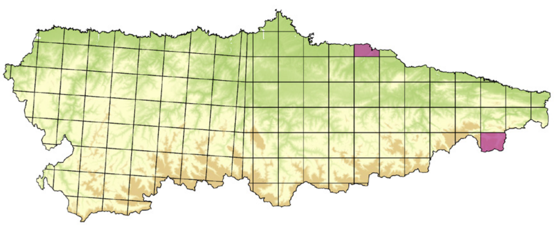
Ophrys insectifera



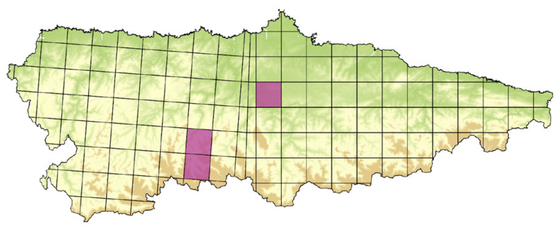
Ophrys lupercalis



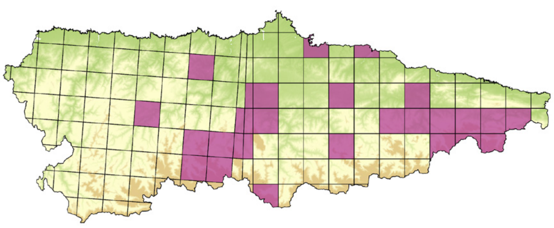
Ophrys lutea



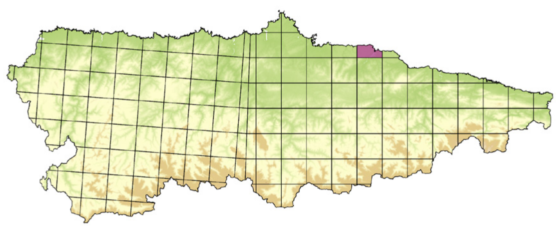
Ophrys passionis



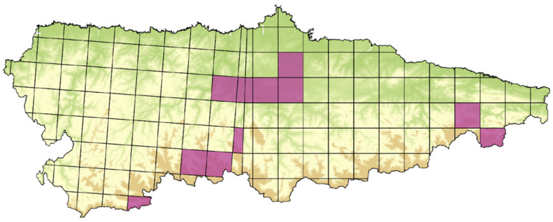
Ophrys scolopax



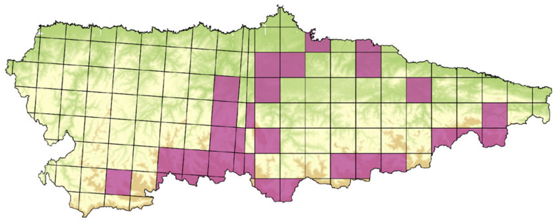
Ophrys speculum



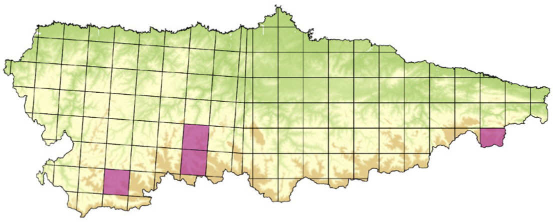
Ophrys sphegodes



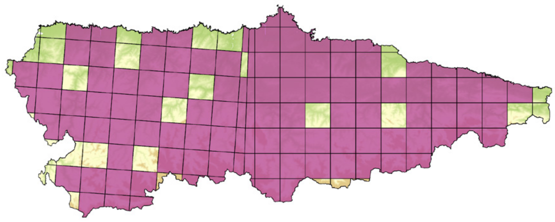
Orchis anthropophora



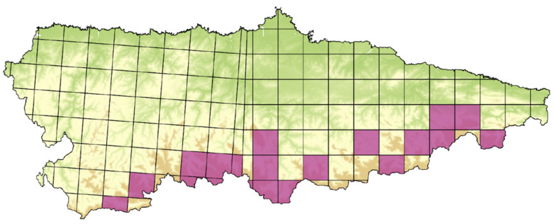
Orchis langei



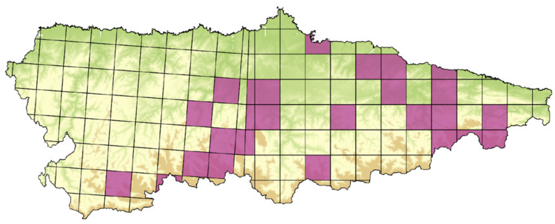
Orchis mascula



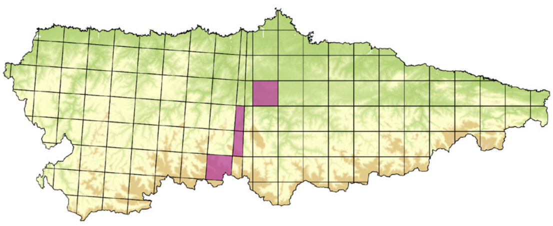
Orchis pallens



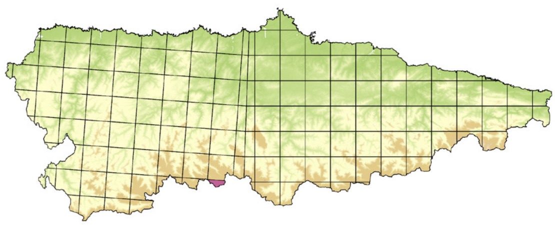
Orchis provincialis



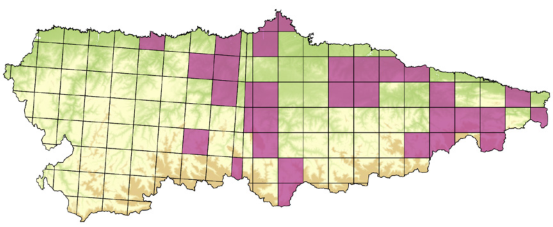
Orchis purpurea



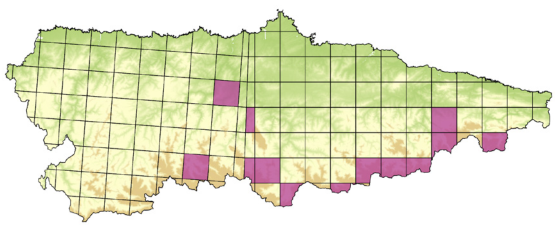
Orchis spitzelii



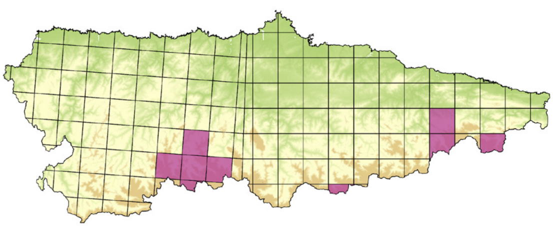
Platanthera bifolia



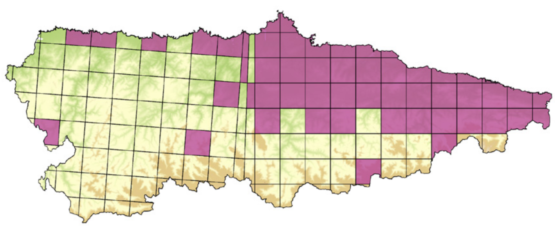
Platanthera chlorantha



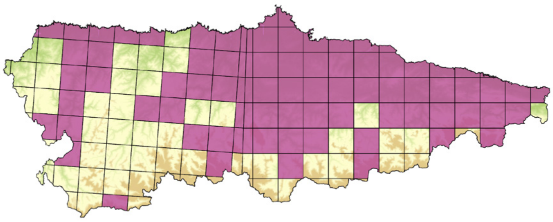
Pseudorchis albida



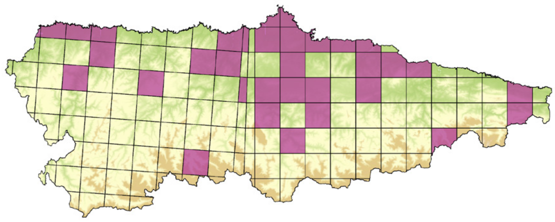
Serapias cordigera



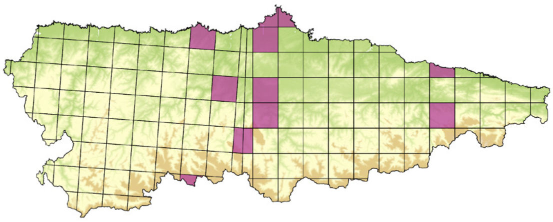
Serapias lingua



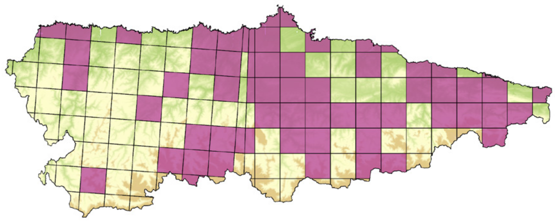
Serapias parviflora



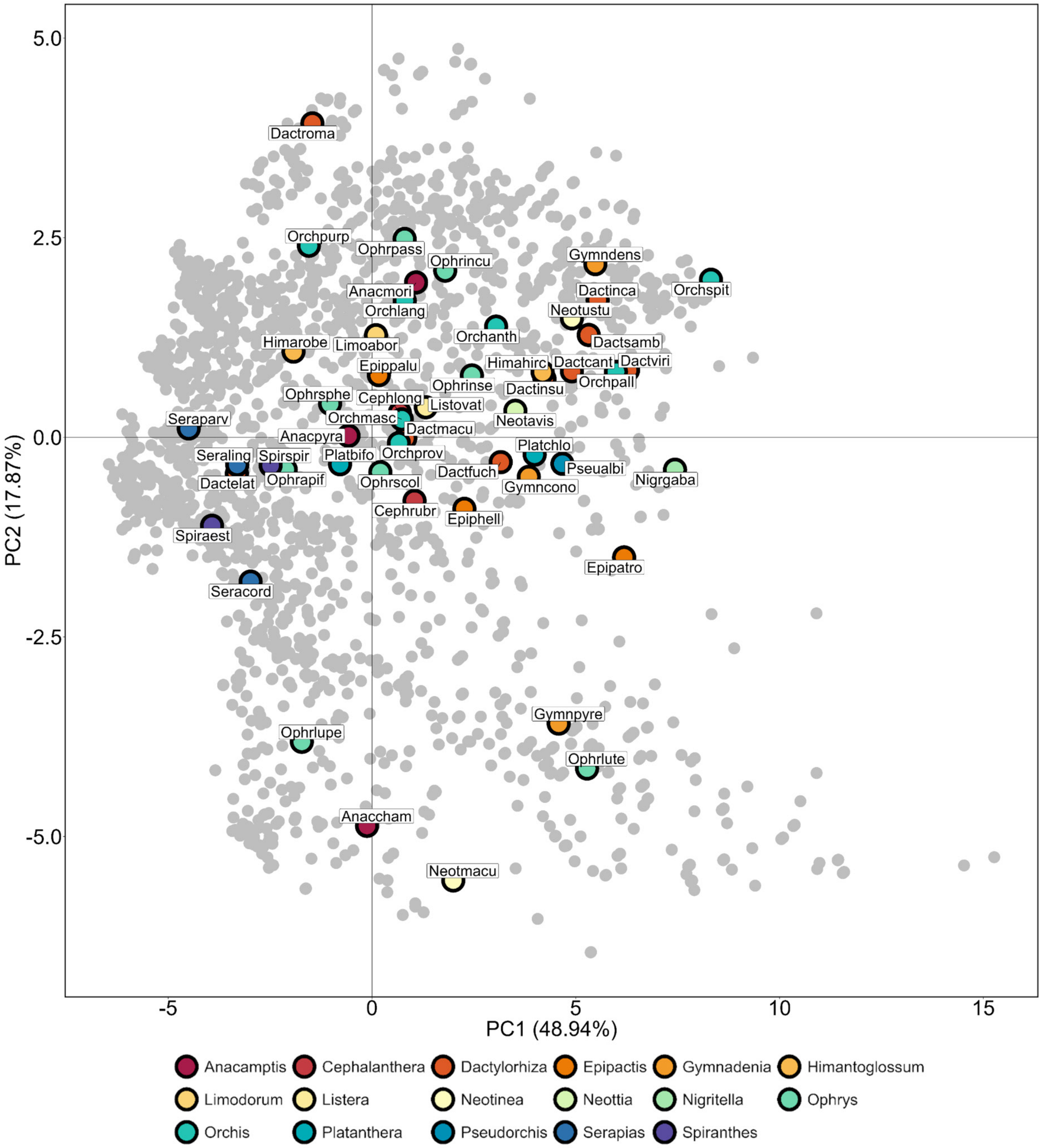
Spiranthes aestivalis



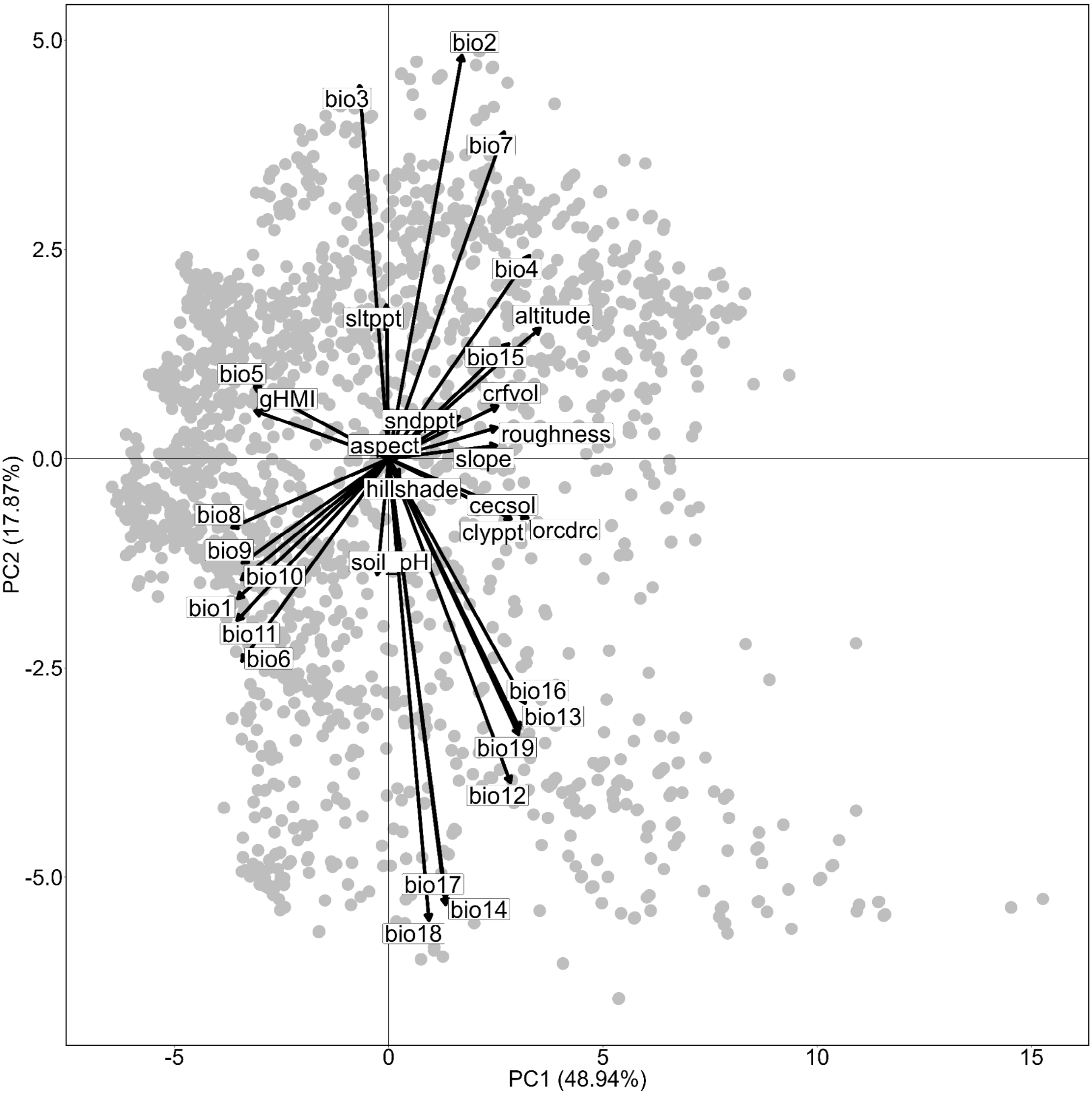
Spiranthes spiralis



Appendix 3A. Principal Component Analysis (PCA) of the orchids present in the Principality of Asturias. Grey dots (●) represent all unique georeferenced records per species and square kilometer, while color dots represent the centroid for each species in the environmental space. Centroids are colored by genus.



Appendix 3B. Principal Component Analysis (PCA) of the orchids present in the Principality of Asturias. Grey dots (●) represent all unique georeferenced records per species and square kilometer, while arrows represent the contribution of each environmental (bioclimatic, edaphic, topographic, anthropogenic) variable to PC1 and PC2.



Appendix 3C. Principal Component Analysis (PCA) of the orchids present in the Principality of Asturias. Relative contribution for each variable to PC1 and PC2. The value of those variables whose contribution is lower than -0.2 or higher than 0.2 are highlighted.

	bio1	bio2	bio3	bio4	bio5	bio6	bio7	bio8
PC1	-0.235	0.114	-0.045	0.219	-0.209	-0.228	0.180	-0.244
PC2	-0.111	0.321	0.297	0.162	0.057	-0.161	0.260	-0.055

	bio9	bio10	bio11	bio12	bio13	bio14	bio15	bio16
PC1	-0.228	-0.229	-0.236	0.189	0.204	0.089	0.187	0.212
PC2	-0.083	-0.096	-0.129	-0.258	-0.215	-0.355	0.091	-0.195

	bio17	bio18	bio19	aspect	hillshade	slope	roughness	altitude
PC1	0.089	0.063	0.202	0.013	0.017	0.168	0.168	0.236
PC2	-0.349	-0.368	-0.220	0.001	-0.013	0.011	0.025	0.104

	Soil pH	cecsol	clyppt	crfvol	orcdrc	sltppt	sndppt	gHMI
PC1	-0.018	0.191	0.191	0.170	0.216	-0.004	0.110	-0.208
PC2	-0.092	-0.048	-0.048	0.042	-0.047	0.123	0.034	0.038

Appendix 4. Whittaker biome diagram. Grey dots (●) represent the environmental space of all Principality of Asturias, while white dots (o) represent the occurrences of orchids within the territory that have been recorded with a spatial accuracy lesser than 1 km.