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MACRO AND MICRO SCALE FACTORS INFLUENCING PRESENCE AND DISTRIBUTION OF FOREST ORCHIDS IN THE FORESTE CASENTINESI, MONTE FALTERONA AND CAMPIGNA NATIONAL PARK

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List of acronyms (a-z)

ABAL	*Abies alba*
AICc	Akaike information criterion correction
AOPNFC	Archive of Orchids of Parco Nazionale Foreste Casentinesi
ASP	Aspect
AUC	Area Under Curve
AUMX	Autotrophic/Mixotrophic species
BIO 1-19	Bioclimate variables
CAM	Camaldoli site
CEDA	*Cephalanthera damasonium*
CELO	*Cephalanthera longifolia*
CEPHA	*Cephalanthera* genus
CERU	*Cephalanthera rubra*
CHP	Cumulative Human Pressure
CMCC-ESM2	Earth System Model of the Euro-Mediterranean Center on Climate Change
CMIP6	Coupled Model Intercomparison Project Phase 6
CMP	Campigna site
CRS	Current Range Size
CV	Coefficient of Variation
CWD	Coarse Woody Debris
D	Diameter
DACTY	*Dactylorhiza* genus
DAMA	*Dactylorhiza maculata* s.l.
DBH	Diameter at Breast Height
ELV	Elevation
EN	Endangered
EPAP	*Epipogium aphyllum*
EPEX	*Epipactis exilis*
EPGR	*Epipactis greuteri*
EPHE	*Epipactis helleborine*
EPIPA	*Epipactis* genus
EPIPO	*Epipogium* genus

EPLE	*Epipactis leptochila*
EPMI	*Epipactis microphylla*
EPPU	*Epipactis purpurata*
EV	Environmental Variable
FASY	*Fagus sylvatica*
FC	Feature Combinations
GCM	Global Climate Model
GHG	Greenhouse gas
GIROS	Gruppo Italiano per la Ricerca sulle Orchidee Spontanee
H	Height
HSM	Habitat Suitability Model
IPCC	Intergovernmental Panel on Climate Change
IR	Index of Regeneration
IUCN	International Union for Conservation of Nature
LC 01-12	Land Cover variables
LC	Least Concern
LQHPT	MaxEnt model feature combinations parameters: L = linear, Q = quadratic, H = hinge, P = product,T = threshold
L, T, K, F, R, N	Ellenberg indicator values: L, Light; T, Temperature; K, Continentality; F, Moisture; R, Soil Reaction; N, Nutrients
MH	Fully Mycoheterotrophic species
MOG	Mature and Old-Growth forests
MTSPS	Maximum Test Sensitivity Plus Specificity
NARROW	Narrow range and rare orchid species
NENA	*Neottia nidus-avis*
NEOTT	*Neottia* genus
NP	National Park
NT	Near Threatened
OC	Orchid Community
OR	Omission Rate
OTBR	Other broadleaves
PA	Protected Area
PCA	Principal Component Analysis
PNFC	Parco Nazionale delle Foreste Casentinesi, Monte Falterona e Campigna

RM	Regularization Multipliers
ROC	Receiver Operating Characteristic
SDM	Species Distribution Model
SDT	Stand Dead Tree
SI	Structural Indicators
SLP	Slope
SOIL 1-11	Soil variables
SRC	Species Range Change
SSP	Shared Socioeconomic Pathway
VER	La Verna site
VIF	Variance Inflation Factor
WIDE	Widespread orchid species

List of *Orchidaceae* taxa (genera, species, and subspecies)

Anacamptis Rich. 1817	
Anacamptis berica Doro 2020	
Anacamptis coriophora (L.) R. M. Bateman, Pridgeon & M. W. Chase 1997 subsp. *fragrans* (Pollini) R.M. Bateman, Pridgeon & M.W. Chase 1997	
Anacamptis laxiflora (Lam.) R.M. Bateman, Pridgeon & M.W. Chase 1997	
Anacamptis morio (L.) R. M. Bateman, Pridgeon & M. W. Chase 1997 subsp. *morio*	
Anacamptis pyramidalis (L.) Rich. 1817	
Cephalanthera Rich. 1818	
Cephalanthera damasonium (Mill.) Druce 1906	
Cephalanthera longifolia (L.) Fritsch 1888	Syn. *Cephalanthera ensifolia* (Ehrh.) Rich. 1817
Cephalanthera rubra (L.) Rich. 1817	
Corallorhiza Gagnebin 1775	
Corallorhiza trifida Châtel. 1760	
Cypripedium L. 1753	
Cypripedium calceolus L. 1753	
Dactylorhiza Neck. ex Nevski 1935	
Dactylorhiza maculata (L.) Soó 1962	
Dactylorhiza maculata (L.) Soó subsp. *fuchsii* (Druce) Hyl. 1966	
Dactylorhiza maculata (L.) Soó subsp. *saccifera* (Brongn.) Diklić 1976	
Dactylorhiza sambucina (L.) Soó 1962	Syn. *Orchis sambucina* L. 1755
Dactylorhiza viridis (L.) R. M. Bateman, Pridgeon & M. W. Chase 1997	Syn. *Coeloglossum viride* (L.) Hartm. 1820
Epipactis Zinn 1757	
Epipactis exilis P.Delforge 2004	Syn. *Epipactis gracilis* B.Baumann & H.Baumann 1988
Epipactis greuteri H. Baumann & Künkele 1981	Syn. *Epipactis flaminia* P.R.

	Savelli & Aless. 1994
Epipactis helleborine (L.) Crantz 1769	
Epipactis leptochila (Godfery) Godfery 1921	
Epipactis microphylla (Ehrh.) Sw. 1800 subsp. *microphylla*	
Epipactis muelleri Godfery 1921	
Epipactis palustris (L.) Crantz 1769	
Epipactis placentina Bongiorni et Grünanger 1993	
Epipactis purpurata Sm. 1828	
Epipogium Borkh. 1792	
Epipogium aphyllum Sw. 1814	
Goodyera R.Br. 1813	
Goodyera repens (L.) R.Br. 1813	
Gymnadenia R.Br. 1813	
Gymnadenia conopsea (L.) R.Br. 1813	
Gymnadenia densiflora (Wahlenb.) A.Dietr. 1839	
Habenaria repens Nutt. 1818	
Himantoglossum Spreng. 1826	
Himantoglossum adriaticum H. Baumann 1978	
Himantoglossum comperianum (Steven) P.Delforge 1999	
Himantoglossum robertianum (Loisel.) P.Delforge 1999	
Limodorum Boehm. 1760	
Limodorum abortivum (L.) Sw. 1799	
Mexipedium V.A.Albert & M.W.Chase 1992	
Neotinea maculata (Desf.) Stearn 1975	
Neotinea tridentata (Scop.) R.M.Bateman, Pridgeon & M.W.Chase 1997	
Neotinea ustulata (L.) R.M.Bateman, Pridgeon & M.W.Chase 1997	
Neottia Guett. 1754	
Neottia cordata (L.) Rich. 1817	
Neottia nidus-avis (L.) Rich. 1817	
Neottia ovata (L.) Bluff & Fingerh. 1838	
Ophrys L. 1753	

Ophrys apifera Huds. 1762	
Ophrys appennina Romolini & Soca 2011	
Ophrys bertolonii Moretti 1823 subsp. *bertolonii*	
Ophrys classica Devillers-Tersch. & Devillers 2000	
Ophrys funereal Viv. 1824	
Ophrys insectifera L. 1753	
Ophrys minipassionis Romolini & Soca 2011	
Orchis Tourn. ex L. 1753	
Orchis anthropophora (L.) All. 1785	
Orchis mascula (L.) L. 1755	
Orchis mascula (L.) L. 1755 subsp. *mascula*	
Orchis mascula (L.) L. subsp. *speciosa* (Mutel) Hegi 1909	
Orchis militaris L. 1753	
Orchis pallens L. 1771	
Orchis provincialis Balb. ex Lam. & DC. 1806	
Orchis purpurea Huds. 1762	
Orchis simia Lam. 1779	
Paphiopedilum Pfitzer 1886	
Phragmipedium Rolfe 1896	
Platanthera Rich. 1817	
Platanthera bifolia (L.) Rich. 1817	
Platanthera chlorantha (Custer) Rchb. 1829	
Selenipedium Rchb.f. 1854	
Serapias L. 1753	
Serapias vomeracea (Burm.f.) Briq. 1910	
Spiranthes Rich. 1817	
Spiranthes cernua (L.) Rich. 1817	
Spiranthes lucida (H.H.Eaton) Ames 1908	
Spiranthes odorata (Nutt.) Lindl. 1840	
Spiranthes sinensis (Pers.) Ames 1908	
Spiranthes spiralis (L.) Chevall. 1827	

List of other taxa (genera, species, and subspecies)

Vascular plants
Abies alba Mill.
Acer campestre L.
Acer opalus Mill.
Acer platanoides L.
Acer pseudoplatanus L.
Alnus cordata (Loisel.) Duby
Alnus glutinosa (L.) Gaertn.
Alnus incana (L.) Moench
Anemonastrum narcissiflorum (L.) Holub subsp. *narcissiflorum*
Arenaria serpyllifolia L. subsp. *serpyllifolia*
Astragalus monspessulanus L.
Avenella flexuosa (L.) Drejer subsp. *flexuosa*
Bombycilaena erecta (L.) Smoljan.
Brachypodium rupestre (Host) Roem. & Schult.
Bromopsis erecta (Huds.) Fourr.
Bromus hordeaceus L.
Calluna vulgaris (L.) Hull
Cardamine bulbifera (L.) Crantz
Cardamine chelidonia L.
Carex L.
Carex pendula Huds.
Carex sylvatica Huds.
Carpinus betulus L.
Castanea sativa Mill.
Centaurea jacea L. subsp. *gaudinii* (Boiss. & Reut.) Gremli
Cichorium intybus L.
Clinopodium vulgare L.
Convolvulus arvensis L.
Coronilla minima L.
Coronilla scorpioides (L.) W.D.J.Koch
Cytisophyllum sessilifolium (L.) O.Lang
Cytisus scoparius (L.) Link subsp. *scoparius*

Digitalis micrantha Roth ex Schweigg.
Doronicum columnae Ten.
Eupatorium cannabinum L.
Euphorbia cyparissias L.
Festuca Tourn. ex L.
Fraxinus excelsior L.
Fraxinus ornus L. subsp. *ornus*
Galium lucidum All.
Galium odoratum (L.) Scop.
Gentiana verna L.
Gentianella campestris (L.) Börner subsp. *campestris*
Geranium nodosum L.
Geranium robertianum L.
Helleborus viridis L. subsp. *bocconei* (Ten.) Peruzzi
Hepatica nobilis Schreb.
Heracleum sphondylium L.
Hypericum montanum L.
Hypericum richeri Vill. subsp. *richeri*
Juncus L.
Juniperus communis L.
Larix decidua Mill.
Lolium arundinaceum (Schreb.) Darbysh.
Lotus corniculatus L.
Lotus dorycnium L.
Matteuccia struthiopteris (L.) Tod.
Melica uniflora Retz.
Murbeckiella zanonii (Ball) Rothm.
Mycelis muralis (L.) Dumort. subsp. *muralis*
Nardus stricta L.
Onobrychis viciifolia Scop.
Ononis spinosa L.
Ostrya carpinifolia Scop.
Petasites albus (L.) Gaertn.
Petasites hybridus (L.) G.Gaertn., B.Mey. & Scherb. subsp. *hybridus*

Phegopteris connectilis (Michx.) Watt
Picea abies (L.) H.Karst.
Pinus nigra J.F.Arnold
Pinus strobus L.
Pinus sylvestris L.
Polygonatum verticillatum (L.) All.
Populus canescens (Aiton) Sm.
Populus nigra L.
Poterium sanguisorba L.
Prunus spinosa L. subsp. *spinosa*
Pseudotsuga menziesii (Mirb.) Franco
Quercus cerris L.
Quercus pubescens Willd. subsp. *pubescens*
Ribes multiflorum Kit. ex Roem. & Schult. subsp. *multiflorum*
Rubus canescens DC.
Rubus idaeus L. subsp. *idaeus*
Rubus ulmifolius Schott
Salix alba L.
Sanicula europaea L.
Saxifraga oppositifolia L. subsp. *oppositifolia*
Saxifraga paniculata Mill.
Senecio doronicum (L.) L.
Sesleria italica (Pamp.) Ujhelyi
Solanum dulcamara L.
Sorbus aucuparia L.
Spartium junceum L.
Stellaria graminea L.
Teucrium chamaedrys L.
Thliphthisa purpurea (L.) P.Caputo & Del Guacchio subsp. *purpurea*
Tilia platyphyllos Scop.
Ulmus glabra Huds.
Vaccinium myrtillus L.
Viola eugeniae Parl.

Moss
Sphagnum L.
Insects
Andrena nigroaenea (Kirby, 1802)

Abstract

Terrestrial forest *Orchidaceae* in temperate ecosystems, particularly in Italy, remain critically underexplored. This study examines the environmental factors shaping the distribution and abundance of forest orchids within the "Parco Nazionale delle Foreste Casentinesi, Monte Falterona e Campigna" (PNFC), a protected area in the Northern Apennines (Central Italy). Detailed studies were conducted on the distribution of individual *Orchidaceae* species, delineating their current occurrence and identifying areas of significant floristic interest. The analysis of key environmental drivers at a macro scale was performed using Habitat Suitability Models (HSMs). These models predicted habitat suitability for *Cephalanthera rubra*, *Epipactis microphylla*, and *Limodorum abortivum* under current and future climate scenarios (2030 and 2050). Precipitation, temperature seasonality, and soil characteristics emerged as critical factors influencing distribution. Low precipitation values during the driest and warmest months could limit orchid occurrence in the Park under climate future conditions. The generated maps could guide conservation efforts by highlighting areas of habitat loss or gain and informing priority actions. Field studies in three high-value forest sites — Campigna, Camaldoli, and La Verna — analysed structural forest variables, including deadwood, regeneration, and old-growth features. At the micro scale, factors such as the presence of large trees, coarse woody debris volume, and structural complexity positively influenced the abundance of mycoheterotrophic orchid species (*Neottia nidus-avis* and *Epipogium aphyllum*) within the orchid community. In contrast, the abundance of *Cephalanthera* and *Epipactis* appeared influenced by forest composition and regeneration rates. Rare and threatened species benefited from overall deadwood density. The results underscore the importance of targeted forest management strategies to preserve orchid diversity, naturalness, and habitat quality.

1. Introduction

1.1. Aim of the PhD Project

The role of terrestrial forest *Orchidaceae* species in temperate ecosystems is quite underexplored, particularly in Italy. The Apennine range harbors a remarkable floristic and vegetational heritage, with unique biocenoses often protected within the network of natural reserves spanning the peninsula. The northern portion, the "Appennino Tosco Romagnolo" mountains, acts as a transitional zone between the Alpine range and the southern Apennines, which stretch over 1200 km. Furthermore, the phytogeographical importance of this area is heightened by its function as a watershed, dividing the Tyrrhenian slopes to the west and the Adriatic slopes to the east. Over millennia, these regions have become a crossroads for species, many of which find their southern or northern distributional limits — both Italian and European — within this area (e.g. *Matteuccia struthiopteris*, *Phegopteris connectilis*, *Ribes multiflorum* subsp. *multiflorum*, etc.)[1].

The primary aim of this project is to investigate, first broadly and then more specifically, the environmental drivers that influence the presence and distribution of wild orchids within a highly significant phytogeographical region of the Northern Apennines (Central Italy): the "Parco Nazionale delle Foreste Casentinesi, Monte Falterona and Campigna" National Park (hereinafter referred as PNFC or the Park). The structure of the project follows a progression from a general overview of the topic to increasingly detailed analyses of ecological and management-related themes.

The initial phase involved a comprehensive bibliographic review of the state of orchidological research within the protected area, consulting floristic and vegetational checklists dating back to 1860. This was followed by the development of a floristic database containing records of wild orchids, termed the AOPNFC (Archive of Orchids of Parco Nazionale Foreste Casentinesi). This archive, comprising over 5600 records as of the 2024 year, formed the basis for the creation of the *Atlas of Orchids of the Park*, a monograph detailing the biology and ecology of the species within the protected area (PA), highlighting their occurrences in the Park and their distributions (Pica & Laghi [2], Chapter 2). Through this effort, orchids within the PA were classified based on their rarity, and distribution maps were provided to the Park's managing authority. Areas prioritized for conservation were identified based on species richness and the rarity of the reported species.

This approach clarified the composition of the orchid community within the PA and highlighted the vulnerabilities of certain species groups in relation to the habitats they depend on. Among these, forest orchid species that are specialised in forest environments require significant attention due to

the Park's predominantly forested nature. Moreover, the more specialized they are in the forest, the more dependent they are on the characteristics of the forest (i.e.: natural level, soil, vegetation, and related structure quality). This foundational work supports subsequent analyses of the ecology of forest orchids.

Forest *Orchidaceae*, especially terrestrial species in temperate climates, have historically garnered limited research interest compared to other orchid groups, such as those in open habitats (e.g., grasslands, pastures) or highly threatened genera and species within the same climatic zone. Understanding their responses to climate change, as well as the roles of soil and topographic factors, the natural progression of forest habitats toward mature successional stages, and the impacts of human activity, represents a cornerstone challenge in biodiversity conservation. Orchids are considered indicators of habitat quality, as they can provide valuable insights into environmental conditions [3,4].

In a world facing rapid social and environmental change, global protected areas should play a crucial role in preserving biomass. Orchids are recognized globally as important umbrella and flagship species within ecosystems [5]. Analyzing macro-environmental factors influencing their presence and distribution under current and future conditions provides a framework for more efficient allocation of conservation resources.

To address these challenges, the project applied distribution modeling (Habitat Suitability Models, HSMs, or Species Distribution Models, SDMs) to predict habitat suitability for certain forest orchids within the PNFC. Using occurrence data for three forest species (*Cephalanthera rubra*, *Epipactis microphylla*, and *Limodorum abortivum*) and a dataset of selected environmental variables (EVs), habitat suitability was predicted under current and future climate conditions using MaxEnt-based HSMs. The results were published in a research paper (Pica et al. [6], Chapter 3).

The study revealed the sensitivity of these species to macro-environmental factors such as soil characteristics and projected precipitation regimes for two future scenarios (2030 and 2050) based on Shared Socioeconomic Pathways (SSPs). The most advantageous application of this research for management involves generating current and future distribution maps that identify individual cells of habitat loss or gain. These maps serve as valuable tools for the Park authority, enabling prioritization of orchids and habitat conservation within the protected area.

In any protected area, even those with limited forest cover, forest management is a cornerstone of effective stewardship. The intensity of forest management — or lack thereof — can significantly influence understory vegetation. Understanding the role of structural components of live and dead

forest biomass in supporting forest orchids is fundamental to their conservation and the associated habitats.

Key structural variables such as density, volume, species composition, regeneration, and deadwood could determine the presence or absence of certain orchid species or groups. To investigate these effects, a study was conducted within three high-value forest areas of the PNFC: Campigna, Camaldoli, and La Verna. These sites, which include biogenetic reserves and sacred forest complexes historically preserved by monastic orders, were the focus of detailed field surveys involving nine plots (three for each site).

Field measurements included canopy diameters and heights, the presence and dimensions of deadwood, and the extent of forest regeneration. For each plot, total basal area, volume, and regeneration density values were calculated, as were species-specific values. Plots were also classified by old-growth indicators, including large tree volume and total deadwood volume. Structural indicators were screened and correlated with the orchid community data.

Preliminary published results (Pica et al. [7], Chapter 4), indicate differential responses among genera (e.g., *Epipactis* and *Cephalanthera*) with similar trophic regimes (autotrophic/mixotrophic) to variations in species composition (dominance of *Abies alba* or *Fagus sylvatica*) and established regeneration. Mycoheterotrophic species responded positively to old-growth indicators such as large tree volume, plot heterogeneity, and lying deadwood volume. Narrow-distribution species showed correlations with total deadwood, both standing and lying.

This research quantified the influence of structural forest variables on orchid communities, offering practical management guidelines for the Park authority. Depending on the targeted orchid group, different interventions — ranging from non-intervention to altering forest density and volume or managing regeneration and deadwood — could be applied. Such studies bridge the gap between orchidological research and the implementation of forest management protocols that account for ecological relationships among functional species groups.

1.2. The *Orchidaceae* family

The *Orchidaceae* family is among the largest plant families worldwide, surpassed in species diversity only by the *Asteraceae* [8,9]. This family accounts for approximately one-tenth of all living Angiosperm species and is represented in all areas of the globe. Orchids thrive in a wide variety of habitats worldwide [10-12]. The only exceptions are permafrost regions, sandy deserts, and submerged aquatic habitats, although a few species, such as *Habenaria repens*, exhibit anatomical adaptations for a semi-aquatic and floating lifestyle [13-16].

Since only a few genera have been extensively studied, it is not possible to know the exact size of this family, and estimates of species numbers vary. Estimates suggest the total number of orchid species falls between 25,000 and 33,000 [17-21], grouped into 704 to 850 genera based on various sources [17,20,21]. Most species are distributed in the tropical and subtropical regions of Asia, the Americas, Australia, and Africa, with Antarctica being the only exception [22,23]. In Europe (including the Proche Orient, the Mediterranean region of North Africa, the Canary Islands, Madeira, and the Azores), the number of species varies depending on the sources: 115 [24], 645 [25], and 163 [10]. These numbers continue to grow due to the ongoing discovery of new species worldwide [26-29].

At the systematic level, European and Italian orchids belong to three subfamilies: *Cypripedioideae*, *Epidendroideae*, and *Orchidoideae*.

- *Cypripedioideae*: distributed mainly in temperate and tropical regions, *Cypripedioideae* are among the most basal subfamilies of orchids, often recognized for their distinctive slipper-shaped labellum, which acts as a trap for pollinators. This subfamily includes five genera (*Cypripedium, Mexipedium, Paphiopedilum, Phragmipedium*, and *Selenipedium*) with approximately 170 species [30,23]. Members of this group are primarily terrestrial or lithophytic, with some epiphytic representatives, and are often found in shaded habitats with moist, humus-rich soils. The genus *Cypripedium*, widely distributed across the Northern Hemisphere, includes species like *Cypripedium calceolus*, which is considered a flagship species for conservation due to its sensitivity to habitat disturbance [31].
- *Orchidoideae*: distributed worldwide, are divided into 7 tribes with about 3,630 species grouped into 215 genera. The tribes present include *Orchideae* (subtribe *Orchidinae*: genera *Anacamptis*, *Dactylorhiza*, *Gymnadenia*, *Himantoglossum*, *Neotinea*, *Ophrys*, *Orchis*, *Platanthera*, *Serapias*) and *Cranichideae* (subtribes *Goodyerinae*: genus *Goodyera*, and *Spiranthinae*: genus *Spiranthes*) [32,33].

- *Epidendroideae*, practically distributed worldwide, are divided into 16 tribes comprising about 18,000 species grouped into 650 genera. The tribes present include *Nervilieae* (subtribe *Epipogiinae*: genus *Epipogium*), *Epidendreae* (subtribe *Calypsoinae*: genus *Corallorhiza*), and *Neottieae* (genera *Cephalanthera*, *Epipactis*, *Limodorum*, *Neottia*) [34].

Italy has historically ranked among the European countries with the richest orchid flora. The "Gruppo Italiano per la Ricerca sulle Orchidee Spontanee - GIROS" Association [35] listed 230 species and subspecies in 30 genera, while the Portal to the Flora of Italy [36-46] recorded 217 species and subspecies in 29 genera. Pignatti et al. [47] listed 141 species and subspecies in 30 genera. The year 2024 marks the publication in Italy of two systematic works addressing *Orchidaceae*. The first is the monograph "Orchidee d'Italia" in the updated edition of GIROS [48], while the second is the updated checklist of the native flora of Italy by Bartolucci et al. [49,50]. The former considered 267 taxa, while the latter recorded 237 taxa. However, significant nomenclatural disparities exist between the two. In the former, some genera (e.g., *Ophrys*) are treated at the species level, whereas in the latter, many are reduced to the subspecies level.

In recent years, the systematics of the family, initially based exclusively on macromorphology, has been revolutionized by the application of more recent investigation techniques, including karyomorphology, molecular analysis (DNA, isoenzymes, etc.), and studies of plant-pollinator interactions [51-57].

1.3. Threats and Conservation

The *Orchidaceae* family is recognized for hosting a significant number of endangered species, especially within terrestrial orchids [58-60]. Human activities, through habitat alteration or direct harm to populations, pose a major threat to these species [61-63]. Additionally, climate change is known to significantly influence the distribution and presence of certain species within specific regions [64-66]. Consequently, the conservation of these species and their habitats has become a global imperative to prevent their continued decline [67,68]. Orchids are often regarded as umbrella and flagship species that not only protect themselves but also benefit other species within their ecosystems by guiding conservation efforts [5,69-73]. Their appeal helps attract public attention to other, often overlooked, organisms, encouraging the adoption of land management policies more mindful of environmental concerns. Orchids, with their particular allure, help people connect with the plant world and the intricate processes that regulate nature, promoting the conservation of the habitats they occupy.

Despite their evolutionary success and cosmopolitan distribution, the *Orchidaceae* are not exempt from conservation challenges. In fact, their close, one-sided dependencies on other organisms—such as mycorrhizal fungi and pollinating insects — along with the strategies they employ to attract these pollinators, make them particularly vulnerable to environmental changes compared to many other plants. These reasons support the use of orchids as indicators of habitat quality [3,4].

The decline of terrestrial orchids in temperate regions is primarily attributed to the loss and degradation of their natural habitats [74,75]. However, human efforts can play a significant role in preserving these environments and ensuring the continued presence of these species [11,76-78]. Additionally, climate change may have varying effects on temperate terrestrial orchids. Depending on the species and geographical location, these plants may respond differently to changes in climate conditions, either benefiting or suffering from alterations in temperature and precipitation [79-82]. Therefore, more research is needed to understand the full impact of these factors on orchid populations.

The potential increase in herbivorous mammal populations, such as wild boars and hedgehogs, can disrupt and directly destroy entire orchid populations, as their underground structures may serve as a food source for these animals. In some areas, particularly for rare and sensitive species, effective wildlife management strategies should be implemented to control the numbers of these and other herbivores that feed on orchids, such as hares, rabbits, roe deer, red deer, and fallow deer. These animals often damage the flower spikes, thereby preventing or limiting reproduction. In the United States, it was observed that overgrazing by white-tailed deer, even for a short period, had significant negative effects on several orchid species that were grazed. Once the issue was addressed, it took between 3 and 10 years for the plants to return to their pre-grazing flowering conditions [83]. In another long-term study on the same deer species, a slow but significant decline, or near-total disappearance, of 90% of the recorded orchid species was observed when ungulates were present in large numbers, compared to when they were scarce [84].

Due to systematic land drainage and water regulation projects, orchids that are closely linked to wetland habitats are experiencing drastic reductions or even global extinctions. For example, *Epipactis palustris* is threatened by river regulation works, while the survival of *Anacamptis laxiflora* could be supported by maintaining even small wetland areas and preventing the continuous extraction of spring water, or conversely, the abandonment of springs used for watering, or the rapid downstream flow of water.

Climate change can affect the pollination rates of orchids. In the United Kingdom, male *Andrena nigroaenea* bees are emerging earlier than in the past, when orchids are still in bud, and subsequently focus primarily on mating with females [86]. Similar shifts in timing could have serious negative consequences for the entire *Ophrys* genus, which already experiences low pollination rates, or potentially for other genera as well. Recent studies in the Alpine mountains showed a general increase in the altitudinal range of various orchids [82]. This trend is further evidenced by the discovery of *Dactylorhiza viridis* (= *Coeloglossum viride*) at much higher elevations than historically recorded in Europe [87].

The harvesting of orchids poses a significant threat to their survival. In Turkey, rhizotubers from various genera such as *Anacamptis*, *Himantoglossum*, *Ophrys*, *Orchis*, *Serapias*, and *Spiranthes* are collected, dried, and ground into a starchy flour known as *salep*, which is used not only in medicinal preparations but also in culinary dishes, including soups, beverages, and desserts like ice cream and sweets. One of the species commonly used for *salep* production is *Anacamptis morio* s.l. [56,87]. In the past, Turkey produced up to 45 tons of *salep* in favorable years, with 1,000 to 4,000 rhizotubers needed to produce just one kilogram of flour. This level of harvest pressure has had devastating effects on wild orchid populations, including the near extinction of *Himantoglossum comperianum* in Turkey [88]. In contrast, orchid collection for culinary purposes is not common in other regions. The practice of collecting entire plants for research is now rare, and although the ornamental collection was highly damaging in the past and continues to be discouraged, it is now minimal [89,90].

Some orchid species, when accidentally or intentionally introduced to new areas, particularly tropical environments, may naturalize. While rarely invasive, species such as *Epipactis helleborine*, first recorded in New York State in 1879, are now widespread across much of the eastern United States and Canada [91-94]. In Europe, four species of *Spiranthes* (*Spiranthes cernua*, *S. lucida*, *S. odorata*, and *S. sinensis*) have been recorded as casual aliens, likely escaped from cultivation [10].

When it comes to the conservation of orchids, the most effective strategy is undoubtedly in situ conservation. This approach focuses on safeguarding orchids in their natural environments or supporting their survival through targeted management plans, such as habitat restoration, maintenance, pollination assistance, and reintroduction programs. For species that are listed as vulnerable (VU), endangered (EN), critically endangered (CR), or extinct in the wild (EW) on the IUCN Red List, ex situ conservation methods become essential. These techniques include the use of seed banks, orchid cultivation, and the cultivation of their mycorrhizal partners [95], whether through in vitro methods or in specialized facilities like botanical gardens and arboreta [90,96].

1.4. Temperate forest *Orchidaceae*: an overview

The remarkable diversity of the *Orchidaceae* family includes taxa with similar ecological adaptations to specific environmental conditions. Among these are orchids that inhabit forested areas. A significant proportion of forest *Orchidaceae* are tropical epiphytes, which grow attached to the stems and branches of trees used solely as structural support, with the aid of their aerial roots [97]. These species have been extensively studied by the scientific community due to their wide distribution, ecological complexity, and potential applications, including ornamental, therapeutic, and nutritional uses [98,99]. Epiphytic orchids have been examined not only in relation to macro-environmental factors such as climate, soil, geography, and topography but also in connection to more localized factors. These include host characteristics like bark pH, bark roughness, stem diameter, deciduous or evergreen nature, growth habit (shrub/tree), host age and height, canopy cover, and bark water-holding capacity [100-102].

The focus of this research is to deepen the understanding of temperate terrestrial forest orchids, particularly European species, with regard to their ecology and responses to various environmental factors. Unlike tropical orchids, European orchids are predominantly terrestrial, although certain Italian and European genera that grow exclusively on *Sphagnum* moss carpets are sometimes considered epiphytic. The absence of epiphytic orchids in temperate biomes is primarily due to the combination of low winter temperatures and extreme dry summer air conditions, both of which are unfavorable for their survival. Most European orchids have underground storage organs called rhizotubers, which serve functions of nutrient storage and vegetative propagation. These rhizotubers renew with each growing season and their shape and size vary across genera, particularly in forest-adapted taxa like *Cephalanthera*, *Epipactis*, and *Neottia*, where underground structures consist of a rhizome with numerous thread-like roots.

The interconnections between forests and orchids have increasingly drawn the attention of researchers, who have explored the ecological dimensions of these interactions [103-107]. Temperate European orchids have been studied concerning biotic and abiotic factors influencing their presence, abundance, and distribution [11,76,108-110], including species typically found in forest habitats [111-113]. The growth of temperate terrestrial forest orchids is influenced not only by climatic and soil factors but also by biotic interactions [111,114,115]. These orchids depend on forest ecosystems for survival, utilizing carbon derived from surrounding trees through mutualistic mycorrhizal associations between higher plants and fungi [116]. These relationships, whether

facultative or obligatory, are crucial for completing the life cycle of orchids. For certain species, fungi serve as indispensable partners across all life stages [117-120].

While no orchid species is strictly parasitic on plants, some could parasitize fungi [121,122], and at least one exhibits adaptations to insectivory [123]. Obligate or fully mycoheterotrophs, such as *Epipogium aphyllum* and *Neottia nidus-avis*, lack chlorophyll and rely exclusively on symbiosis with fungi that decompose organic matter in the soil. Partial mycoheterotrophs, or mixotrophs, like *Corallorhiza trifida*, *Limodorum abortivum*, and *Epipactis* genus species, possess chlorophyll and complement their autotrophic nutrition with fungal-derived nutrition. Genera such as *Cephalanthera*, *Epipactis*, and *Dactylorhiza* include species with well-documented degrees of mixotrophy [118,124-127] and others that occupy a trophic continuum between autotrophy and mixotrophy [128-130]. In the past, these plants were often described as saprophytic [131]. However, contemporary studies suggest that some mycoheterotrophs obtain carbon from the decomposition of woody debris such as leaf litter and deadwood by parasitizing saprotrophic fungi, as evidenced by ^{14}C analyses [122]. In the forests of temperate biomes, rich in litter [132,133], the dense canopy and limited sunlight reaching the ground have led these plants to specialize their trophic regime. This intricate ecological interdependence underscores the complexity of orchid interactions within forest ecosystems and the challenges of studying these relationships.

While temperate orchids from open habitats, such as *Ophrys* and *Orchis*, have historically garnered significant research attention, particularly from systematic and ecological perspectives [134-136], forest orchids remain comparatively underexplored. Interest in forest-specific orchids has grown in recent years, particularly for highly protected and endangered species like *Cypripedium calceolus* [137]. Research has focused on the impact of forest cover on their fitness and population dynamics [138-140]. However, less threatened temperate forest orchids lacking legal protection or found outside protected areas remain underrepresented in studies, particularly concerning the effects of forest cover changes. This research bias often favours charismatic and visually striking flowering plants that attract more attention and funding in conservation science [141]. Many European forest *Orchidaceae* lack such appealing morphological or chromatic traits, which, combined with their small size and limited floral displays, make them less captivating than their counterparts in open habitats. These observations emphasize the need for further investigation into this group of *Orchidaceae*.

According to Djordjević & Tsiftsis [11], factors influencing the presence of terrestrial orchids, and consequently those species specialized to live in forests, are numerous, and while they act in

synergy with each other, some are particularly crucial. One of the main aspects highlighted in the study is the importance of climatic factors, such as temperature and precipitation, which are decisive for the distribution of terrestrial orchids. Forest orchids, in fact, are strongly influenced by the microclimate created by the forest canopy, which offers more stable conditions compared to open habitats. Soil characteristics, such as pH and moisture retention capacity, are equally important, as forest species rely on soil that maintains constant moisture for survival. Furthermore, soil type can influence the presence of microorganisms necessary for mycorrhizal symbiosis, which is essential for orchid germination and growth. Light also plays a fundamental role in forests, affecting the presence and abundance of species. At the same time, geographical factors such as elevation, topography, and the various types of trees, shrubs, and herbaceous vegetation influence their ecology. Finally, human activities and the challenges posed by climate change intersect with these other factors.

1.5. Study area

The “Parco Nazionale delle Foreste Casentinesi, Monte Falterona e Campigna” Protected Area, is located in the “Appennino Tosco-Romagnolo” mountains, straddling the border between the Emilia-Romagna and Toscana regions, across the provinces of Forlì-Cesena, Arezzo, and Firenze. The Park covers an area of 36,400 hectares and includes 11 municipalities: five in the province of Forlì-Cesena (Bagno di Romagna, Portico-San Benedetto, Premilcuore, Santa Sofia, Tredozio), four in the province of Arezzo (Bibbiena, Stia-Pratovecchio, Poppi, Chiusi della Verna), and two in the province of Florence (Londa, San Godenzo). A distinctive feature of the Park is the Apennine ridge, oriented northwest-southeast, which geomorphologically divides the territory into two main slopes (Tuscan slope and Romagna slope). Along the ridge, the elevations reach their highest points with “Monte Falco” Mt. (1657 m a.s.l.) and “Monte Falterona” Mt. (1654 m a.s.l.). Valleys originate and extend from the ridge, exhibiting distinct characteristics on the two slopes. On the Romagna side, the terrain features narrow, steep, and deeply incised valleys arranged like comb teeth relative to the main watershed. This area includes the mountainous portions of the Tramazzo, Montone, Rabbi valleys, and the three branches of the “Fiume Bidente” river (Campigna-Corniolo, Ridracoli, Pietrapazza). In contrast, the Tuscan side is characterized by gentler slopes and includes portions of the Mugello and Casentino regions, with an eastern extension reaching “Monte Penna” Mt. (1289 m a.s.l.) and the Franciscan sanctuary of La Verna. From a geological perspective, the Romagna slope is dominated by marl-arenaceous formations, consisting of sandstones and marls interspersed with calcareous breccias and marl limestones. On the Tuscan slope, the predominant rock type is Macigno sandstone, subdivided into two types: Chianti Macigno and Mugello Macigno. In the

southeastern Tuscan part of the Park, the La Verna area features outcrops of massive limestone overlaying a chaotic complex of clayey rocks. The Park is situated in a temperate macrobioclimate and temperate oceanic bioclimate, exhibiting a weak euroceanic subtype on the two sides, both the Tyrrhenian and the Adriatic; in contrast, the ridge area displays a semi-continental weak subtype [142]. The area can be divided into two different ombrotypes, namely a semi-arid lower horizon on the two sides and a semiarid upper horizon in the ridge area [142]. In terms of thermotype, three different classifications can be identified: supratemperate lower horizon for the lower areas of the two sides, supratemperate upper horizon for the central area that rises up to the ridge, and a third thermotype, orotemperate lower horizon, at the two highest peaks of the Park territory [142]. The area shows mesic temperatures and abundant rainfall, with maximum precipitation occurring between October and February and a minimum between June and August. Winters are moderately cold, while summers are relatively cool and humid. The average annual temperatures at higher altitudes (e.g., Campigna and Camaldoli, approximately 1100 m a.s.l.) range between 8.0 and 8.4 °C. Precipitation levels are high, exceeding 1750 mm annually. Overall, much of the Park's climate can be classified as oceanic semi-continental.

With over 84% of its surface covered by forests and woodlands, the PNFC can truly be considered a predominantly forested Park. The forests embody the Park's essence, shaped by millennia of history and tradition, as well as a forward-thinking approach to natural conservation. This combination has made the Park's forests one of the most valuable and well-preserved forest complexes in Europe. From a vegetational perspective, Viciani & Agostini [143], in the Park's Vegetation Map, classify the forest vegetation into various phytocoenoses based on phytosociological principles. Below, the main categories are presented, focusing on the *Orchidaceae* species typical of each:

Beech Forests of the Upper, Lower Montane Zones, and Semi-natural Fir Stands

Beech forests, dominated by European beech (*Fagus sylvatica*), cover about 30% of the Park's area. A smaller portion is found at higher altitudes along the "Toscano-Romagnolo" mountain ridge, above 1300–1400 m a.s.l., characterized by high-mountain beech forests on cool, deep, and humus-rich soils, hosting species like *Polygonatum verticillatum* and others typical of nutrient-rich environments (*Cardamine bulbifera*, *Galium odoratum*, *Geranium nodosum*, *G. robertianum*). In upper montane beech forests, species like sycamore maple (*Acer pseudoplatanus*), silver fir (*Abies alba*), rowan (*Sorbus aucuparia*), and wych elm (*Ulmus glabra*) occur sporadically. Typical *Orchidaceae* are: *Corallorhiza trifida*, *Dactylorhiza maculata*, *Epipactis exilis*, *E. greuteri*, *E. helleborine*, *E. leptochila*, *E. microphylla*, *E. purpurata*, *Neottia nidus-avis*, *Orchis pallens*.

At lower altitudes, roughly between 900–1000 m and 1300–1400 m a.s.l., lower montane beech forests dominate, representing the most extensive forest type in the Park. These forests exhibit significant variation depending on local geomorphology, with the most common types being pure beech forests and mixed beech-fir forests (often featuring variable amounts of silver fir) on nutrient-rich, developed soils. These areas host a range of herbaceous species like *Cardamine chelidonia*, *Carex sylvatica*, *Melica uniflora*, and other eutrophic or moisture-indicating species. Semi-natural silver fir plantations, established for silvicultural purposes, resemble these forests in their floristic assemblages. In the Romagnolo side, fir-beech forests are common, especially in the "Riserva Naturale Integrale di Sasso Fratino" reserve and "Foresta di Campigna" forest, featuring additional broadleaf species such as European ash (*Fraxinus excelsior*), Norway maple (*Acer platanoides*), Italian maple (*Acer opalus* s.l.), large-leaved lime (*Tilia platyphyllos*), and wych elm (*Ulmus glabra*). In the Tuscan side, semi-mesophilic beech forests occur at lower altitudes on less-developed soils, often intermixed with submontane mixed broadleaf species like Turkey oak (*Quercus cerris*), hop hornbeam (*Ostrya carpinifolia*), sweet chestnut (*Castanea sativa*), and thermophilic herbaceous species such as *Helleborus viridis* subsp. *bocconei*, *Hepatica nobilis*, *Hypericum montanum*. Typical *Orchidaceae* are: *Cephalanthera damasonium*, *C. longifolia*, *C. rubra*, *Corallorhiza trifida*, *Dactylorhiza maculata* s.l., *Epipactis exilis*, *E. greuteri*, *E. helleborine*, *E. leptochila*, *E. microphylla*, *E. muelleri*, *E. placentina*, *E. purpurata*, *Epipogium aphyllum*, *Limodorum abortivum*, *Neottia nidus-avis*, *N. ovata*, *Orchis mascula* s.l., *O. pallens*, *Platanthera bifolia*, *P. chlorantha*.

Oak Forests and Mixed Deciduous Broadleaf Woods

These communities occupy the hilly and lower montane zones, from 400 m to about 900–1000 m a.s.l., where they are gradually replaced by lower montane beech forests. Environmental factors (altitude, exposure, temperature, precipitation, etc.) result in diverse vegetational types, broadly grouped into two distinct categories with different floristic assemblages.

The first category includes mesophilic and semi-mesophilic submontane and hill forests. Mesophilic types are found in cooler and moister areas, with mixed tree populations dominated by Turkey oak (*Quercus cerris*), alongside hop hornbeam (*Ostrya carpinifolia*), sweet chestnut (*Castanea sativa*), field maple (*Acer campestre*), Italian maple (*Acer opalus* s.l.), European beech (*Fagus sylvatica*), sycamore maple (*Acer pseudoplatanus*), and hornbeam (*Carpinus betulus*). The herbaceous layer features species typical of beech forests, such as *Geranium nodosum*, *Melica uniflora*, *Mycelis muralis*, *Sanicula europaea*, among others. The second category (semi-mesophilic forests)

represents transitional formations between cooler, wetter forests and more thermoxerophilic ones. The main tree species include Turkey oak (*Quercus cerris*) and European hop hornbeam (*Ostrya carpinifolia*), along with manna ash (*Fraxinus ornus*), field maple (*Acer campestre*), Italian maple (*Acer opalus* s.l.), chestnut (Castanea sativa), European hornbeam (*Carpinus betulus*), and occasionally downy oak (*Quercus pubescens*). The herbaceous component of these formations consists of species with differing ecological requirements, ranging from species of open areas to those indicative of varying temperature and water availability conditions.

The second category consists of more thermophilic and xerophilic forests. The most frequent type, which predominates on the Tuscan side, is represented by oak forests and mixed woodlands with Turkey oak (*Quercus cerris*), European hop hornbeam (*Ostrya carpinifolia*), manna ash (*Fraxinus ornus*), and chestnut (*Castanea sativa*), along with a good presence of downy oak (*Quercus pubescens*), which is more thermophilic and less demanding in terms of water, sometimes becoming dominant. The herbaceous layer is mainly composed of species associated with warmer and moderately dry environments. Species such as *Brachypodium rupestre*, *Clinopodium vulgare*, *Digitalis micrantha*, *Euphorbia cyparissias*, *Sesleria italica*, and *Teucrium chamaedrys* are present. There is an even more xeric variant, particularly found on the Romagna side, with a nearly steppe-like aspect, dominated by downy oak (*Quercus pubescens*) and frequently containing European hop hornbeam (*Ostrya carpinifolia*) and manna ash (*Fraxinus ornus*). Species such as *Cytisophyllum sessilifolium* and *Juniperus communis* can be found in the shrub layer, while *Brachypodium rupestre*, *Sesleria italica*, etc., dominate the herbaceous layer. Typical *Orchidaceae* species include: *Anacamptis morio, A. pyramidalis, Cephalanthera damasonium, C. longifolia, C. rubra, Dactylorhiza maculata* s.l.*, D. sambucina, Epipactis helleborine, E. microphylla, E. muelleri, Limodorum abortivum, Neotinea maculata, N. tridentata, Neottia nidus-avis, N. ovata, Ophrys apifera, O. appennina, O. bertolonii, O. classica, O. insectifera, O. minipassionis, Orchis anthropophora, O. mascula* s.l.*, O. militaris, O. provincialis, O. purpurea, O. simia, Platanthera bifolia,* and *P. chlorantha.*

Conifer Reforestation

Conifer reforestation is widespread and well-represented within the Park territory. The most interesting characteristic is undoubtedly their local variability: they coexist in the upper valley of Bidente di Corniolo (FC) with both entirely artificial recent plantations, with limited or absent natural regeneration, and older plantations with abundant regeneration of spontaneous species and a well-structured, diversified flora. The species most frequently used for reforestation within the Park

are the Norway spruce (*Picea abies*) and Douglas fir (*Pseudotsuga menziesii*), followed by other conifers mainly used in unfavorable and degraded environments, such as certain pines (*Pinus nigra* s.l., *P. sylvestris*, *P. strobus*) and larch (*Larix decidua*). Typical *Orchidaceae* species include: *Anacamptis morio, A. pyramidalis, Cephalanthera damasonium, C. longifolia, C. rubra, Dactylorhiza maculata* s.l.*, D. sambucina, Epipactis helleborine, E. microphylla, E. muelleri, Goodyera repens, Limodorum abortivum, Neotinea maculata, Neottia cordata, N. nidus-avis, N. ovata, Ophrys apifera, O. classica, O. insectifera, O. minipassionis, Orchis mascula* s.l.*, O. provincialis, O. purpurea, O. simia,* and *Platanthera chlorantha.*

Chestnut Groves (semi-natural and fruit-bearing)

The chestnut tree (*Castanea sativa*) is a native component of the mixed mesophilic forests of the Apennines, particularly on siliceous substrates. However, it has always been planted and promoted by humans for the production of chestnuts and timber, both key resources for past populations. The depopulation of mountain and sub-mountain areas led to the abandonment of the typical fruit orchard forest (called "selva castanile"), which was progressively converted into coppice or high forest, transforming a typically artificial formation into a semi-natural forest, often mixed, which hosts numerous herbaceous and shrub components of the adjacent vegetation (particularly of the mixed oak forests that have replaced it). In the Park, fruit-bearing chestnut groves are still quite widespread. It is important to note that these forests are definitely deserving of protection. Typical *Orchidaceae* species include: *Anacamptis morio, A. pyramidalis, Cephalanthera damasonium, C. longifolia, C. rubra, Dactylorhiza maculata* s.l.*, Epipactis helleborine, E. microphylla, E. muelleri, Limodorum abortivum, Neotinea maculata, Neottia nidus-avis, N. ovata, Ophrys insectifera, Orchis mascula* s.l.*, O. militaris, O. provincialis, O. purpurea, O. simia, Platanthera bifolia,* and *P. chlorantha.*

Riparian Hygrophilous Forests

Riparian and alluvial tree formations are typically azonale vegetation, meaning they are directly linked to the presence of water rather than specific climatic conditions. They are widespread in both sectors of the Park, located along watercourses, in the bottoms of valleys and ravines, and at lower altitudes. The dominant tree species is the black alder (*Alnus glutinosa*), accompanied by white willow (*Salix alba*), black poplar (*Populus nigra*), gray poplar (*P. canescens*), white alder (*Alnus incana*), and various species from neighboring forests. The herbaceous layer is characterized by hygrophilous species such as *Carex pendula*, *Eupatorium cannabinum*, *Heracleum sphondylium*, *Petasites hybridus*, *P. albus*, and *Solanum dulcamara*. This category also includes broadleaf reforestation in humid sites, dominated by the non-native Neapolitan alder (*Alnus cordata*). Typical

Orchidaceae species include: *Anacamptis morio, A. pyramidalis, Cephalanthera damasonium, C. longifolia, Dactylorhiza maculata* s.l.*, Epipactis helleborine, E. palustris, Neotinea tridentata, Neottia nidus-avis, N. ovata, Ophrys apennina, O. bertolonii, O. classica, Orchis mascula* s.l.*, O. militaris, O. provincialis, O. purpurea,* and *O. simia.*

Open Areas of the Park

Open habitats constitute approximately 16% of the protected area and are extremely important for the conservation of valuable flora and fauna. Many *Orchidaceae* species are intrinsically linked to the maintenance of open areas such as meadows, pastures, and shrublands. Viciani & Agostini [142] identified categories that represent the complex fragmentation of open habitats, differentiating them by altitudinal zones. On the ridge, vegetation includes montane shrublands and grasslands, comprising meadows, pastures, montane heathlands and shrublands, as well as vegetation of grassy ledges and scree slopes. At lower elevations, vegetation transitions to submontane and hilly zones, including shrublands, meadows, pastures, and vegetation on eroded slopes. From an ecological perspective, the shrublands present are considered secondary successional stages resulting from the colonization of forest clearings in deciduous broadleaf woodlands. On the summit of "Monte Falco" Mt., small remnants of primary grassy prairies are present, relics of subalpine vegetation preserved over time by the particular climatic conditions of the ridge but currently under significant decline. In both the Tuscan and Romagnolo sides of the Park, pastures are common. These are also secondary in origin, deriving from the destruction of pre-existing forest formations.

Montane Meadows, Pastures, Heathlands, and Shrublands

These habitats are characterized by small, fragmented areas located at higher elevations, often above the forest limit, on leached, acidic, and nutrient-poor soils. They form a vegetative continuum where shrublands, pastures, and meadows intermingle. Typical montane heathlands and shrublands are dominated by *Vaccinium myrtillus* and/or *Calluna vulgaris*. Montane shrublands are primarily composed of *Cytisus scoparius*, with frequent occurrences of *Juniperus communis* and occasional *Rubus idaeus*. The herbaceous layer often includes acidophilous and subalpine species such as *Hypericum richeri* and *Anemonastrum narcissiflorum*. Montane meadows and pastures, generally referred to as "nardeti" are dominated by *Nardus stricta* and various *Festuca* species, alongside *Avenella flexuosa*, *Stellaria graminea*, *Viola eugeniae*, and others. In very moist or seasonally waterlogged areas, hygrophilous communities dominated by *Carex* sp. and *Juncus* sp. are established. On the exposed summits of "Monte Falco" Mt., small, highly localized sites with relict vegetation occur on very limited surfaces, often just a few dozen square meters. Species found here

include *Doronicum columnae*, *Gentiana verna*, *Gentianella campestris*, *Murbeckiella zanonii*, *Saxifraga oppositifolia*, *S. paniculata*, *Senecio doronicum*, and *Viola eugeniae*. Typical *Orchidaceae* species are: *Anacamptis morio*, *Dactylorhiza maculata* s.l., *D. sambucina*, *D. viridis*, *Gymnadenia conopsea*, *Neotinea ustulata*, *Neottia ovata*, *Orchis mascula* s.l., *O. pallens*, *Platanthera bifolia*, *P. chlorantha*.

<u>*Submontane and Hilly Shrublands, Meadows, and Pastures*</u>

These open habitats at lower elevations are well-represented in the Park and encompass vegetation on diverse substrates. Submontane and hilly shrublands are abundant and generally develop on neutral soils with adequate nutrient levels. Dominant species include *Prunus spinosa*, *Rubus ulmifolius* and *R. canescens*, *Crataegus monogyna*, *Juniperus communis*, and *Spartium junceum*. On acidic to subacidic substrates, species like *Cytisus scoparius* and *Calluna vulgaris* may become dominant. Submontane and hilly meadows and pastures are highly diversified due to anthropogenic disturbance and there are commonly on neutral soils. Dominant species include *Bromopsis erecta* and *Brachypodium rupestre*, accompanied by *Galium lucidum*, *Lolium arundinaceum*, *Lotus corniculatus* s.l., *Onobrychis viciifolia*, *Ononis spinosa* s.l., *Poterium sanguisorba* s.l., and others. Some species differentiate these grasslands further: *Bromus hordeaceus* s.l., *Cichorium intybus*, and *Convolvulus arvensis* indicate post-cultivation successional stages, while *Centaurea jacea* subsp. *gaudinii*, *Lotus dorycnium*, and *Teucrium chamaedrys* highlight more xerophilous aspects. On eroded slopes, often with rocky, exposed substrates, steppe-like grasslands occur, particularly on the Romagnolo side of the Park. These are associated with marl and marl-clay outcrops, characterized by instability and water scarcity. The vegetation is sparse and dominated by perennials such as *Thliphthisa purpurea*, *Astragalus monspessulanus*, *Coronilla minima*, and *Sesleria italica*, alongside annuals like *Arenaria serpyllifolia*, *Bombycilaena erecta*, and *Coronilla scorpioides*. Typical *Orchidaceae* species are: *Anacamptis coriophora* subsp. *fragrans*, *A. berica*, *A. morio*, *A. pyramidalis*, *Cephalanthera longifolia*, *Dactylorhiza maculata* s.l., *D. sambucina*, *D. viridis*, *Gymnadenia densiflora*, *Himantoglossum adriaticum*, *Neotinea maculata*, *N. tridentata*, *N. ustulata*, *Neottia ovata*, *Ophrys apifera*, *O. appennina*, *O. bertolonii*, *O. classica*, *O. funerea*, *O. insectifera*, *O. minipassionis*, *Orchis anthropophora*, *O. mascula* s.l., *O. militaris*, *O. provincialis*, *O. purpurea*, *O. simia*, *Platanthera chlorantha*, *Serapias vomeracea*, *Spiranthes spiralis*.

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2. Atlas of Orchids of the Foreste Casentinesi Forests, Monte Falterona and Campigna National Park. Guide to species with identification keys

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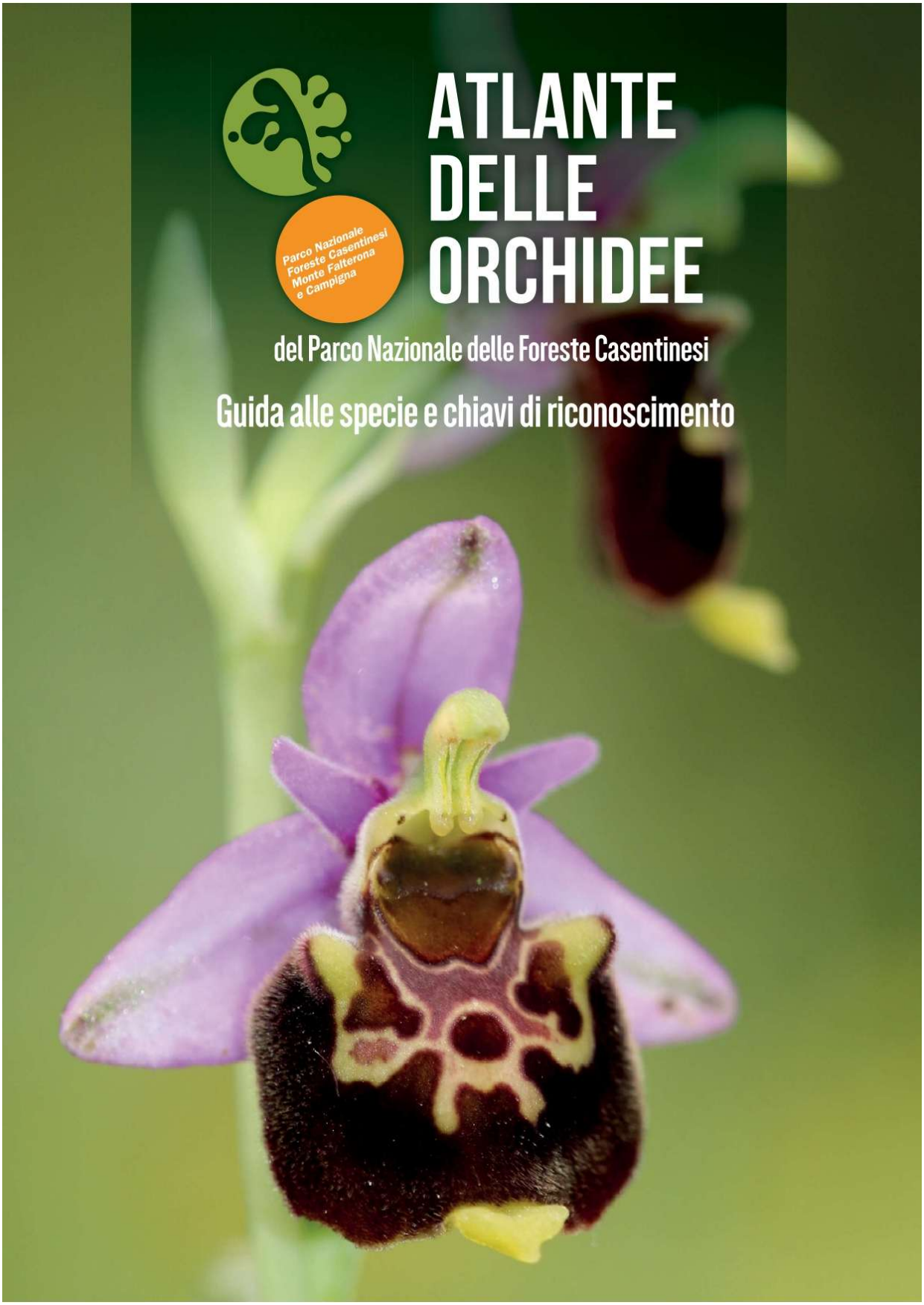

ATLANTE DELLE ORCHIDEE

del Parco Nazionale delle Foreste Casentinesi, Monte Falterona e Campigna

Guida alle specie e chiavi di riconoscimento

Antonio Pica & Paolo Laghi

Crediti

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2.2. Book overview

The *Orchid Atlas* was published and officially presented in June 2023 to mark the 30th anniversary of the FCNP. The volume spans 356 pages, divided into 36 chapters and subchapters, and is enriched with 385 figures, 52 maps, and 5 tables. The preface was written by Luca Santini, the current president of the Park.

The book is designed to cater to a broad audience, including enthusiasts, botanists, orchidologists, as well as casual visitors and tourists to the Park. It provides comprehensive and accessible information about the fascinating world of *Orchidaceae*. The opening chapters introduce readers to orchids and the *Orchidaceae* family, followed by sections on morphology, biology, ecology, threats, and conservation. These are supplemented by chapters focusing on the Park's habitats and the environments where orchids thrive. A historical overview of orchidological research within the Park is included, along with details on the methods and materials used in the study. This section concludes with dichotomous keys for identifying the genera present and several in-depth discussions, such as one dedicated to the orchids of the Valbonella Botanical Garden.

The heart of the volume comprises 50 detailed profiles of each species (distributed across 17 genera) found in the Park. Each profile features a series of informative and diagnostic photographs, highlighting key identification traits to assist even novice orchid enthusiasts. The profiles also include maps showing the species' distribution within the protected area and across Italy, descriptions of morphological characteristics, accounts of the species' historical and current presence in the Park's habitats, and insights into their ecology and pollinators. Each profile is rounded out with bibliographic references and detailed field data collected through a Citizen Science project. This initiative involved "Orchid Hunters," including enthusiasts, AIGAE guides, researchers, volunteers, and nature photographers trained during recognition courses organized as part of the project. For each genus covered, dichotomous keys are provided to facilitate accurate species identification in the field, aiding in the classification of plants and supporting the annual update of species distribution data.

The book concludes with additional chapters discussing doubtful or potential species in the protected area, *lusus naturae* and chromatic forms observed in the Park, individual contributions from field surveyors, a glossary, bibliography, acknowledgments, and credits.

2.3. Introduction

The research leading to the creation of the Atlas was conceived with multiple objectives. The first was to synthesize knowledge about the spontaneous orchids in the Park, which had remained fragmented for many years across various floristic and vegetational checklists, notes, technical reports, and publications related to the study area. This fragmentation had prevented the managing authority from developing management plans that accounted for the presence of orchids in specific habitats. The second objective was to provide the managing authority with tools that are both easily accessible and practical for use in territorial management processes. For a protected area, it is essential to have information on the distribution of all orchid species within the site, presented both graphically (digital distribution maps) and as a database of occurrences that can be continuously updated. Finally, the third objective was to advance the dissemination of the area's natural heritage. This aims not only to educate visitors and local inhabitants within the Park's boundaries but also to actively involve them in research and database updates through citizen science initiatives.

The first chapter of the book introduces the world of orchids from a historical perspective, highlighting their cultural significance as symbols of elegance and purity, or conversely, as symbols of fertility, sexuality, and carnal love. It also examines orchids scientifically, emphasizing their role as examples of natural selection and ecological interaction with their environment. Orchids have evolved intricate relationships with other organisms for survival, making them critical components of ecosystems. Through these varied perspectives, orchids emerge as extraordinary plants that uniquely combine aesthetics, culture, and science.

The second chapter systematically introduces the *Orchidaceae* family. It begins with an overview of their global distribution and the specific habitats they have adapted to. This is followed by an analysis of the family's dimensions in terms of species diversity and a taxonomic framework at global, European, and local levels. European and Italian orchids are categorized within three subfamilies: *Cypripedioideae*, *Epidendroideae*, and *Orchidoideae*, though only the latter two are found in the Park. The chapter also discusses the scientific debate concerning the geological era in which the *Orchidaceae* family originated.

The third chapter delves deeply into the morphology, biology, and ecology of wild orchids, with a focus on the genera and species present in the Park. It details the structural components of terrestrial orchids, from their hypogeal parts (rhizomes and tubers) to the epigeal structures (leaves, scapes, inflorescences), paying particular attention to the flower and reproductive organs. Variations in coloration are also discussed. Subsequent sections address biological and ecological aspects, such as

pollination mechanisms across genera, seed and inflorescence characteristics, trophic regimes, and the crucial role of mycorrhizae in orchid life cycles—factors essential for understanding their distribution within the Park.

The fourth chapter examines the threats faced by orchids in their natural habitats, including anthropogenic influences, herbivory by wild ungulates, and climate change. Conservation strategies are discussed, focusing on both in situ and ex situ methods and the legislative frameworks at various scales that protect orchids. This chapter also includes case studies on conservation efforts at the Valbonella Botanical Garden (a facility within the Park) and the management of seminatural habitats.

The fifth chapter provides an in-depth description of the protected area's territory, including its primary vegetation types. It outlines forested and open habitats across different altitudinal zones, identifying typical orchids associated with each environmental condition. A dedicated section summarizes the Natura 2000 network habitats that host orchid species and their abundance. The chapter concludes by introducing unusual orchid-growing habitats, such as public and private gardens and cemeteries.

2.4. Materials and ethods

The chapters of the book following the fifth have been included in this section as they form the core of the scientific research and provide the necessary foundation for developing the results. Due to their importance, they have been presented in their entirety. The floristic data explored and analyzed in the volume encompass many works published over a period of more than 150 years (from 1860 to 2022). The data utilized primarily fall into the following categories (Table 1).

Table 1. Types of floristic data used into research.

Bibliographic Data	Field Data
Local floristic checklists	Unpublished data obtained from field research conducted by the authors
Data related to herbarium specimens and publications reporting their information	Unpublished archived data obtained from field research by other collaborators
Data derived from academic theses or research grants/fellowships	Data collected and validated from citizen science reports, including analysis of material

	published on social networks (web, Facebook, WhatsApp, etc.)
Floristic data extracted from vegetation studies	-
Minor floristic contributions	-
Open-access plants mapping projects	-

For the historical analysis of the Tuscan side, we used the renowned *Prodromo della Flora Toscana* by Caruel [1] as the primary reference. Théodore Caruel (1830–1898), an Italian botanist of Franco-English origin and former student of Filippo Parlatore (1816–1877), reports several records of *Orchidaceae* in his work: *Cephalanthera longifolia* (referred to as *C. ensifolia*) for «La Lama in Casentino»; *Neottia nidus-avis* and *Dactylorhiza sambucina* (referred to as *Orchis sambucina*) for La Verna («L'Alvernia in Casentino»). Regarding one of these species, *Orchis pallens*, he writes: «I found this species in June 1857 in fir and beech forests at Poggiaccio near Campigna in Casentino».

Following Caruel's monumental work are the findings of Marcucci [2,3], who reports numerous species from locations such as «Verna» (La Verna), «Falterona» (Monte Falterona, Mt.), and Camaldoli, along with those of Baroni [4], who frequently cites Marcucci [2,3]. Some of these records, along with others mentioned in Caruel [1], originate from earlier herbarium collections by prominent scientific figures, including the Italian botanist, naturalist, and physician Antonio Bertoloni (1775–1868); the Italian chemist and botanist Antonio Targioni Tozzetti (1785–1856); and the Italian botanist, geographer, and anthropologist of French origin Carlo Pietro Stefano Sommier (1848–1922).

On the Romagna side, the floristic and vegetational knowledge—and consequently the understanding of orchids—owes much to the extraordinary research of the naturalist Pietro Zangheri (1889–1983) from Forlì. From a young age, Zangheri extensively explored Romagna region, from the coastal pine forests to the mountain ridge. Over the course of his studies, Zangheri made significant contributions to the knowledge of orchids within the current boundaries of the PNFC. His works document dozens of *Orchidaceae* records, first in his *Sguardo preliminare alla flora e vegetazione dell'alto Appennino Romagnolo con particolare riguardo alla foresta di Campigna* [5] and even more so in his renowned volumes *Repertorio Sistematico e Topografico della Flora e Fauna Vivente e Fossile della Romagna* [6] and *Flora e vegetazione del medio ed alto Appennino Romagnolo* [7]. Contemporary with Zangheri, other authors also expanded the

understanding of *Orchidaceae* in the PNFC during that period, particularly in the Sasso Fratino area [8,9].

Herbarium specimens (*exsiccata*) are crucial evidence of the exploratory process within the Park's territory, including in the field of orchidology. For the Tuscan side, Matteini [10] reports numerous *Orchidaceae* collected by botanists and researchers in the La Verna area from the early 19th century to the late 20th century. These are complemented by the samples cataloged in the La Verna herbarium [11–13] and the numerous *exsiccata* housed in the M. Padula Herbarium [13,14]. Recently, Romolini & Sodi [15] critically reviewed specimens of the genus *Epipactis* deposited in the Herbarium Centrale Italicum of Florence (HCI). Some of these, collected since 1863 within the current Park boundaries, have updated the historical distribution of this genus in the area under investigation.

For the Romagna side, Zangheri [6,7] mentions collections by S. Sommier, K. Siemon, and A. Targioni Tozzetti, as well as unpublished data by P. Baccarini, based on field notes and herbarium collections made during explorations of the Campigna-M. Falco sector.

In subsequent years, the Park's territory witnessed significant national orchidological discoveries. In two locations on the Romagna side, populations of *Epipactis purpurata* were found, representing the first confirmed and documented records for Italy [16]. The same study reported the first observation of *E. exilis* (cited as *E. gracilis*) in the Park at the foothills of "Monte Falco" Mt., along with the presence of an *Epipactis* species similar to *E. greuteri* but with distinct morphological differences. A few years later, these plants were described as a new species, *E. flaminia* [17], now synonymized with *E. greuteri*.

Among the major works containing distribution data on *Orchidaceae* within the PNFC's territory, although not exclusively focused on the family, are the comprehensive *Atlante della Flora protetta della regione Emilia-Romagna* by Alessandrini & Bonafede [18] and *Indagine sulla flora protetta, rara e minacciata del Parco* by Sirotti [19]. Additionally, explorations of the Campigna area and nearby regions (Santa Sofia, Forlì - Cesena) by the nascent "Gruppo Italiano per la Ricerca sulle Orchidee Spontanee" (GIROS) association [20,21] should be noted. The first synthesis of orchidological knowledge in the Park and an update on species distribution was later presented in Sirotti et al. [22]. These data were subsequently incorporated into the vascular flora checklist of the protected area [23] and its subsequent updates [24,25].

Several notable findings post-2000 include the discovery of a *Neottia cordata* station on the Romagna side of the Park [26]; the first report of *Neotinea maculata* in the protected area [27,28],

followed by further confirmations [29,30]; and various updates on the distribution of rare species in the Park, such as *Goodyera repens* [31], *Epipactis exilis* [32], *Epipogium aphyllum* [33–35], *Corallorhiza trifida* [36], and *Himantoglossum adriaticum* [37]. Romolini et al. [38,39] first documented the presence of *Epipactis placentina* and updated the distribution and nomenclature of other species in the Park. Among the most recent and significant discoveries are two new orchids for the Park, which further enrich its flora: *Anacamptis berica* and *Ophrys minipassionis* [40–43].

In Italy, there were examples of floristic atlases dedicated exclusively to the distribution of *Orchidaceae* since several decades. These works cover territories of varying extents, ranging from large macro-regions [44], administrative regions [45–47], and provinces [48–50], to increasingly smaller areas, such as individual protected areas and municipalities [51–53]. The importance of these tools lies not only in their contribution to expanding orchidological knowledge for territories of different sizes but also in their role as basic data for conservation projects and actions implemented by public and private entities.

The process of data collection and storage, whether bibliographic or field-based, follows the protocol outlined by Perazza [54]. This protocol, widely used in numerous *Orchidaceae* cartographic studies, remains valid today, adapted to the needs of this research and supported by advancements in GPS surveying technologies [44,45,53]. The bibliographic review is the starting point of the research: previous data, from publications spanning 1860 to 2022, were analyzed and entered into a Microsoft® Excel® database, which serves as the repository for *Orchidaceae* records. Documents consulted for each species are detailed in specific sheets. Each row (record) was assigned to a pair of geographic coordinates (georeferenced data); the data, originating from diverse and heterogeneous sources, were georeferenced with varying levels of accuracy based on the nature of the data (e.g., precise location, derived from a toponym, or cell scale). Additional features, directly or indirectly derived, were associated with these records (e.g., author, bibliographic references, location, altitude, province, observation date, habitat, Natura 2000 site code, vegetation type, and notes). Records lacking precise information or referring to overly broad areas were excluded from map creation.

The database also incorporated presence data derived from unpublished reports by local experts and relevant associations who voluntarily shared their independently collected data. A significant portion of the database records came from the field survey campaign conducted in the Park during 2020–2021. Field data collection also focused on exploring areas with limited or no previous data.

To further extend the investigation within the protected area, a citizen science campaign was launched. This involves research activities to which everyone can contribute. Data collection by

novice “orchid hunters” was facilitated by targeted training for participants (including AIGAE hiking guides, amateur photographers, botanists and naturalists, Carabinieri Forestali, volunteer ecological guards, university students, and curious citizens). Training included specific courses on orchid recognition within the Park [55–60], in collaboration with the Valbonella Botanical Garden [61], along with guidelines to standardize surveys with adopted protocols. Subsequently, all data, following validation and verification by the authors of this volume, were incorporated into the Park's *Orchidaceae* database.

To align the distribution of individual *Orchidaceae* species with graphical and conservation needs, the cartography (Figure 1) was created using the UTM WGS84 grid with cells of 4 km² (2 km per side). This approach is similar to the most recent Italian orchid cartographic studies [45,53,62] and faunal cartography efforts conducted in the Park [63–65]. The cell size adopted allows detailed coverage of all Park areas, yielding a readable graphic output capable of capturing even small presence variations across the territory. The resulting grid comprises 127 cells. For border cells, data within the quadrant were used even if located outside the protected area’s perimeter. Cell no. 41, which does not include any Park area but is entirely surrounded by it, was also surveyed to avoid an unjustified distributional gap. In cases where data fell on the border of two or more cells, records were evaluated individually and assigned to one or more quadrants based on the extent of the area investigated by the author (when available).

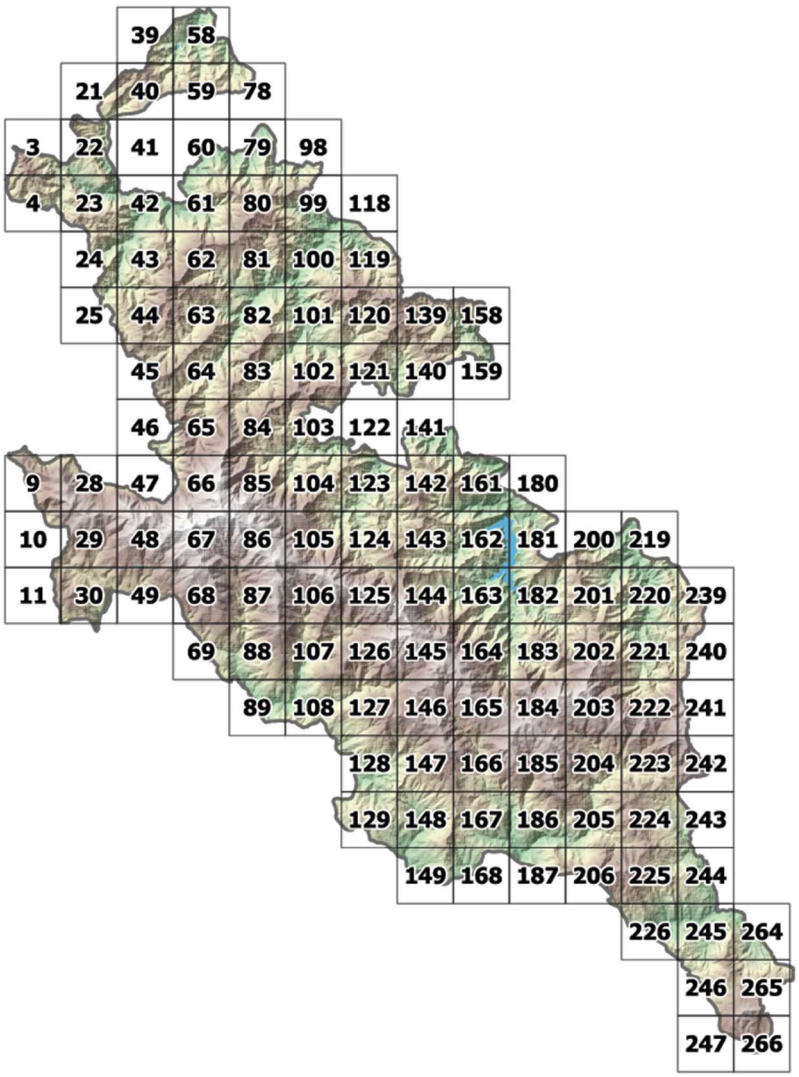


Figure 1. Study area divided into numbered 4 km² cells.

The maps of single species sheets show the presence/absence of orchids within specific grid cells and indicate the type of temporal data recorded (from historical to the most recent records). However, they provide no information about species abundance. The mapping for the Atlas and spatial analyses were carried out using QGIS 3.28.2 "Firenze" [66]. The geomorphology of the area and the distribution of altitudes were represented using a shaded DEM raster [67]. The list of reference toponyms for each cell (chosen among the most significant or those located at the centroid of each grid) is following (Table 2).

3	Il Briganzone - Balze di Cornacchia
4	Poggio Sodo - Il Bagnatoio
9	Pian del Vaio - Buca di Parisi
10	Campo Ritroso
11	C. Lavacchio - P.gio Calvaliani
21	Val Mora
22	C.se Pian Baruzzoli
23	M. di Londa - Acquacheta
24	Il Masseto
25	Pian de Bocci
28	P.gio Arsiccio
29	P.gio Porciglie - Pallereta
30	P.gio A Scheggi
39	P.gio della Solista
40	Colle del Tramazzo
41	C. Rio Celle - Susinelli
42	S. Benedetto in Alpe
43	Pian Casciano - C. Rio del Faggio
44	P.gio dei Tramiti Monte di Gralli di sotto
45	Valico dei Tre Faggi
46	C. le Fosse - Pian dei Giunchi
47	La Pianaccia
48	Monte Acuto
49	Bocca Pecorina - Barinco
58	La Castellina - Case Ponte
59	Fonte del Bepi
60	Frassineta
61	Rio Canetole - Caprincolle
62	C. Bucine
63	Ponticelli - C. Cerreta
64	C. Pian di Castagno - Valdonnetto
65	P.gio di Giogo - C. Sassello
66	Balze delle Rondinaie Pian delle Fontanelle
67	M. Falterona
68	Rif.o Vitareta - Il Lago
69	Mad.na di Montalto - Camping Falterona
78	Pian di Rupino - Bocconi
79	C. Tre Sassi
80	M. Gemelli
81	P.gio Fornello
82	Le Concolle - Castel dell'Alpe
83	C. Val di Sparviera - P.gio delle Culle
84	Pian del Grado - C. Torni
85	F.so del Satanasso
86	La Burraia
87	C. Oia - R.gio Morgante
88	Pian di Cotozzo
89	Ponte Biforco
98	Passo della Valbura (o Valico del Manzo)
99	F.so di Giumella
100	C. Petriccio
101	Fiumicello
102	M. Ritoio - Ca di Marcaccio
103	C.se Montecavallo - F.te del Bercio
104	Il Poderone
105	Campigna
106	Aia delle Guardie
107	L'Imposto - C. Vitrignesi
108	C.se Gaviserri - La Chiusa
118	Premilcuore
119	F.so dell'Orco
120	C.se I Piani - Belvedere Finestrone
121	P.so della Braccina
122	Corniolino - Lago
123	C.se Fiumari - S. Agostino
124	Rif.o Ballatoio - P.gio Ricopri
125	P.gio Pian Tombesi
126	Aia di Dorino
127	C. Prato alle Cogna - C. Vellano
128	Valagnesi
129	P.gio Tondo - C. Capecchi
139	P.gio Penna - Mandriolo di sopra
140	Valpisella - Valbonella
141	Corniolo
142	P.gio Squilla - Ronco dei Preti
143	Le Pozzacchere - Ciriegiolino
144	P.gio Scali - Fonte del Maresciallo
145	La Scossa
146	M. Faggiolo
147	C.Asqua - P.gio Muschioso
148	Moggiona
149	Lierna
158	Rif.o Pinone - Rio di Riborsia
159	Sasso - Stabiella
161	C.Val della Via - Ridracoli
162	Pratovecchio - P.gio della Gallona
163	La Seghettina
164	P.gio Cornacchia
165	S.cro Eremo - Prato alla Penna
166	Camaldoli
167	Vivaio Cerreta
168	Freggina
180	Il Poggiolo - Le Putine
181	Ca di Sopra - Campo dei Peri
182	Molino di Carpinone
183	La Lama - P.gio Fonte Murata
184	P.so Fangacci - Aia di Guerrino
185	F.so di Serravalle - P.gio Brogli
186	Serravalle
187	P.gio D'Oro - Faeta
200	Casanova dell'Alpe - La Casaccia
201	Pod.e Romiceto - Maestà di Valdora
202	Pa.so della Bertesca - Le Grigiole
203	P.gio allo Spillo - P.so della Crocina
204	Badia Prataglia
205	T. Archiano - Pian del Ponte
206	P.gio Baralla
219	Ponte del Faggio - Cetoraio
220	Pietrapazza - Felcitino
221	Eremo Nuovo - Campo della Sega
222	P.so dei Lupatti
223	Cancellino - Storca
224	Pod.e la Motta - Sala Nuova
225	Pod.e Bellaria
226	T. Corsalone - M.o di Giona
239	M. Castelluccio
240	M. Carpano - I Prati
241	Villaggio Ravenna Montana
242	P.so dei Madrioli
243	Corezzo
244	M.o di Corezzo
245	Rimbocchi - Siregiolo
246	Pod. Il Vinco - Melete
247	P.gio Casale - Vezzano
264	Montefatucchio
265	M. Penna - P.gio dello Spicchio
266	La Verna - Chiusi della Verna

Table 2. List of reference toponyms for each cell, according to the adopted numbering system.

2.5. Results

The summary information of the research is grouped in the following tables and maps. A total of 5,562 records were collected, of which 5,317 (95.6%) were useful for mapping the species present in the Park. The remaining 245 records (4.4%) either did not have the necessary requirements for precise georeferencing or fell outside the study area. These records were classified as NC (not mapped). The percentage of unexplored cells is 3.9%.

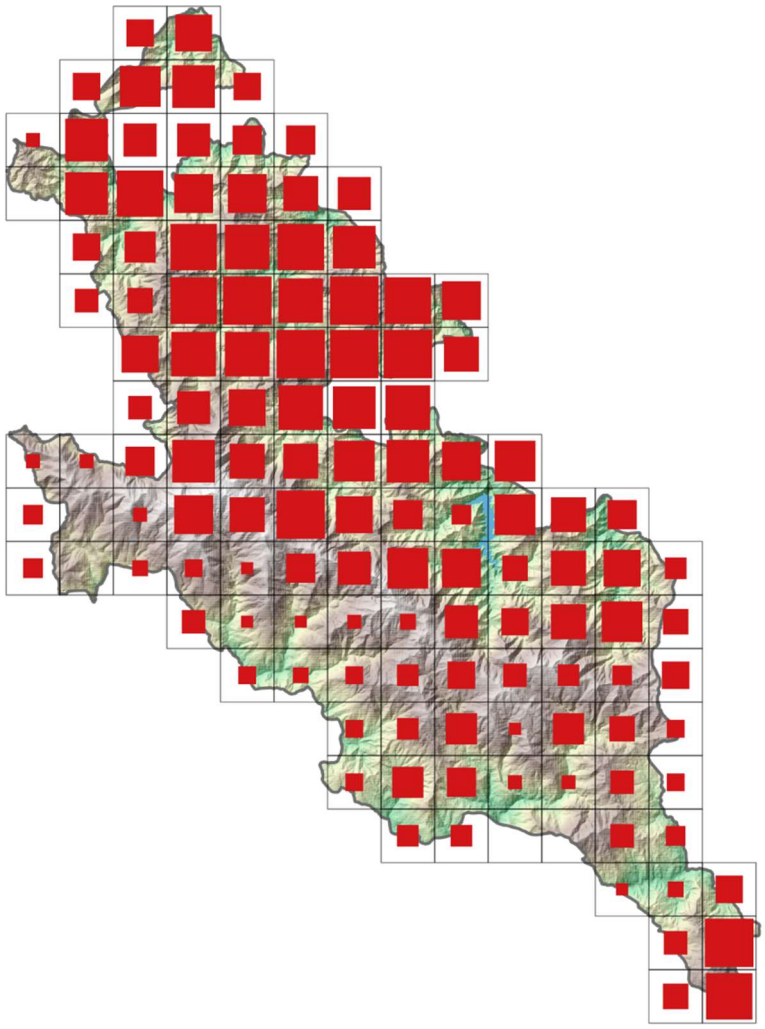


Figure 2. The number of observations ranges from 1 to 192, represented by the size of the red indicator.

Following the investigation, some cells appear to be very rich in terms of the number of species present, while others are relatively poor. This disparity results either from the actual scarcity of orchids (due to unsuitable habitats, settlements, etc.) or from a lesser research effort. The Tuscan side of the Park seemingly hosts a lower number of orchid species. However, this is primarily due to a combination of historical and environmental factors: geo-morpho-pedological, climatic, and vegetational differences between the Tuscan and Romagnolo sides are not, in isolation, sufficient to explain the gaps found in the distribution of various species. Among the contributing factors, we must also consider the lower research effort applied in the Tuscan areas. Although exploration of the Casentino area began well before that of the Romagnolo side of the Park [1-4], most of the reports concentrate on the areas of Camaldoli and La Verna, with a significant data gap for other

areas. In the Florentine side, the findings appear even more fragmented, with the only contribution to floristic knowledge for the more internal areas coming from Sabato & Valenziano [68]. Other Florentine reports are limited to ridge areas on the border between Toscana and Emilia-Romagna (regions where the three provinces covered by the Park meet). The Romagnolo side, on the whole, is much more thoroughly explored, often systematically, with few gaps, and many areas with well-documented and verified orchid presence (e.g., the Campigna and Passo della Braccina cells). A key factor in the Romagnolo knowledge process was the meticulous investigative work of Pietro Zangheri and subsequent researchers [18, Massimo Milandri unpublished data 1988-2021]. The knowledge contributed by this Atlas and the associated field research work, far from being a sufficient record of the park's orchid distribution and diversity, has helped to fill significant gaps in its distribution. Today, the volume and the related research work constitute a starting point rather than an endpoint for a future series of studies in the Park's territory.

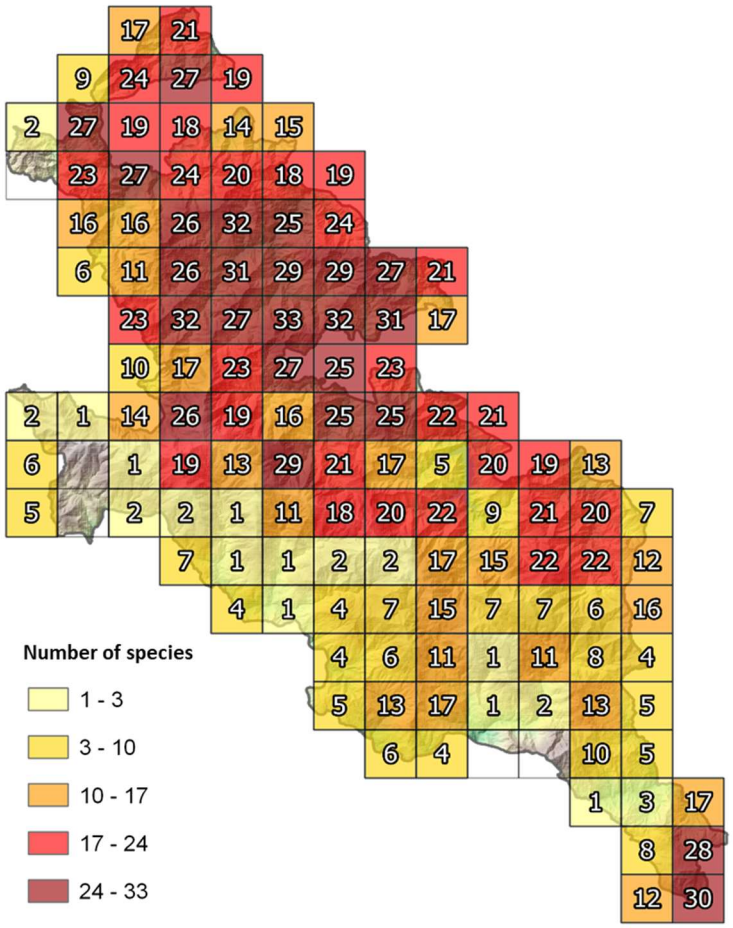


Figure 3. Orchid richness (number of species per cell) in the Park.

Among the 50 species present, the most widespread in the Park area are *Orchis purpurea* and *Dactylorhiza maculata* s.l., with a frequency exceeding 70% of the total cells. These are followed by *Anacamptis morio*, *Cephalanthera damasonium*, *Epipactis helleborine*, *Neottia nidus-avis*, and *Neottia ovata*, all occurring in more than 60% of the cells. Among the less frequent species, reported in less than 5% of the cells, are *Anacamptis berica*, *Epipactis leptochila*, *Epipactis placentina*, *Epipogium aphyllum*, *Goodyera repens*, *Neottia cordata*, and *Serapias vomeracea*.

Table 3. Number of cells occupied by each species (absolute and relative).

Taxa	Cells of occurence (n. 127)	%
Anacamptis berica	4	3.1
Anacamptis coriophora subsp. *fragrans*	19	15.0
Anacamptis morio	84	66.1
Anacamptis pyramidalis	61	48.0
Cephalanthera damasonium	80	63.0
Cephalanthera longifolia	76	59.8
Cephlanthera rubra	57	44.9
Corallorhiza trifida	9	7.1
Dactylorhiza maculata subsp. *fuchsii*; *D. maculata* subsp. *saccifera*	91	71.7
Dactylorhiza sambucina	33	26.0
Dactylorhiza viridis	11	8.7
Epipactis exilis	13	10.2
Epipactis greuteri	14	11.0
Epipactis helleborine	78	61.4
Epipactis leptochila	2	1.6
Epipactis microphylla	43	33.9
Epipactis muelleri	30	23.6
Epipactis palustris	14	11.0
Epipactis placentina	3	2.4
Epipactis purpurata	9	7.1
Epipogium aphyllum	4	3.1
Goodyera repens	5	3.9

Gymnadenia conopsea; *G. densiflora*	71	55.9
Himantoglossum adriaticum	28	22.0
Limodorum abortivum	58	45.7
Neotinea maculata	13	10.2
Neotinea tridentata	41	32.3
Neotinea ustulata	24	18.9
Neottia cordata	2	1.6
Neottia nidus-avis	85	66.9
Neottia ovata	78	61.4
Ophrys apifera	52	40.9
Ophrys appennina	49	38.6
Ophrys bertolonii subsp. *bertolonii*	36	28.3
Ophrys classica	58	45.7
Ophrys funerea	13	10.2
Ophrys insectifera	43	33.9
Ophrys minipassionis	10	7.9
Orchis anthropophora	6	4.7
Orchis mascula subsp. *mascula*; *O. mascula* subsp. *speciosa*	76	59.8
Orchis militaris	12	9.4
Orchis pallens	14	11.0
Orchis provincialis	59	46.5
Orchis purpurea subsp. *purpurea*	91	71.7
Orchis simia	50	39.4
Platanthera bifolia	35	27.6
Platanthera chlorantha	59	46.5
Serapias vomeracea	5	3.9
Spiranthes spiralis	40	31.5

2.5.1. How to read the Atlas sheets

This section, which represents the most important part of the Atlas, contains descriptive profiles of the 50 species recorded within the National Park. To facilitate species identification, the profiles are preceded by a dichotomous key to the genera. The genera are organized alphabetically, and for each one, general information is provided about its distribution, the species it comprises, and its etymology. If a genus includes multiple species, it is followed by a dichotomous key to the species, similar to the general key, designed to aid in identifying the different species within the genus.

While using a dichotomous key may seem challenging at first, just a few attempts will reveal its utility. The key advice is to carefully read both options provided for each step, thoroughly observe small distinguishing features with the help of a magnifying glass, and use the accompanying explanatory illustrations as a guide.

Each species profile includes:

- A map of the Park showing the species' distribution within the protected area and its regional distribution across Italy.
- Pictograms indicating the species' altitudinal range within the Park (from 400 m to 1650 m a.s.l., divided into 200 m intervals).
- The flowering period within the Park.
- The vegetative period within the Park (expressed across the 12 months of the calendar year).

Additionally, an Abundance Index (A.I.) is provided, calculated based on the percentage of occupied grid cells relative to the total (Figure 4).

Figure 4. Abundance Index categories used in species sheets.

The first section of the text focuses on nomenclature, including the scientific name, common name (in Italian, English, or French), basionym (abbreviated as Bas.), synonyms (abbreviated as Sin.), and the etymology of the species epithet. This is followed by a morphological description and a brief overview of the national habitats where the species can be found.

The paragraph titled "*Distribution nel Parco"* provides details about the species' distribution within the Park, the types of vegetation where it can be observed, and the coded Natura 2000 habitats where it has been recorded.

In the section "*Presenza storica nel Parco*", a summary of the species' historical records is provided, starting from herbarium specimens and/or the earliest observations within the current administrative boundaries of the protected area.

The *Notes* section highlights other relevant characteristics of the species, including taxonomy, biology, and ecology, as well as any additional information useful for distinguishing the species. This section also includes data on fruiting rates and known pollinators in the Western Palearctic (a "*" denotes species confirmed to be present in the protected area based on a database provided by the Park).

The final section relates to the data used to outline the species' distribution within the Park. In the *Field Data* paragraph, unique abbreviations—typically the initials of contributors who provided original data for mapping the species' distribution—are listed. These abbreviations are followed by symbols indicating the type of data provided:

- "!" for new records for one or more grid cells,
- "*" for confirmed records for one or more grid cells,
- "!*" for both new and confirmed records for one or more grid cells.

The *Bibliographic Data* paragraph lists references in the literature used to extract distribution information. Bibliographic records marked with "NC" (Not Cartographed) indicate the presence of a species within the study area but lack precise geolocation data, and therefore, are not represented on the map. Bibliographic records referring to species outside the study area or too vague (e.g., "Casentino," "Bibbiena," "Pratovecchio," etc.) have been omitted from the list and not mapped.

For the cartographic representation, data were divided into the following time intervals (Figure 5).

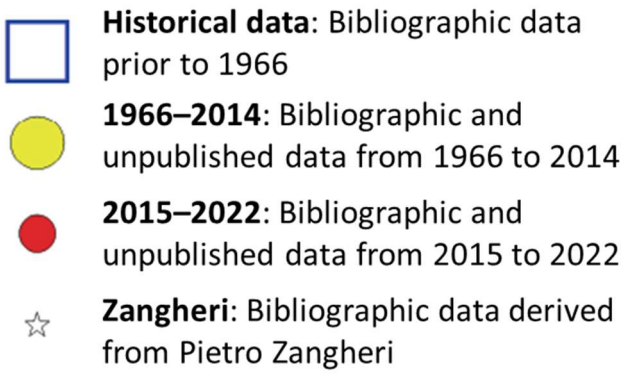


Figure 5. Temporal classification of occurrence data used in distribution maps.

For the nomenclature and the descriptive section of the species and genera profiles, references include Bartolucci et al. [69–79], collectively cited as the Portal of the Flora of Italy [80], GIROS [81], POWO [82], Romolini & Souche [83], Delforge [84], Doro [85], Biagioli et al. [86], and Perazza & Lorenz [44]. Vegetation types are based on the Vegetation Map of the Park [87]. Habitat classifications follow the Natura 2000 Habitat Map [65]. For the "Notes" section, particularly the list of pollinators, data are drawn from Claessen & Kleynen [88], Van Der Cingel [89], and other studies cited individually in the text; nomenclature follows GBIF [90]. The dichotomous keys for species identification are based on GIROS [81,91], Delforge [84], and Nimis et al. [92].

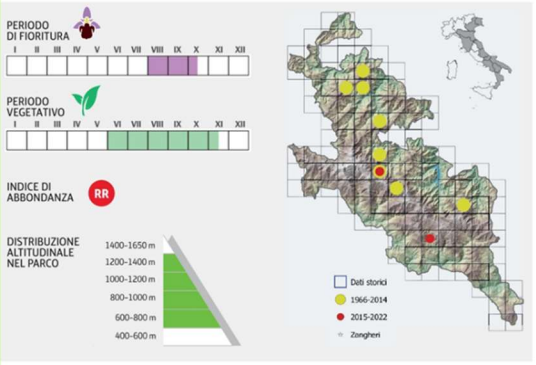
2.5.2. Descriptive and Distributional Species Sheets

Following the section on research materials and methods, the volume includes descriptive and distributional profiles for the 50 species present within the protected area. Due to space constraints, it was decided not to include all the profiles here but instead to provide a selection of illustrative examples. Nevertheless, the updated distribution of individual species profiles is freely accessible on the webGIS platform “Arca della Biodiversità” of the Park, available at the following link: https://biodiversita.parcoforestecasentinesi.it/it/#/it/maps. The platform is updated annually with new records and discoveries of orchids within the Park's area.

Below are some example sheets extracted from the volume (*Epipactis purpurata*, *Limodorum abortivum* and *Neottia nidus-avis*).

Epipactis purpurata

G.E. Smith 1828



Nome comune:

Elleborina violacea

Violet helleborine

Sin.: *Epipactis viridiflora* Hoffm. ex Krock.; *E. helleborine* subsp. *varians* (Crantz) H. Sund.; *Epipactis pollinensis* B. & H. Baumann.

Etimologia: in riferimento al colore violaceo caratteristico di questa pianta.

Descrizione: Pianta alta 20-70 cm, solitaria o spesso in gruppi, con apparato ipogeo costituito da rizoma. Scapo eretto, robusto, grigio-verdastro ± sfumato di violetto e con peluria grigiastra verso l'alto. Foglie basali assenti, le cauline 4-12 ± spiralate, piccole, carenate, rigide con colorazione verde-brunastra soffusa di violetto, 5-10 × 1-3 cm, le superiori bratteiformi. Infiorescenza ± densa (10-50 cm), in genere composta da 5-50 (fino a 100), questi disposti ± unilateralmente, di media grandezza, allogami, ben aperti, leggermente profumati, penduli o suborizzontali. Brattee inferiori più lunghe del fiore. Sepali ovato-lanceolati (8-13 × 4-6 mm), pubescenti all'esterno e con colorazione verdastra fuori e verde-biancastra all'interno. Petali subeguali con leggera sfumatura violacea. Labello diviso in ipochilo ed epichilo, con ipochilo cupuliforme, nettarifero, bruno-violaceo all'interno, epichilo cordiforme (3.5-5 × 4.5-6 mm), con bordi ondulati, increspati, ribattuto all'indietro, munito alla base

di due cuscinetti verrucosi violacei. Clinandrio ben sviluppato, viscidio funzionale. Pollinii coerenti. Ovario fusiforme con evidenti costolature, glabro o appena pubescente, verde-violaceo, portato da un pedicello lungo 2-5 mm, violaceo.

Habitat: Faggete, boschi ombrosi di conifere e latifoglie.

Distribuzione nel Parco: Rarissima nel Parco, un tempo maggiormente diffusa. Dai dati recenti risulta assente o scarsamente presente nelle aree dove era segnalata in passato. È strettamente legata alle abetine ma la si trova anche nelle faggete. La sua distribuzione si limita attualmente al versante forlivese e aretino del Parco. Rinvenuta nei seguenti habitat codificati dalla Rete Natura 2000: 9130; 9180*; 9210*; 9220*.

Presenza storica nel Parco: Segnalata nel Parco per la prima volta nel versante forlivese nel 1984 (M. Bucine, S. Benedetto in Alpe): la stazione, con oltre 100 esemplari, rappresenta di fatto la prima segnalazione certa per il territorio italiano (Savelli *et al.* 1988). Non più riconfermata in tempi recenti (Sirotti *et al.* 2005). Viene riportata anche una stazione per l'abetina di Campigna, scoperta nel 1986 (Savelli *et al.* 1988). Quest'ultima, potenzialmente a rischio per l'impatto legato al forte afflusso turistico estivo (Sirotti *et al.* 2005) e agli interventi selvicolturali, è stata riconfermata di recente solo fino al 2018 (R. Romolini, F. Sodi & G. Pandeli *in litteris*). Nell'ultimo biennio di ricerche purtroppo non è stata più osservata.

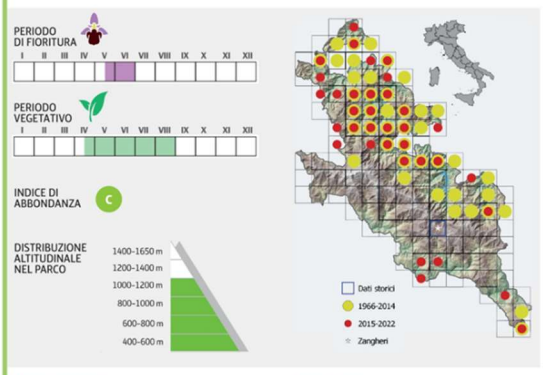
Note: Pianta micoeterotrofica parziale. È inserita nel "Libro rosso delle Piante d'Italia" (Conti *et al.* 1992). È una specie allogama con una struttura florale e meccanismi di impollinazione simili a quelli di *E. helleborine*; anche il suo nettare è tossico ed è impollinata principalmente da Vespe. Tasso di fruttificazione che varia dal 65,5% al 95,9% (media 82,5%).

Impollinatori (nel Paleartico Occidentale): Coleoptera (*Coccinella septempunctata** Linnaeus, 1758); Diptera (*Episyrphus balteatus De Geer, 1776*); Hymenoptera (*Apis mellifera** Linnaeus, 1758; *Bombus pascuorum** (Scopoli, 1763); *Dolichovespula media* (Retz., 1783); *Dolichovespula sylvestris* (Scopoli, 1763); *Polistes dominula* (Christ, 1791); *Vespula austriaca* (Panzer, 1799); *Vespula germanica* (J.C.Fabricius, 1793); *Vespula rufa* (Linnaeus, 1758); *Vespula vulgaris* (Linnaeus, 1758)].

Dati di campo: API!; MM!; PL*; PLI*; RSP*.
Dati bibliografici: Savelli *et al.* (1988); Alessandrini & Bonafede (1996); Biagioli (1996); Sirotti (1998); Sirotti *et al.* (2005); Viciani *et al.* (2010); Romolini *et al.* (2016); Viciani & Agostini (2016, 2020).
Cit. sub: *E. viridiflora*.

Limodorum abortivum

(Linnaeus) Swartz 1799



Nome comune:

Fior di legna, Limodoro, Fiammone

Violet limodore

Bas.: *Orchis abortiva* Linnaeus 1753

Sin.: *Epipactis abortiva* (L.) All.; *Ionorchis abortiva* (L.) Beck

Etimologia: il nome specifico 'abortivum' non ha nulla a che vedere con presunte proprietà abortive, ma si riferisce al fatto che spesso i fiori appassiscono prima di sbocciare.

Descrizione: Pianta alta 20-80 cm, con apparato ipogeo costituito di un corto rizoma e un fascio di radici ingrossate. Scapo eretto, robusto, talvolta sinuoso, compatto, di colore violaceo o bruno-violaceo. Foglie cauline ridotte a squame guainanti lo scapo, le inferiori bruno-violacee, le superiori verdastre sfumate di viola. Brattee erbacee squamiformi, violacee, lanceolate, leggermente più lunghe dell'ovario. Infiorescenza a racemo lunga 10-33 cm, lassa, allungata e cilindrica con 4-25 fiori grandi, eretti e appressati al fusto, di colore viola con le parti basali più chiare, spesso poco aperti. Sepali laterali lanceolati (16-25 × 5-11 mm), opposti e patenti, di colore viola chiaro con nervature scure, sepalo mediano più largo dei laterali, concavo all'estremità e ripiegato a cappuccio in avanti sul gimnostemio, con apice ottuso. Petali più corti e più stretti dei sepali, ± concolori ai sepali. Labello 14-22 mm articolato in ipochilo e epichilo, il primo concavo, stretto, il secondo cuorifor-

me, dilatato, con bordi ondulati e rialzati e con striature scure disposte a ventaglio. Sperone nettarifero presente, lungo ± quanto l'ovario, arcuato verso il basso, più sottile all'apice. Ginostemio robusto ed eretto, un po' curvato in avanti, di colore violaceo. Antera ovale, rivolta verso il basso. Masse polliniche di colore giallo chiaro poco coerenti. Ovario oblungo, ristretto alla base in un breve peduncolo, lungo 14-25 mm.

Habitat: Specie diffusa nelle fasce altitudinali collinari e basso montane mentre tende a rarefarsi fino a scomparire nei tratti più propriamente montani; in pianura è rarissima. Boschi radi e termofili, cespuglieti, radure, scarpate stradali.

Distribuzione nel Parco: Comune nel Parco, in genere non è abbondante e presenta alcune lacune distributive sul territorio. Predilige gli habitat boschivi quali i rimboschimenti di conifere e le faggete della fascia montana inferiore, nonché i boschi misti submontani e collinari, più termofili. A volte la si può osservare ai margini di arbusteti e praterie. Rinvenuta nei seguenti habitat codificati dalla Rete Natura 2000: 5130; 6210(*); 9130; 9220*.

Presenza storica nel Parco: Zangheri (1942) la indica per l'Eremo di Camaldoli riportando un dato di Baccarini; contestualmente esprime dubbi sulla sua presenza nel versante romagnolo. Successivamente Sabato & Valenziano (1975) ne indicano la presenza per l'area di Rincine-M. Massicaia, nel versante fiorentino, ma il dato risulta non cartografabile e per di più mai verificato. Le prime segnalazioni certe per il versante romagnolo dell'area protetta sono da attribuirsi a Alessandrini & Bonafede (1996) per la seconda metà degli anni 80. A queste seguono diverse conferme per il versante aretino, nell'area di La Verna (Siemoni *et al.* 1989-1998, Sirotti *et al.* 2005). Per il versante fiorentino, la sua presenza è stata confermata nel 2016 (P. Laghi, dati inediti).

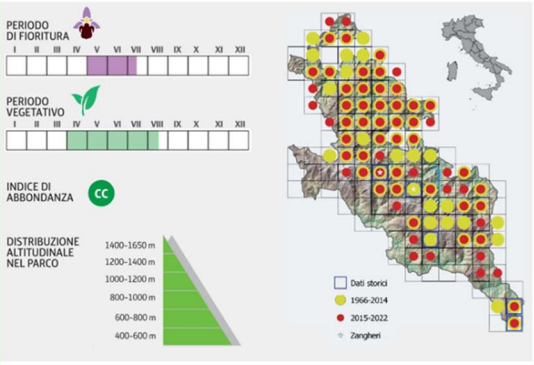
Note: Pianta che possiede clorofilla ma con fotosintesi inefficiente dipendente per la sua nutrizione (micoeterotrofia parziale o mixotrofia) da diversi funghi del genere *Russula*, spesso *Russula delica* (Girlanda *et al.* 2006, Mossberg & Pedersen 2017); raramente associata al Tartufo nero (*Tuber melanosporum*). Specie soprattutto autogama e a volte cleistogama; occasionalmente ricorre all'allogamia, soprattutto dovuta a Imenotteri, che ricercano l'abbondante nettare racchiuso nel lungo sperone. Tasso di fruttificazione che varia dal 73% al 100% (media 88.7%).

Impollinatori (nel Paleartico Occidentale): Coleoptera (*Tropinota hirta* (Poda, 1761)); Hymenoptera (*Anthophora affinis* Brullé, 1832; *Anthophora dispar* Lepeletier, 1841; *Anthophora plumipes* (Pallas, 1772); *Habropoda tarsata* (Spinola, 1838); *Lasioglossum marginatum** (Brullé, 1832); *Osmia caerulescens** (Linnaeus, 1758); *Rhodanthidium septemdentatum* (Latreille, 1809)).

Dati di campo: API*; APDA*; APFDI; APMM!*; DAI; DLSG*; FB*; GM!*; MB*; MM!*; MMNA!*; PL*; RBI; RSP!*; VC*.
Dati bibliografici: Zangheri (1942); Sabato & Valenziano 1975[ns]; Alessandrini & Bonafede (1996); Siemoni *et al.* (1989-1998); Sirotti & Fariselli (2002); Sirotti *et al.* (2005); Viciani *et al.* (2010, 2020); Viciani & Agostini (2016, 2020); Lelli *et al.* (2019); iNaturalist (2021).

Neottia nidus-avis

(Linnaeus) L.C.M. Richard 1817



Nome comune:

Nido d'uccello

Bird's Nest

Bas.: *Ophrys nidus-avis* Linnaeus 1753

Sin.: *Epipactis nidus-avis* (L.) Crantz; *Malaxis nidus-avis* (L.) Bernh.

Etimologia: il nome specifico deriva dal latino e fa riferimento alla forma di nido di uccello dell'apparato radicale.

Descrizione: Pianta alta 10-50 cm, giallo-brunastra, provvista di apparato ipogeo costituito da un rizoma orizzontale avvolto da numerose radici carnose, corte, affastellate e intrecciate tra loro. Scapo robusto, eretto, cilindrico, grosso. Foglie 4-6 ridotte a squame giallastre o marroni, guainanti il caule (2-6 cm). Brattee membranacee, lineari-lanceolate, lunghe poco meno dell'ovario. Infiorescenza a racemo densa per numerosi fiori verso l'alto, ± rada in basso, di forma cilindrica o globosa allungata, alta 5-20 cm. Fiori di grandezza media, con leggero odore di miele. Sepali e petali ovato-lanceolati, concavi a formare un casco (4-6 mm) ± lasso e aperto. Labello (9-12 mm) rivolto verso il basso, lungo circa il doppio dei sepali, con base a cupola nettarifera evidenziata da una macchia scura mentre l'apice, più chiaro, è a sua volta ben diviso in due lobi divergenti, larghi e arcuati, ottusi all'estremità. Sperone assente. Ginostemio lungo e biancastro. Masse polliniche di colore giallo chiaro,

compatte all'inizio e poi friabili. Ovario allungato (8-10 mm), subcilindrico.

Habitat: Boschi ombrosi di latifoglie e conifere.

Distribuzione nel Parco: Comunissima e ben diffusa nel Parco, è possibile trovarla in tutti i versanti. È indissolubilmente legata all'ambiente boschivo: vegeta nelle faggete soprattutto quelle della fascia montana inferiore, nei boschi submontani e collinari e nei rimboschimenti di conifere. Rinvenuta nei seguenti habitat codificati dalla Rete Natura 2000: 5130; 9110; 9130; 9180*; 9210*; 9220*.

Presenza storica nel Parco: Specie la cui presenza è storicamente conosciuta per il Parco, viene riportata nel versante aretino da Caruel (1860-64) per La Verna e da Marcucci (1881, 1889) per Camaldoli. Seguono alcune raccolte d'erbario che si estenderanno dai primi del '900 con Martelli, Alessandri e Baccarini fino a metà del secolo con Pichi Sermolli e Corradi (Matteini 1968). Per il versante romagnolo viene riportata da Zangheri (1942, 1966a,b) per l'area di Campigna e di Poggio Scali (con sue osservazioni personali e con raccolte di Fiori, Baccarini e Pampanini) e da Allegri (1960) e Hofmann (1965) per Sasso Fratino. Le conoscenze sulla distribuzione di *N. nidus-avis* si sono accresciute successivamente nel corso degli anni espandendosi su tutti e tre i versanti, grazie ai contributi di numerosi autori (Sirotti *et al.* 2005, Viciani & Agostini 2020).

Note: L'infiorescenza, disseccata, spesso rimane visibile fino alla successiva stagione di fioritura. La specie è minacciata da cinghiali ed istrici, che ne ricercano e divorano gli organi ipogei (Sirotti *et al.* 2005). Questa specie sembra particolarmente legata a boschi fortemente ombreggiati e si riduce o scompare quando la copertura arborea diminuisce (Stewart 1992). Tutte le parti della pianta sono completamente prive di clorofilla, la specie è incapace di svolgere la fotosintesi clorofilliana e dipende interamente per il suo nutrimento dalla simbiosi fungina instaurata durante la fase di germinazione con *Rhizomorpha neottiae*, e, successivamente, con un gruppo di funghi ectomicorrizici della famiglia delle *Sebacinaceae* come *Sebacina incrustans*, nonché *S. epigaea* e *Tremelloscypha gelatinosa*; è possibile che *N. nidus-avis* tragga le sue risorse dagli alberi circostanti, una strategia di frode micorrizica simile a quelle osservate ad oggi in altre piante micoeterotrofe studiate (McKendrick *et al.* 2002, Selosse *et al.* 2002). Inoltre, dato che sono state rilevati più volte *Ceratobasidiaceae* e *Russulaceae* in diverse specie di *Neottia*, la probabilità che siano loro micobionti è elevata (cfr. Yagame *et al.*

2016). In *N. nidus-avis* è nota la cleistogamia anche sotterranea; normalmente ricorre all'autogamia e, accidentalmente, ad un certo grado, più o meno occasionale, di fecondazione incrociata. Frequentemente visitata da Ditteri.

Tasso di fruttificazione che varia dal 72,2% al 97,1% (media 88,3%).

Impollinatori (nel Paleartico Occidentale): Diptera [*Syrphus ribesii* (Linnaeus, 1758); *Metalimnobia* cf. *quadrimaculata* (Linnaeus, 1761)]; Hymenoptera [*Myrmica** Latreille, 1804 sp.]; Thysanoptera* Haliday, 1836.

Dati di campo: ABGT*; AN*; API*; APDA*; APFD!; APLE!; APLS*; APMM!*; APPL*; APVC*; DLSG*; FB!*; GCO*; GM*; IZ*; LC*; LE!*; MM!*; MMNA*; PLI*; PLM*; PV*; RB!; RSP*; RT*; VC*; VR*.

Dati bibliografici: Caruel (1860-64); Marcucci (1881, 1889); Baroni (1897-1908); Allegri (1960)[pc]; Hofmann (1965); Zangheri (1942, 1966a,b); Matteini (1968); Sabato & Valenziano (1975)[pc]; Massei (1981); Padula (1983[pc], 1988, 2008); Siemoni *et al.* (1989-1998); Alessandrini & Bonafede (1996); Ferrarini (1998); Miozzo (1999); Sirotti & Fariselli (2002); Viciani & Gabellini (2002); Bottacci *et al.* (2003); Montanari (2005)[pc]; Sirotti *et al.* (2005); Gonnelli *et al.* (2006, 2009); Zingarelli (2006); Frignani *et al.* (2009); Viciani *et al.* (2010, 2020); Gonnelli & Bottacci (2012); Laghi (2013b,c); Viciani & Agostini (2016, 2020); Lelli *et al.* (2019); Inaturalist (2021).

2.6. Discussion and conclusion

The publication of this volume does not represent a conclusion but rather a “new” starting point for research within the Park. This is because, until now, only very specific reports were available for the rarest species, while for the more common ones, data were often vague in spatial terms. The lack of georeferenced data in the past has caused significant management issues. For rare species, only areas with historical occurrences were safeguarded, whereas for common species, knowledge of their distribution was never expanded. In both cases, the understanding of the family remained fragmented.

This initial cartographic work has provided the PNFC Authority with a management tool of primary importance. Many of the species present are protected by European, national, and local directives and are often included in national red lists or under assessment by the IUCN. Notable species of interest within the Park include *Epipactis greuteri* and *E. placentina*, both classified as endangered (EN) on the IUCN Red List [93,94], as well as *E. microphylla*, which is considered near threatened (NT) [95]. Additionally, two policy species [96], *Himantoglossum adriaticum* and *Orchis provincialis*, are present, along with others listed in the “Italian flora red lists” [96,97]: *Epipactis palustris*, *E. exilis*, *Ophrys appennina*, *O. bertolonii subsp. bertolonii*, *O. classica*, *O. minipassionis*. *Epipactis purpurata* is also included in the "Red Book of Italian Plants” [98].

It is noteworthy that many of the species present in the Park and included in various protection lists are orchids specialized in forest habitats. In a protected area predominantly covered by forests, these environments become safe havens for their conservation and reproduction. Prioritizing the protection of these areas is one of the primary objectives of a protected area. These species are simultaneously uncommon or rare in the rest of Italy, making the territories that host them critical for maintaining suitable habitats. Mapping their precise distribution and increasing field research is increasingly necessary. New areas that appear less suitable or have not yet been thoroughly explored may host important populations of these species.

For example, in the case of *Epipactis greuteri*, research has led to the discovery of new occurrences in parts of the Park outside of the known distribution areas, similarly for the rare *E. placentina*, *E. purpurata*, and *E. exilis*. This is particularly interesting as it has allowed for an expansion of the known Italian distribution of these species, which remains fragmented in some cases [99,100].

Species typical of more open environments (grasslands, meadows, shrublands, etc.) have also revealed intriguing dynamics worth investigating further. Some species, historically reported in open ridge areas of the National Park, appear to be in decline compared to past distributions

(historical records from 1966–2014), such as *Orchis pallens*, *Dactylorhiza sambucina*, and *D. viridis*. In most areas, these species have been significantly impacted by ungulates, as reported by many local testimonies and directly observed in the field.

Conversely, some typically Mediterranean species seem to have expanded their distribution within the Park over the years, such as *Himantoglossum adriaticum* and *Neotinea maculata*. This is inferred by observing the number of recent records (from 2015 to 2022). For instance, in *Neotinea maculata*, only 2 (16%) out of a total of 12 grid cells contain records predating 2015. For *H. adriaticum*, of the 28 occurrence grid cells, 19 (68%) were identified in recent years.

The role of citizen science has proven fundamental in this research and is expected to become increasingly significant globally [101] thanks to tools and applications now accessible to everyone [102]. The contributions of local residents and frequent visitors to the Park have been crucial to the investigation process [103]. By the end of 2024, over 450 reports were recorded through citizen science channels. Some of these reports have led to the discovery of a new species never previously found in the PNFC (*Himantoglossum robertianum*, [104]) and new occurrences (e.g., *Epipactis placentina*). This underscores the importance of increasing citizen science involvement in scientific research within protected areas.

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3. Forest orchids under future climate scenarios: habitat suitability modelling to inform conservation strategies

Research paper

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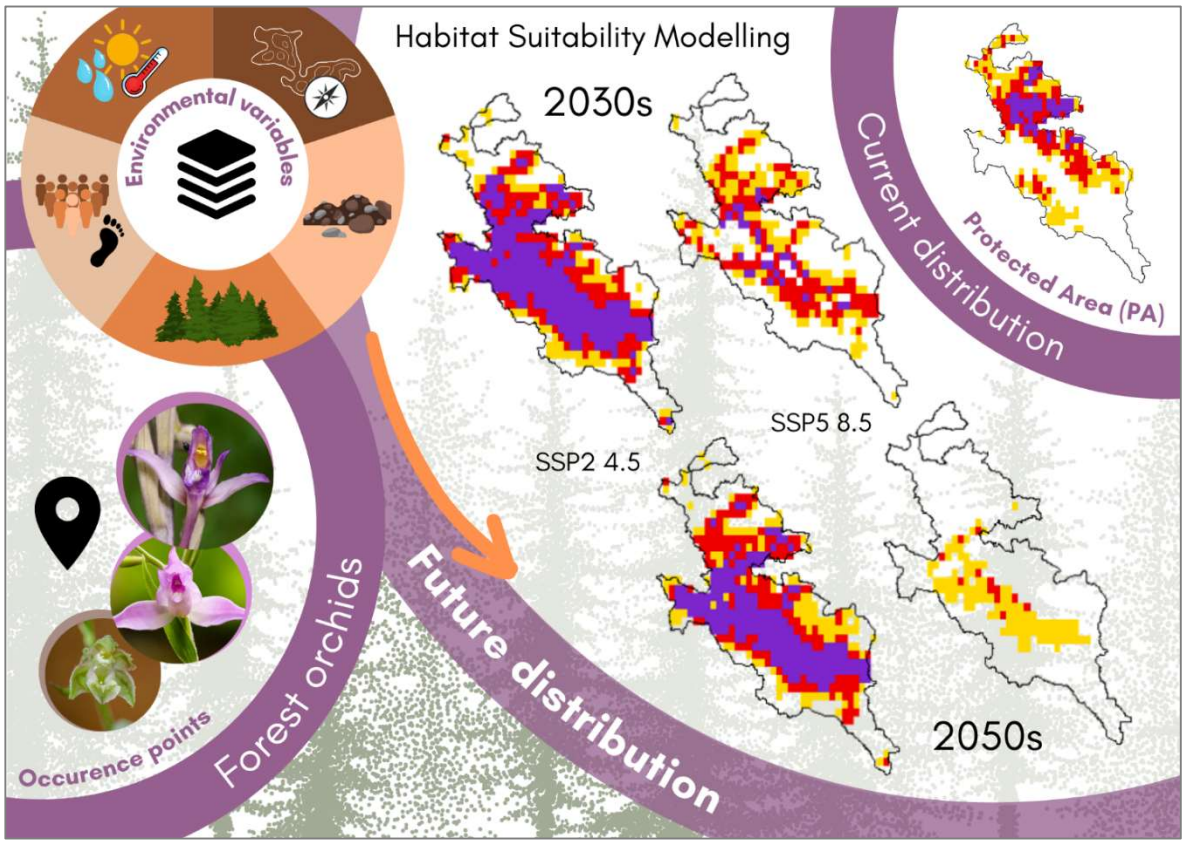
3.1. Graphical abstract



3.2. Abstract

Orchidaceae is one of the largest and most diverse families of flowering plants in the world but also one of the most threatened. Climate change is a global driver of plant distribution and may be the

cause of their disappearance in some regions. Forest orchids are associated with specific biotic and abiotic environmental factors, that influence their local presence/absence. Changes in these conditions can lead to significant differences in species distribution. We studied three forest orchids belonging to different genera (*Cephalanthera*, *Epipactis* and *Limodorum*) for their potential current and future distribution in a protected area (PA) of the Northern Apennines. A Habitat Suitability Model was constructed for each species based on presence-only data and the Maximum Entropy algorithm (MaxEnt) was used for the modelling. Climatic, edaphic, topographic, anthropogenic and land cover variables were used as environmental predictors and processed in the model. The aim is to identify the environmental factors that most influence the current species distribution and the areas that are likely to contain habitats suitable for providing refuge for forest orchids and ensuring their survival under future scenarios. This will allow PA authorities to decide whether to invest more resources in conserving areas that are potential refuges for threatened species.

Keywords: biodiversity; protected areas (PAs); climate change; landscape ecology; *Cephalanthera*; *Epipactis*; *Limodorum*

3.3. Introduction

The *Orchidaceae* is one of the largest plant families in the world, with many accepted species second only to the *Asteraceae* [1,2]. They are found in a wide variety of environments across the globe [3–5]. The number of orchid species is estimated to range from approximately 25,000 to 33,000 [2,6–9], belonging to 704–850 genera, according to various sources [6,9,10]. Furthermore, new orchid discoveries worldwide continue to increase these numbers [11–14]. In Europe, the number of species ranges from approximately 163 [3] to around 645 [15]. The most recent checklist of native flora indicates that there are 237 taxa of *Orchidaceae* in Italy [16,17], while other authors report 267 taxa [18].

The *Orchidaceae* family is widely recognised as having a significant number of endangered species, particularly among the terrestrial orchids [19–21]. Human activities, either by altering their natural habitats or by directly harming individual populations, are a major threat to these species [22–24]. Moreover, it has been observed that climate change can have a significant impact on the presence and distribution of certain species in a given territory [25–27]. As a result, the conservation of these species and their habitats has become a global priority to counteract their continued decline [28–30]. Orchids are widely recognised as umbrella and flagship species that can guide the conservation process to protect not only themselves but also other species growing in their habitats [29,31–35].

Habitat suitability models (HSMs) are broadly used to make prediction about potential distribution of habitats capable of hosting species at different scales, ranging from global [36,37] to local [38,39]. One of the most commonly used modelling methods for investigating the distribution of plant and animal species is the maximum entropy (MaxEnt) algorithm [40]. It is based on presence-only data and is known for its efficiency and also for turning out robust results, even when occurrence data is limited [41–46]. Species distribution models are frequently used to better conserve species, identify priority protection areas and plan effective interventions [47–52].

The disappearance of terrestrial orchids from temperate climates is mainly caused by the loss and deterioration of natural habitats [53,54]. However, human actions can help maintain past environmental conditions and ensure the presence of these species [4,55–57]. Furthermore, climate change may affect temperate terrestrial orchids in different ways. Depending on the species and region, they may respond positively or negatively to changes in climate parameters [58–61]. Consequently, further investigation is required to identify the impact of the aforementioned factors on these species.

The target species of this study are *Cephalanthera rubra* (L.) Rich., *Epipactis microphylla* (Ehrh.) Sw. and *Limodorum abortivum* (L.) Sw. These are three temperate terrestrial orchids whose native range is centred in Europe [10] and they belong to a widespread group of species known as forest orchids, which are mainly found in forest habitats. Forest orchids have a close relationship with the forest ecosystem as they can take up carbon from surrounding trees through mutualistic associations between higher plants and fungi, called mycorrhizae. These associations may or may not be obligatory to ensure their life cycle [62–64] and in the case of the species under investigation they are intimately associated with fungi throughout their life stages [63,65,66]. The target species exhibit a discontinuous presence with considerable gaps in the study area [67]. It is crucial to underscore that these species are linked to forest habitats, which are included in the Habitats Directive 92/43/EEC and are classified as priority (Natura 2000 code 9180*, 9210*, 9220*) or have a limited distribution within the PA (Natura 2000 code 9110, 9130, 91M0) [68]. Furthermore, the number of available occurrence points was considered sufficient to model species with the HSM approach [69].

Previous studies have extensively explored temperate European orchids, analysing the biotic and abiotic factors that influence their presence, abundance and distribution [4,55,70–72], including species commonly grown in forest environments [73–75]. However, it is important to note that only a limited number of studies have been conducted to assess the potential future distribution of a few species in relation to climate change using a species distribution modelling approach [25,76–79].

The objectives of this study were: (a) to investigate the potential present distribution of three forest orchid species in a protected area (PA) of Northern Apennines (Foreste Casentinesi National Park) and to predict the future distribution of habitats suitable for hosting them using the Habitat Suitability Model (MaxEnt); (b) to evaluate the impact of individual environmental factors on the species; (c) to assess the areas that are most suitable for the species in relation to future projections of global climate change and actual environmental conditions; (d) to provide the necessary guidance for future management and conservation projects by assessing in advance the most suitable areas for the conservation of forest orchids according to the model predictions. The aim is to provide a common methodological approach to help PAs manage and conserve threatened species for the long term while making efficient use of available resources.

3.4. Results

3.4.1. Species Occurrence and Environmental Variables

A total of 149 occurrence records were used in this study to identify target species. These included *C. rubra* (54), *E. microphylla* (37), and *L. abortivum* (58). Following the thinning process, the number of occurrence points was reduced by 37, 21, and 39, respectively, in comparison to the original datasets (Figure 1, Table S1).

Following the application of Pearson's test and Variance Inflation Factor (VIF) (Table S2), the initial 46 environmental variables (EVs) were reduced to 12 for *C. rubra*, 7 for *E. microphylla*, and 13 for *L. abortivum*. Only the first five variables with the highest contribution to the model were isolated and used for the final model for each species (Table 1).

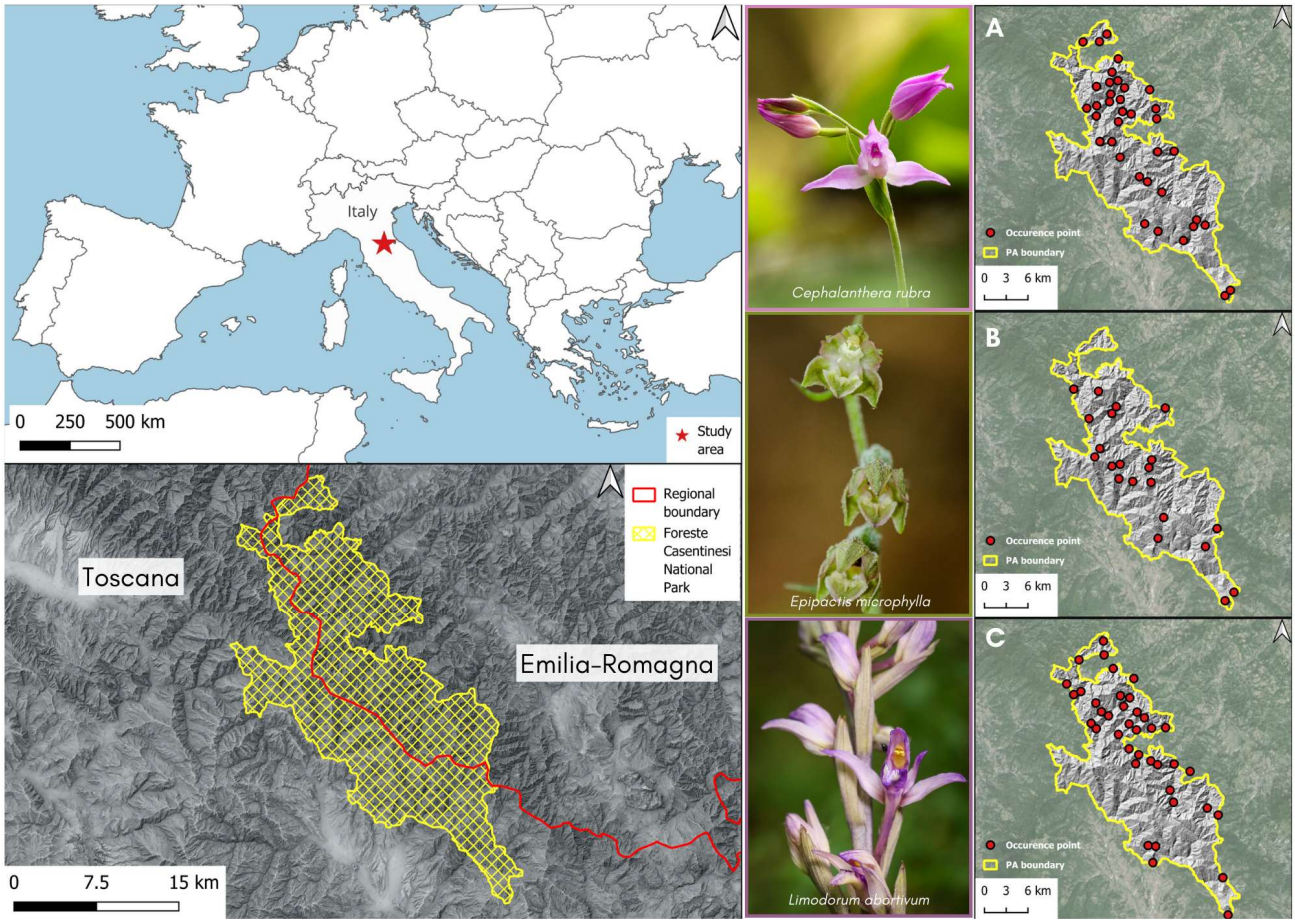


Figure 1. Study area (Foreste Casentinesi National Park, Northern Apennines) and reduced occurrence points of (**A**) *Cephalanthera rubra*, (**B**) *Epipactis microphylla* and (**C**) *Limodorum abortivum*.

Table 1. The environmental variables (EVs) involved in the process of predicting habitat suitability. Only the variables highlighted in bold were included in the final MaxEnt model and actively participated in the modelling process.

ID	Code	Variable Description	Unit
1	BIO1	Annual Mean Temperature	°C
2	BIO2	Mean Diurnal Range (Mean of monthly (max temp—min temp))	°C
3	BIO3	Isothermality (BIO2/BIO7) (×100)	%
4	**BIO4**	**Temperature Seasonality (standard deviation ×100)** [3]	**%**
5	BIO5	Max Temperature of Warmest Month	°C
6	BIO6	Min Temperature of Coldest Month	°C
7	BIO7	Temperature Annual Range (BIO5-BIO6)	°C
8	BIO8	Mean Temperature of Wettest Quarter	°C
9	BIO9	Mean Temperature of Driest Quarter	°C
10	BIO10	Mean Temperature of Warmest Quarter	°C
11	**BIO11**	**Mean Temperature of Coldest Quarter** [3]	**°C**

12	BIO12	Annual Precipitation	mm
13	BIO13	Precipitation of Wettest Month	mm
14	**BIO14**	**Precipitation of Driest Month** [2,3]	**mm**
15	**BIO15**	**Precipitation Seasonality (Coefficient of Variation)** [1,2]	**%**
16	BIO16	Precipitation of Wettest Quarter	mm
17	BIO17	Precipitation of Driest Quarter	mm
18	**BIO18**	**Precipitation of Warmest Quarter** [1]	**mm**
19	BIO19	Precipitation of Coldest Quarter	mm
20	LC01	Evergreen/Deciduous Needleleaf Trees	%
21	LC02	Evergreen Broadleaf Trees	%
22	LC03	Deciduous Broadleaf Trees	%
23	LC04	Mixed/Other Trees	%
24	LC05	Shrubs	%
25	LC06	Herbaceous Vegetation	%
26	LC07	Cultivated and Managed Vegetation	%
27	LC08	Regularly Flooded Vegetation	%
28	LC09	Urban/Built-up	%
29	LC10	Snow/Ice	%
30	**LC11**	**Barren** [3]	**%**
31	LC12	Open Water	%
32	**SOIL1**	**Bulk density of the fine earth fraction** [1,2,3]	**cg/cm³**
33	SOIL2	Cation Exchange Capacity of the soil	mmol(c)/kg
34	**SOIL3**	**Volumetric fraction of coarse fragments (>2 mm)** [1]	**cm³/dm³ (vol‰)**
35	**SOIL4**	**Proportion of clay particles (<0.002 mm) in the fine earth fraction** [2]	**g/kg**
36	SOIL5	Total nitrogen (N)	cg/kg
37	SOIL6	Soil pH	pHx10
38	SOIL7	Proportion of sand particles (>0.05 mm) in the fine earth fraction	g/kg
39	SOIL8	Proportion of silt particles (≥0.002 mm and ≤0.05 mm) in the fine earth fraction	g/kg
40	SOIL9	Soil organic carbon content in the fine earth fraction	dg/kg
41	SOIL10	Organic carbon density	hg/m³
42	SOIL11	Organic carbon stocks	t/ha
43	**SLP**	**Slope** [2]	**degree**
44	ELV	Elevation	meter
45	ASP	Aspect	degree
46	**CHP**	**Cumulative human pressure on the environment** [1]	

([1]) Variable used in the *C. rubra* model; ([2]) Variable used in the *E. microphylla* model; ([3]) Variable used in the *L. abortivum* model.

3.4.2. Model Optimization and Evaluation Results

The standard values of the MaxEnt software (RM = 1 and FC = LQHPT, where RM = regularization multipliers, FC = feature combinations, L = linear, Q = quadratic, H = hinge, P = product and T = threshold) employed in the initial screening phase of the model were modified to optimise the prediction results. The RM parameter was set to take values between 0.5 and 4, with increments of 0.5. This process yielded eight regularization multiplier values, which were associated with six combinations of one or more feature classes (L, LQ, H, LQH, LQHP, LQHPT). This resulted in a total of 48 parametric combinations that the model can take instead of the default parameters to test complexity. The optimal set of parameters was identified by selecting combinations with Akaike information criterion correction delta (ΔAICc) = 0. For *C. rubra*, the optimal parameters were FC = LQHPT and RM = 2.5; for *E. microphylla*, the optimal parameters were FC = L and RM = 0.5; for *L. abortivum*, the optimal parameters were FC = LQHP and RM = 2. The final distribution model built for *C. rubra* with its optimised parameters presents the values of Area Under Curve difference (AUC_{DIFF}) = 0.05 ± 0.06 and 10% training omission rate (OR_{10}) = 0.06; the final distribution model built for *E. microphylla* with its optimised parameters presents the values of AUC_{DIFF} = 0.05 ± 0.04 and OR_{10} = 0.06; the final distribution model built for *L. abortivum* with its optimised parameters presents the values of AUC_{DIFF} = 0.02 ± 0.03 and OR_{10} = 0.09. The accuracy and performance of the model were evaluated using the AUC training value (Figures S7–S9). For *C. rubra*, the value of AUC mean = 0.88 ± 0.03; for *E. microphylla*, the value of AUC mean = 0.91 ± 0.02; for *L. abortivum*, the value of AUC mean = 0.86 ± 0.02.

The Maximum Test Sensitivity Plus Specificity (MTSPS) value obtained from the final MaxEnt model for *C. rubra* was 0.4062. The probability (p) obtained from the model was used to classify the output as follows: unsuitability ($p < 0.4062$), low suitability ($0.4062 < p < 0.6041$), moderate suitability ($0.6041 < p < 0.8021$) and high suitability ($p > 0.8021$). The MTSPS value obtained from the final MaxEnt model for *E. microphylla* was 0.2683. The probability (p) obtained from the model was used to classify the output as follows: unsuitability ($p < 0.2683$), low suitability ($0.2683 < p < 0.5122$), moderate suitability ($0.5122 < p < 0.7561$) and high suitability ($p > 0.7561$). The MTSPS value obtained from the final MaxEnt model for *L. abortivum* was 0.6144. The probability (p) obtained from the model was used to classify the output as follows: unsuitability ($p < 0.6144$), low suitability ($0.6144 < p < 0.7429$), moderate suitability ($0.7429 < p < 0.8715$) and high suitability ($p > 0.8715$).

3.4.3. Contribution of Environmental Variables

The environmental variables influencing the distribution of each species are listed below, derived from the jackknife test applied to them (Figure 2). The higher the contribution, the greater the influence of that variable in the final prediction.

In *C. rubra*, the variables most influencing the distribution in the area, in terms of permutation importance, are the bulk density of the fine earth fraction (SOIL1), the precipitation of the warmest quarter (BIO18), the precipitation seasonality (BIO15), the cumulative human pressure on the environment (CHP) and the volumetric fraction of coarse fragments (SOIL3). Consequently, the variables in question exhibit a corresponding permutation importance in the distribution prediction of 35.5%, 25.2%, 18.5%, 11.4% and 9.5%. In terms of percent contribution to the model, the values are 34%, 24.7%, 8.1%, 27.4% and 5.8%, respectively (Table 2). In *E. microphylla*, the variables most influential in determining distribution in the area, as determined by permutation importance, are the bulk density of the fine earth fraction (SOIL1), the precipitation of the driest month (BIO14), the proportion of clay particles in the fine earth fraction (SOIL4), the slope (SLOPE) and the precipitation seasonality (BIO15). Consequently, the permutation importance of each variable is as follows: 46.6%, 19%, 17.6%, 12.5% and 10.4%. In terms of percent contribution to the model, the values are 45%, 18.3%, 21.4%, 8.6% and 6.7%, respectively (Table 2). Finally, in *L. abortivum*, the variables most influencing the distribution, according to permutation importance, are the temperature seasonality (BIO04), the precipitation of the driest month (BIO14), the bulk density of the fine earth fraction (SOIL1), the mean temperature of the coldest quarter (BIO11) and the barrenness (LC11). Consequently, the permutation importance of each variable is as follows: 39.5%, 35.2%, 17.7%, 6.7% and 1%. In terms of percent contribution to the model, the values are 30.2%, 32.5%, 28.9%, 7.4% and 1%, respectively (Table 2).

Table 2. Permutation importance and percent contribution values obtained from the modelling for each species.

Species	Environmental Variables (EV)	Permutation Importance (%)	Percent Contribution (%)
Cephalanthera rubra	SOIL1	35.5	34
	BIO18	25.2	24.7
	BIO15	18.5	8.1
	CHP	11.4	27.4
	SOIL3	9.5	5.8
Epipactis microphylla	SOIL1	46.6	45
	BIO14	19	18.3

	SOIL4	17.6	21.4
	SLOPE	12.5	8.6
	BIO15	10.4	6.7
	BIO04	39.5	30.2
	BIO14	35.2	32.5
Limodorum abortivum	SOIL1	17.7	28.9
	BIO11	6.7	7.4
	LC11	1	1

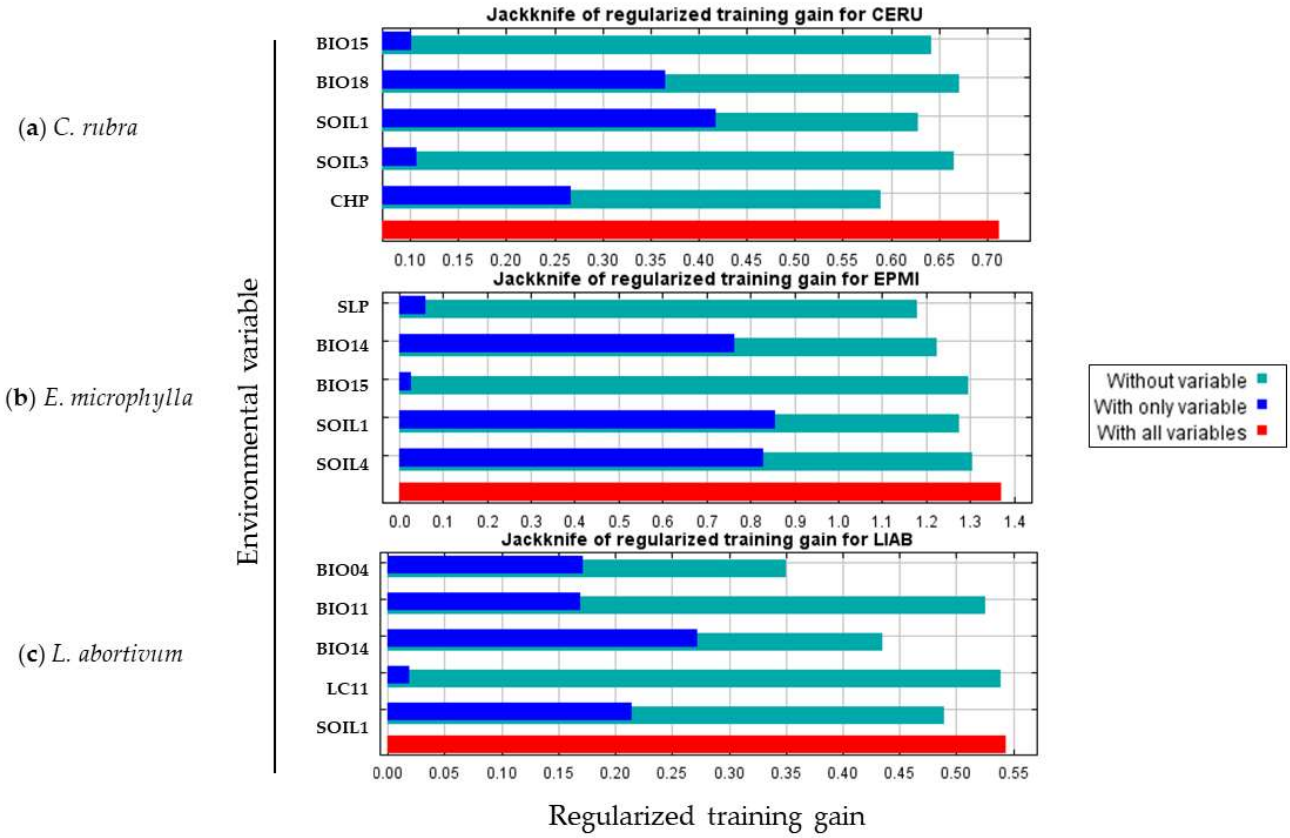


Figure 2. Jackknife of regularized training gain test for *C. rubra* (**a**), *E. microphylla* (**b**) and *L. abortivum* (**c**).

The five most influential variables in the final model for each species are presented below. For each variable, the range of suitable values for the presence of the investigated species was indicated, that is, the values associated with all areas classified as suitable for the species. In addition, the range of optimum values for the species was indicated, that is, only the values associated with the areas classified as high suitable. Furthermore, response curves for each environmental variable included in the final model were generated (Figures S4–S6).

In *C. rubra*, the precipitation seasonality (BIO15) value range was 23.64–32.56% and its optimum was 26.26–32.01%; precipitation of warmest quarter (BIO18) range was 222–273 mm and its

optimum was 232–268 mm; bulk density of the fine earth fraction (SOIL1) range was 83.30–102.81 cg/cm³ and its optimum was 83.30–96.96 cg/cm³; volumetric fraction of coarse fragments (SOIL3) range was 99.46–153.97 cm^3/dm^3 (vol‰) and its optimum was 111.37–148.68 cm^3/dm^3 (vol‰); cumulative human pressure on the environment (CHP) range was 3.00–18.75 and its optimum was 3.00–6.25.

In *E. microphylla*, the precipitation of driest month (BIO14) value range was 60–69 mm and its optimum was 63–69 mm; precipitation seasonality (BIO15) value range was 23.64–32.59% and its optimum was 23.64–31.44%; bulk density of the fine earth fraction (SOIL1) range was 83.30–98.33 cg/cm³ and its optimum was 83.30–91.43 cg/cm³; the proportion of clay particles within the fine earth fraction (SOIL4) value range was 188.77–317.77 g/kg and its optimum was 188.77–244.62 g/kg; slope (SLP) value range was 0.66–16.06 degree and its optimum was 1.43–10.03 degree.

In *L. abortivum*, the temperature seasonality (BIO04) value range was 637.23–665.20% and its optimum was 645.61–661.48%; mean temperature of coldest quarter (BIO11) value range was 1.58–3.77 °C and its optimum was 1.95–3.65 °C; precipitation of driest month (BIO14) value range was 60–68 mm and its optimum was 62–67 mm; land cover class barren (LC11) value range was 0–34% and its optimum was 0–12%; bulk density of the fine earth fraction (SOIL1) range was 83.68–102.81 cg/cm³ and its optimum was 83.68–95.07 cg/cm³.

3.4.4. Prediction of Potential Suitable Habitat Distribution under Current Climate Conditions

The calibrated and optimised MaxEnt prediction model was employed to predict the local distribution of habitats suitable for the presence of the investigated species under current climatic conditions (Figure 3). In *C. rubra* (Figure 3a), the estimated area occupied under current conditions by potentially suitable habitats is 315.28 km², which represents 76.3% of the total area analysed. With regard to the suitability of habitats for the species, the high suitability area covers 56.94 km², the moderate suitability area covers 113.89 km², and the low suitability area covers 144.44 km², respectively representing 13.78%, 27.56% and 34.96% of the total area. Finally, the area with habitats that are potentially unsuitable for the species is 97.92 km² (23.70% of the total) (Table 3). In *E. microphylla* (Figure 3b), the estimated area occupied under current conditions by potentially suitable habitats is 225.69 km² or 54.62% of the total area analysed. In terms of habitat suitability classes that could potentially host the species, the high suitability area covers 38.89 km², the moderate suitability area covers 79.17 km², and the low suitability area covers 107.64 km², respectively representing 9.41%, 19.16% and 26.05% of the total area. Finally, the area with potentially unsuitable habitats for the species is 187.50 km² (45.38% of the total) (Table 4). In *L. abortivum* (Figure 3c), the estimated area occupied under current conditions by potentially suitable

habitats is 217.36 km² or 52.61% of the total area analysed. About the habitat suitability classes for the species, the high suitability area covers 40.97 km², the moderate suitability area covers 82.64 km², and the low suitability area covers 93.75 km², respectively representing 9.92%, 20% and 22.69% of the total. Lastly, the area with potentially unsuitable habitats for the species is 195.83 km² (47.39% of the total) (Table 5).

Table 3. Classification of habitat suitability based on probability values obtained from the final MaxEnt model of *C. rubra*. The area is expressed in square kilometres (km²), with the percentage (%) referring to the total area studied. The percentage increase (% inc.) or decrease (% dec.) is expressed in positive (+) or negative (−) values in comparison to the total area currently occupied.

Time	Scenario	Unit	Tot.	Unsuitability	Low Suitability	Moderate Suitability	High Suitability
Present		km²	315.28	97.92	144.44	113.89	56.94
		%	76.30	23.70	34.96	27.56	13.78
2030s	SSP245	km²	140.28	272.92	85.42	46.53	8.33
		%	33.95	66.05	20.67	11.26	2.02
		% inc./dec.	−55.51	+178.72	−40.87	−59.15	−85.37
	SSP585	km²	294.44	118.75	166.67	81.25	46.53
		%	71.26	28.74	40.34	19.66	11.26
		% inc./dec.	−6.61	+21.28	+15.38	−28.66	−18.29
2050s	SSP245	km²	281.94	131.25	166.67	80.56	34.72
		%	68.24	31.76	40.34	19.50	8.40
		% inc./dec.	−10.57	+34.04	+15.38	−29.27	−39.02
	SSP585	km²	27.08	386.11	25.69	1.39	0.00
		%	6.55	93.45	6.22	0.34	0.00
		% inc./dec.	−91.41	+294.33	−82.21	−98.78	−100.00

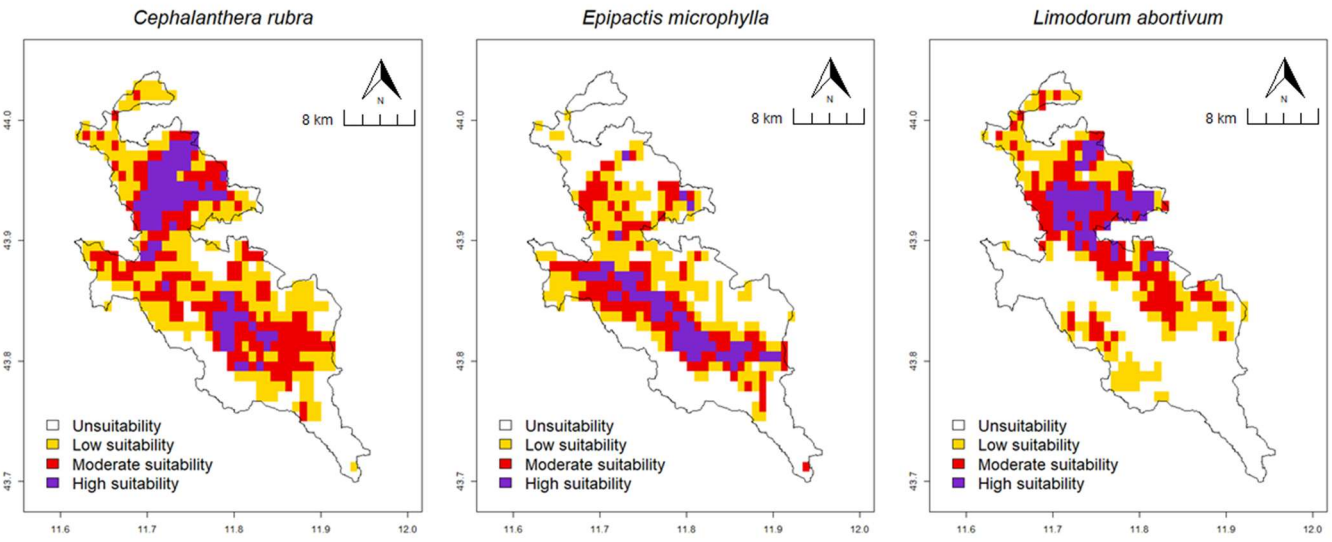
Table 4. Classification of habitat suitability based on probability values obtained from the final MaxEnt model of *E. microphylla*. The area is expressed in square kilometres (km²), with the percentage (%) referring to the total area studied. The percentage increase (% inc.) or decrease (% dec.) is expressed in positive (+) or negative (−) values in comparison to the total area currently occupied.

Time	Scenario	Unit	Tot.	Unsuitability	Low Suitability	Moderate Suitability	High Suitability
Present		km²	225.69	187.50	107.64	79.17	38.89
		%	54.62	45.38	26.05	19.16	9.41
2030s	SSP245	km²	144.44	268.75	97.92	37.50	9.03

		%	34.96	65.04	23.70	9.08	2.18
		% inc./dec.	−36.00	+43.33	−9.03	−52.63	−76.79
	SSP585	km²	198.61	214.58	115.97	64.58	18.06
		%	48.07	51.93	28.07	15.63	4.37
		% inc./dec.	−12.00	+14.44	+7.74	−18.42	−53.57
2050s	SSP245	km²	195.14	218.06	120.83	51.39	22.92
		%	47.23	52.77	29.24	12.44	5.55
		% inc./dec.	−13.54	+16.30	+12.26	−35.09	−41.07
	SSP585	km²	11.81	401.39	11.81	0.00	0.00
		%	2.86	97.14	2.86	0.00	0.00
		% inc./dec.	−94.77	+114.07	−89.03	−100.00	−100.00

Table 5. Classification of habitat suitability based on probability values obtained from the final MaxEnt model of *L. abortivum*. The area is expressed in square kilometres (km²), with the percentage (%) referring to the total area studied. The percentage increase (% inc.) or decrease (% dec.) is expressed in positive (+) or negative (−) values in comparison to the total area currently occupied.

Time	Scenario	Unit	Tot.	Unsuitability	Low Suitability	Moderate Suitability	High Suitability
Present		km²	217.36	195.83	93.75	82.64	40.97
		%	52.61	47.39	22.69	20.00	9.92
2030s	SSP245	km²	320.83	92.36	59.72	95.14	165.97
		%	77.65	22.35	14.45	23.03	40.17
		% inc./dec.	+47.60	−52.84	−36.30	+15.13	+305.08
	SSP585	km²	202.78	210.42	91.67	90.97	20.14
		%	49.08	50.92	22.18	22.02	4.87
		% inc./dec.	−6.71	+7.45	−2.22	+10.08	−50.85
2050s	SSP245	km²	309.03	104.17	75.69	100.69	132.64
		%	74.79	25.21	18.32	24.37	32.10
		% inc./dec.	+42.17	−46.81	−19.26	+21.85	+223.73
	SSP585	km²	79.17	334.03	70.83	8.33	0.00
		%	19.16	80.84	17.14	2.02	0.00
		% inc./dec.	−63.58	+70.57	−24.44	−89.92	−100.00



(a) *(b)* *(c)*

Figure 3. Prediction of potential suitable habitats distribution under current climate conditions elaborated by MaxEnt model: *C. rubra* (**a**), *E. microphylla* (**b**) and *L. abortivum* (**c**).

3.4.5. Prediction of Potential Suitable Habitat Distribution under Future Climate Conditions

The potential distribution of suitable habitats for hosting the three investigated species was estimated for two different scenarios (Shared Socioeconomic Pathways), SSP2 4.5 and SSP5 8.5 (referred below as SSP245 and SSP585) and for two future year intervals, i.e., 2021–2040 and 2041–2060, which are referred to as the 2030s and 2050s, respectively.

In *C. rubra* (Figure 4), the predicted area of habitats suitable for the species under the SSP245 scenario covers 140.28 km² for the 2030s and 281.94 km² for the 2050s, representing 33.95% and 68.24% of the total area, respectively. In the SSP585 scenario, the area of suitable habitat is 294.44 km² for the 2030s and 27.08 km² for the 2050s, representing 71.26% and 6.55% of the total area, respectively. A review of the habitat suitability classes for the SSP245 scenario reveals that the area is classified as follows: for the 2030s, 272.92 km² (66.05%) is unsuitable, 85.42 km² (20.67%) is low suitable, 46.53 km² (11. 26%) is moderate suitable and 8.33 km² (2.02%) is high suitable; for the 2050s, 131.25 km² (31.76%) is unsuitable, 166.67 km² (40.34%) is low suitable, 80.56 km² (19.50%) is moderate suitable and 34.72 km² (8.40%) is high suitable. For the SSP585 scenario area is classified as follows: for the 2030s, 118.75 km² (28.74%) is unsuitable, 166.67 km² (40.34%) is low suitable, 81.25 km² (19.66%) is moderately suitable and 46.53 km² (11. 26%) is high suitable; for 2050s, 386.11 km² (93.45%) is unsuitable, 25.69 km² (6.22%) is low suitable, 1.39 km² (0.34%) is moderate suitable and no area is classified as high suitable (Table 3).

In *E. microphylla* (Figure 5), the prediction of suitable habitats for the species covers an area of 144.44 km² for the SSP245 scenario in the 2030s and 195.14 km² for the 2050s, respectively representing 34.96% and 47.23% of the total area. For the SSP585 scenario, the suitable area is 198.61 km² for the 2030s and 11.81 km² for the 2050s, representing 48.07% and 2.86% of the total area, respectively. Further analysis of the habitat suitability classes for the SSP245 scenario reveals that the area is distributed as follows: for the 2030s, 268.75 km² (65.04%) is unsuitable, 97.92 km² (23.70%) is low suitable, 37.50 km² (9.08%) is moderately suitable and 9.03 km² (2.18%) is high suitable. The area is distributed as follows for the 2050s: 218.06 km² (52.77%) is unsuitable, 120.83 km² (29.24%) is low suitable, 51.39 km² (12.44%) is moderately suitable and 22.92 km² (5.55%) is high suitable. With regard to the SSP585 scenario, the surface area is distributed as follows: for the 2030s, 214.58 km² (51.93%) is unsuitable, 115.97 km² (28.07%) is low suitable, 64.58 km² (15.63%) is moderately suitable and 18.06 km² (4.37%) is high suitable. Finally, the area is distributed as follows for the 2050s: 401.39 km² (97.14%), is designated as unsuitable, 11.81 km² (2.86%) is classified as low suitable and no area is classified as moderate suitable or high suitable (Table 4).

In *L. abortivum* (Figure 6), the projected suitable habitat area for the species under the SSP245 scenario is 320.83 km² for the 2030s and 309.03 km² for the 2050s. This represents 77.65% and 74.79% of the total area, respectively. For the SSP585 scenario, the eligible area is 202.78 km² for the 2030s and 79.17 km² for the 2050s, respectively, representing 49.08% and 19.16% of the total area. Further analysis of the various habitat suitability classes for the SSP245 scenario reveals that the area is distributed as follows: for the 2030s, 92.36 km² (22.35%) is unsuitable, 59.72 km² (14.45%) is low suitable, 95.14 km² (23.03%) is moderately suitable and 165.97 km² (40.17%) is high suitable. For the 2050s, 104.17 km² (25.21%) is unsuitable, 75.69 km² (18.32%) is low suitable, 100.69 km² (24.37%) is moderately suitable and 132.64 km² (32.10%) is high suitable. The distribution of the area for the SSP585 scenario is as follows: for the 2030s, 210.42 km² (50.92%) is unsuitable, 91.67 km² (22.18%) is low suitable, 90.97 km² (22.02%) is moderately suitable and 20.14 km² (4.87%) is of high suitable. Finally, for the 2050s, 334.03 km² (80.84%) is unsuitable, 70.83 km² (17.14%) is low suitable, 8.33 km² (2.02%) is moderately suitable and no area is classified as highly suitable (Table 5).

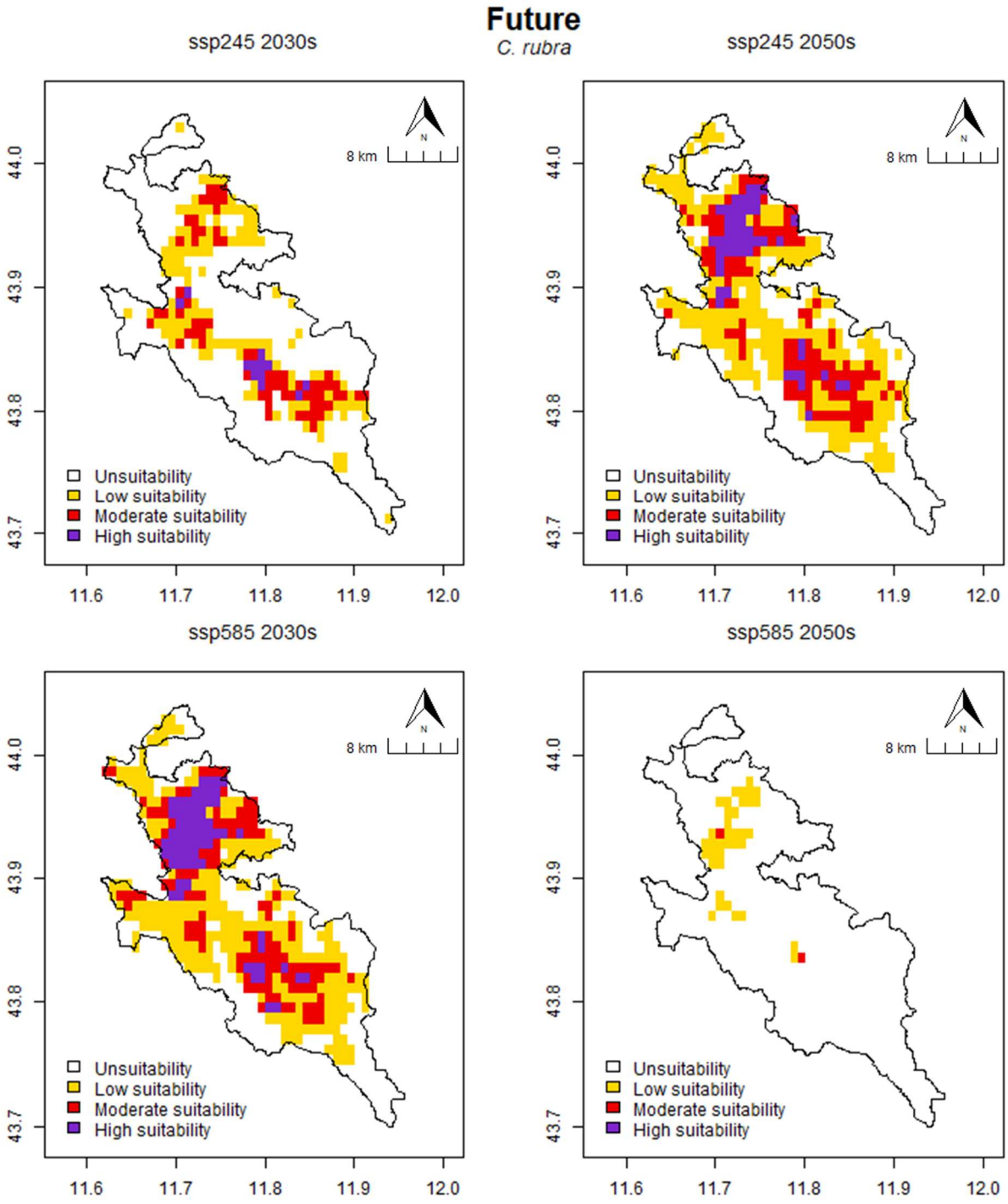


Figure 4. Prediction of potential suitable habitat distribution of *C. rubra* under future climate conditions.

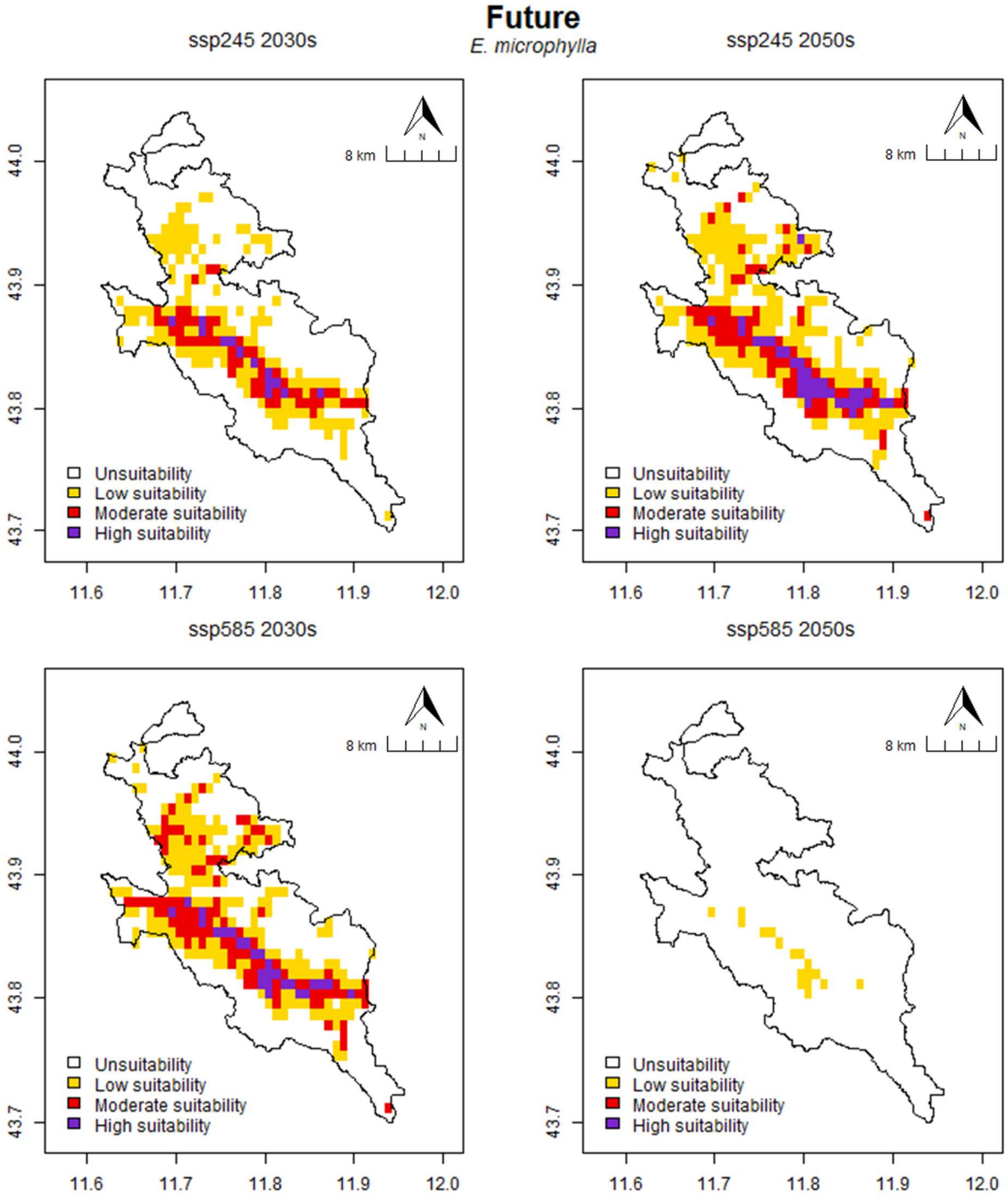


Figure 5. Prediction of potential suitable habitat distribution of *E. microphylla* under future climate conditions.

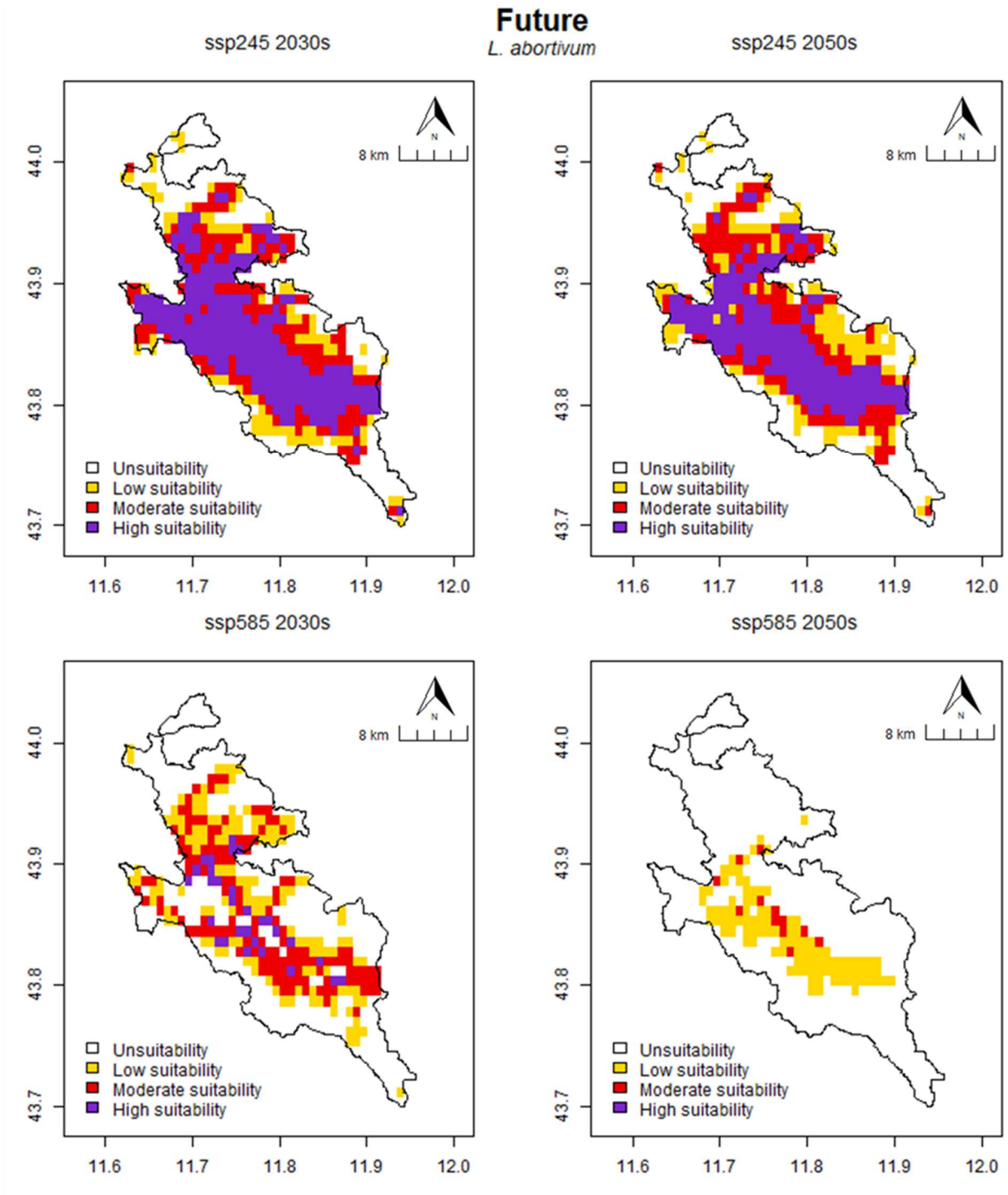


Figure 6. Prediction of potential suitable habitat distribution of *L. abortivum* under future climate conditions.

3.4.6. Distribution Changes under Future Climate Conditions

The future distribution range of each species is presented in three types of cell classes: loss, stable and gain. The loss class corresponds to the number of cells predicted to be lost, the stable class corresponds to the number of cells actually occupied and the gain class corresponds to the number of cells predicted to be gained in relation to the present distribution of each species. In addition, the percentage of cells currently occupied and predicted to be lost (Loss / (Loss + Stable)) is referred to as %Loss, while the percentage of cells predicted to be gained in comparison to the number of cells currently occupied (Gain / (Loss + Stable)) is designated as %Gain. The Species Range Change (SRC) is defined as the percentage of cells predicted to change (loss or gain) in comparison to the number of cells currently occupied (%Gain − %Loss). Finally, the Current Range Size (CRS) is the number of cells currently occupied.

In *C. rubra* (Figure 7), the CRS is 315.28 km² (454 cells). For the SSP245 scenario, in the 2030s, the area predicted to be lost is 175.00 km² (252 cells), the area predicted to be stable is 140.28 km² (202 cells), and no cells are predicted to be gained from the CRS. The percentage loss (%Loss), percentage gain (%Gain) and SRC are 55.51%, 0% and −55.51% respectively. For the 2050s, the occupied area predicted to be lost is 34.03 km² (49 cells), the stable area is 281.25 km² (405 cells) and the gained area is 0.69 km² (1 cell). The percentage loss, percentage gain and SRC are 10.79%, 0.22% and −10.57%, respectively. In the SSP585 scenario, the area predicted to be lost in the 2030s is 23.61 km² (34 cells), the area predicted to be stable is 291.67 km² (420 cells) and the area predicted to be gained is 2.78 km² (4 cells). The percentage loss, percentage gain, and SRC are 7.49%, 0.88%, and −6.61%, respectively. For the 2050s, the occupied area predicted to be lost is 288.19 km² (415 cells), the stable area is 27.08 km² (39 cells), and no cells are gained compared to the CRS. The percentage loss, percentage gain, and SRC are 91.41%, 0%, and −91.41%, respectively (Table 6).

In *E. microphylla* (Figure 8), the CRS is 225.69 km² (315 cells). For the SSP245 scenario, in the 2030s, the area predicted to be lost is 81.25 km² (117 cells), the area predicted to be stable is 144.44 km² (208 cells), and no cells are predicted to be gained from the CRS. The percentage loss (%Loss), percentage gain (%Gain) and SRC are 36.00%, 0% and −36.00% respectively. For the 2050s, the occupied area predicted to be lost is 30.56 km² (44 cells), the stable area is 195.14 km² (281 cells) and no cells were gained in comparison to the CRS. The percentage loss, percentage gain and SRC are 13.54%, 0% and −13.54% respectively. For the SSP585 scenario, for the 2030s, the occupied area predicted to be lost is 27.08 km² (39 cells), and the stable area is 198.61 km² (286 cells) while no cells are gained compared to the CRS. The percentage loss, percentage gain and SRC are 12.00%, 0% and −12.00% respectively. For the 2050s, the occupied area predicted to be lost is

213.89 km² (308 cells), the stable area is 11.81 km² (17 cells) and no cells were gained compared to the CRS. The percentage loss, percentage gain, and SRC are 94.77%, 0%, and −94.77%, respectively (Table 7).

In *L. abortivum* (Figure 9), the CRS is 217.36 km² (313 cells). For the SSP245 scenario, for the 2030s, the occupied area predicted to be lost is 41.67 km² (60 cells), the stable area is 175.69 km² (253 cells) and the gained area is 145.14 km² (209 cells). The percentage loss (%Loss), percentage gain (%Gain) and SRC are 19.17%, 66.77% and 47.60% respectively. For the 2050s, the occupied area predicted to be lost is 44.44 km² (64 cells), the stable area is 172.92 km² (249 cells) and the gained area is 136.11 km² (196 cells). The percentage loss, percentage gain and SRC are 20.45%, 62.62% and 42.17% respectively. For the SSP585 scenario, for the 2030s, the occupied area predicted to be lost is 105.56 km² (152 cells), the stable area is 111.81 km² (161 cells) and the gained area is 90.97 km² (131 cells). The percentage loss, percentage gain and SRC are 48.56%, 41.85% and −6.71% respectively. For the 2050s, the occupied area predicted to be lost is 206.25 km² (297 cells), the stable area is 11.11 km² (16 cells) and the gained area is 68.06 km² (98 cells). The percentage loss, percentage gain and SRC are 94.89%, 31.31% and −63.58% respectively (Table 8).

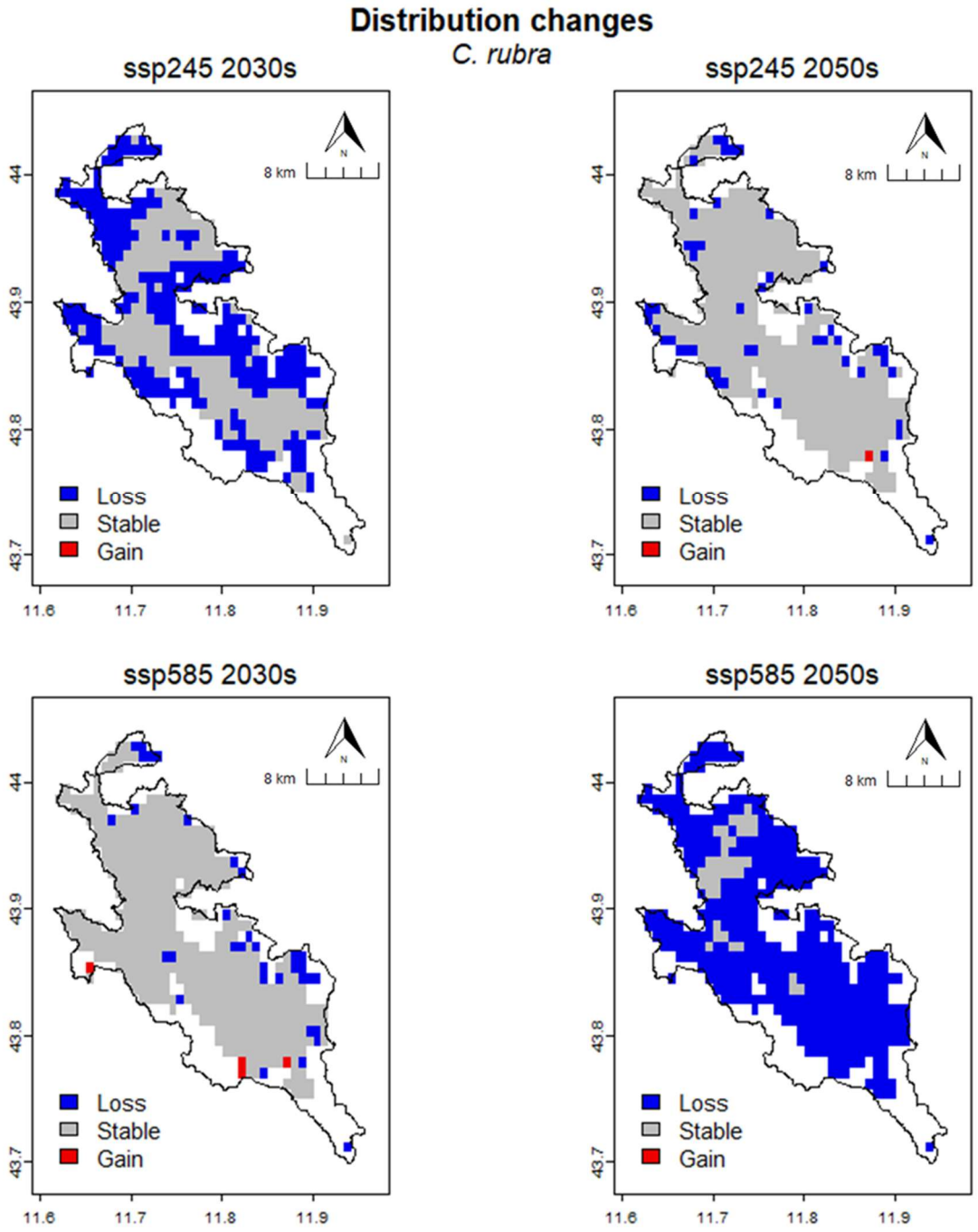


Figure 7. Spatial changing in habitat suitabilty for different climate scenarios in *C. rubra*.

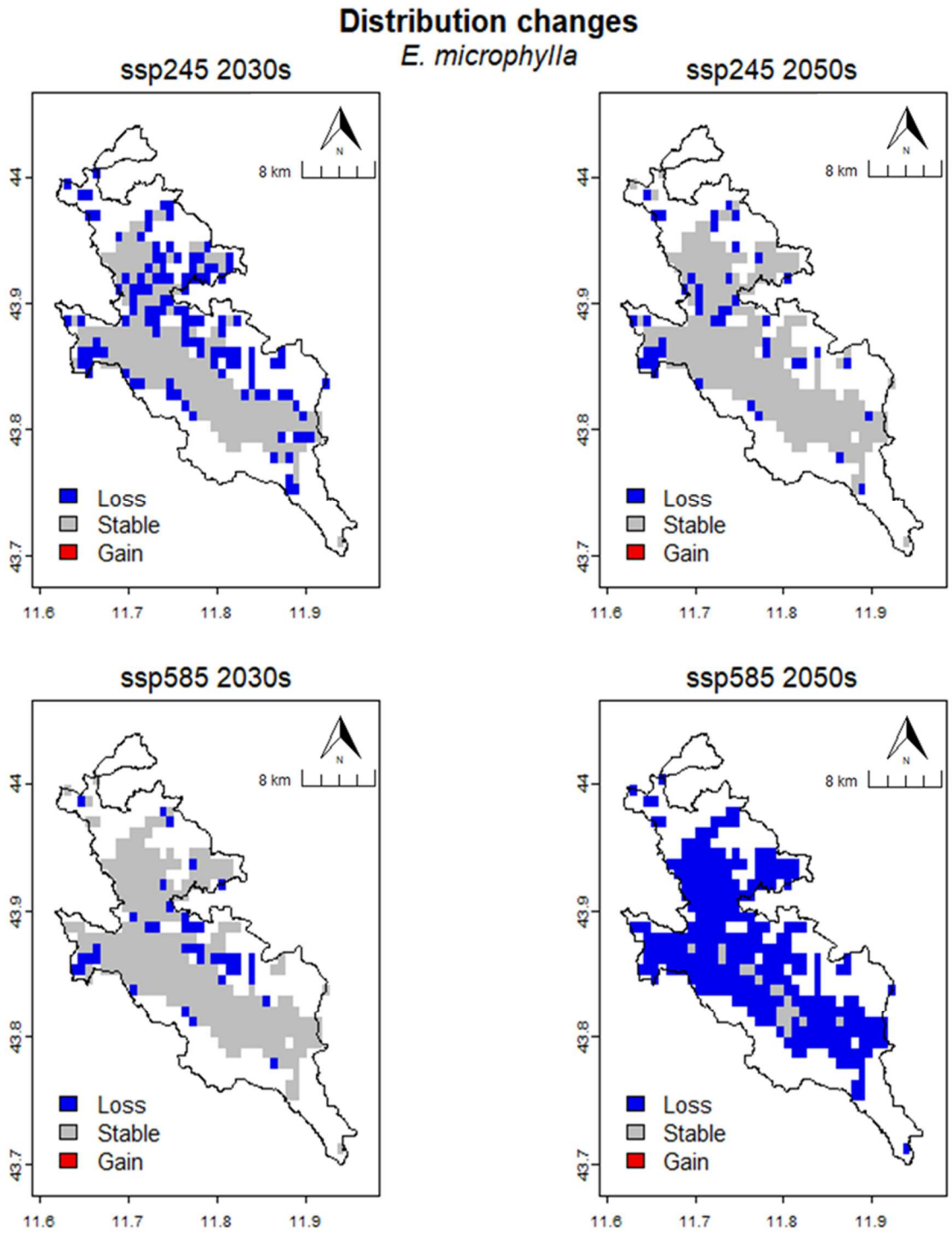


Figure 8. Spatial changing in habitat suitabilty for different climate scenarios in *E. microphylla*.

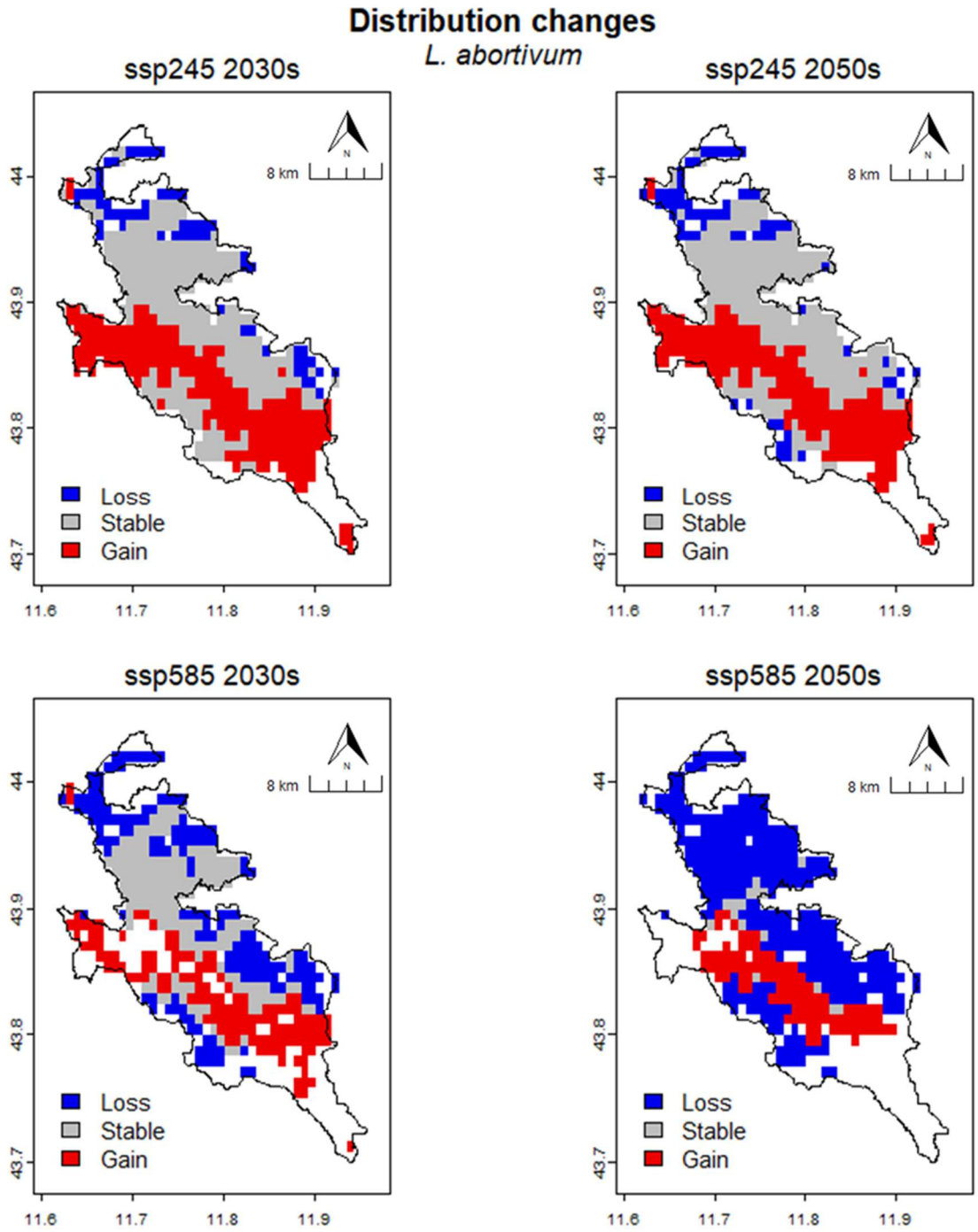


Figure 9. Spatial changing in habitat suitabilty for different climate scenarios in *L. abortivum*.

Table 6. Distribution area changes in *C. rubra* for different climate scenarios at two different periods.

Time	Scenario	Units	CRS	Loss	Stable	Gain	%Loss	%Gain	SRC
Present		cells	454						
		km²	315.28						
2030s	SSP245	cells		252	202	0	55.51	0.00	-55.51

		km²	175.00	140.28	0.00			
	SSP585	cells	34	420	4	7.49	0.88	-6.61
		km²	23.61	291.67	2.78			
2050s	SSP245	cells	49	405	1	10.79	0.22	-10.57
		km²	34.03	281.25	0.69			
	SSP585	cells	415	39	0	91.41	0.00	-91.41
		km²	288.19	27.08	0.00			

Table 7. Distribution area changes in *E. microphylla* for different climate scenarios at two different periods.

Time	Scenario	Units	CRS	Loss	Stable	Gain	% Loss	% Gain	SRC
Present		cells	325						
		km²	225.69						
2030s	SSP245	cells		117	208	0	36.00	0.00	-36.00
		km²		81.25	144.44	0.00			
	SSP585	cells		39	286	0	12.00	0.00	-12.00
		km²		27.08	198.61	0.00			
2050s	SSP245	cells		44	281	0	13.54	0.00	-13.54
		km²		30.56	195.14	0.00			
	SSP585	cells		308	17	0	94.77	0.00	-94.77
		km²		213.89	11.81	0.00			

Table 8. Distribution area changes in *L. abortivum* for different climate scenarios at two different periods.

Time	Scenario	Units	CRS	Loss	Stable	Gain	% Loss	% Gain	SRC
Present		cells	313						
		km²	217.36						
2030s	SSP245	cells		60	253	209	19.17	66.77	47.60
		km²		41.67	175.69	145.14			
	SSP585	cells		152	161	131	48.56	41.85	-6.71
		km²		105.56	111.81	90.97			
2050s	SSP245	cells		64	249	196	20.45	62.62	42.17
		km²		44.44	172.92	136.11			
	SSP585	cells		297	16	98	94.89	31.31	-63.58
		km²		206.25	11.11	68.06			

3.5. Discussion

The model performance and accuracy evaluation yielded satisfactory results. The AUC_{DIFF} and OR_{10} values for the three species were below the threshold values indicated by other studies [80,81]. This indicates that the models developed are not subject to overfitting. The model's accuracy, as assessed by the AUC value of the ROC (Figures S7–S9), can be considered good for *C. rubra* (0.88 ± 0.03) and *L. abortivum* (0.86 ± 0.02) and excellent for *E. microphylla* (0.91 ± 0.02) [82–84]. When considering the distribution of the three potential suitable habitats under current climate conditions, it can be observed that the largest potential suitable area in terms of extent is that of *C. rubra* (315.28 km²), followed by *E. microphylla* (225.69 km²) and *L. abortivum* (217.36 km²), which have similar values. Furthermore, when considering each of the three suitability classes, *C. rubra* exhibits the highest area values. In contrast, *E. microphylla* exhibits higher values of suitable surface area exclusively within the low suitability class, in comparison to *L. abortivum*. The current potential distribution of the three species exhibits distinct patterns. In *E. microphylla*, the highly suitable area is concentrated on the Apennine ridge line, specifically at the higher altitudes of the PA. Conversely, in *L. abortivum*, the areas of highest suitability are concentrated in the lower altitudes of the northern and north-eastern portion of the PA, with some disjunct occupied cells (low suitability and moderate suitability) in the south-western slope. The areas suitable for the presence of *C. rubra* exhibit a more homogeneous distribution throughout the PA, with two distinct high-suitability cores. The largest of these is located in the north-northeast portion of the PA, while the other is situated in the central area of the PA at higher altitudes. The analysis of the individual variables influencing the distribution of the three species in the area under consideration revealed a greater involvement of the variables associated with precipitation (BIO04, BIO11, BIO14, BIO15, BIO18) and the variables associated with the soil (SOIL1, SOIL3, SOIL4). The bulk density of the fine earth fraction (SOIL1) was found to be present in all three species, influencing their distribution. The jackknife test in *C. rubra* and *E. microphylla* shows that this variable contributes most to the model when used in isolation (dark blue bar). The values of this variable range from a minimum of 83.30 cg/cm³ to a maximum of 102.81 cg/cm³. The optimal values for each species are situated within this range and exhibit minimal variation, with *C. rubra* exhibiting the highest optimal value (96.96 cg/cm³) in comparison to the other two species. The bulk density of the soil is dependent upon the presence of soil pores and soil moisture, both of which are fundamental for the presence of orchids [4]. Precipitation seasonality (BIO15) represents one of the climatic variables influencing the distribution of habitats suitable for *C. rubra* and *E. microphylla*. This variable is frequently correlated with the distribution of orchids [85] and can affect their presence in different ways by acting as a limiting factor to their survival. For example, it has been demonstrated that

summer rainfall in rare forest species at the southern limit of their distribution [86] and the slope of the terrain [87] can both exert a significant influence on the distribution of these species. The two species exhibit partial ecological requirements in the study area. The jackknife test with the variable alone indicates that it makes the least contribution to the models of the two species. In *C. rubra*, the precipitation of the warmest quarter (BIO18) value has a strong influence on the distribution. The response curve explains how low precipitation values in the warmer months proportionally limit the probability of suitable habitats. This variable also correlates with the continental distribution of orchids [85], thereby reinforcing the importance of precipitation as a limiting factor [86]. Furthermore, the volumetric fraction of coarse fragments (SOIL3) and the cumulative human pressure on the environment (CHP) also exert a partial influence on the distribution. In the former variable, there is an increase in probability that is proportional to the increase in the fraction of coarse fragments; in the latter, the probability decreases rapidly with increasing human pressure. In *E. microphylla*, the precipitation of the driest month (BIO14) and the proportion of clay particles (0.002 mm) within the fine earth fraction (SOIL4) were found to be very influential factors in determining the distribution. The precipitation of the driest month (BIO14) is an important climatic variable that appears to be related to the distribution of orchids [85]. According to Djordjević and Tsiftsis [4], soil texture can influence moisture content through its retaining capacity. However, there is a lack of studies on orchids [4]. The response curves (Figure S5) indicate that the limiting factor is the low precipitation values in the driest month, and, conversely, the high clay content in the fine earth fraction. The distribution of *L. abortivum* appears to be most effectively explained by temperature seasonality (BIO04) and precipitation of the driest month (BIO14). Temperature seasonality appears to be among the environmental variables most frequently associated with the spread of orchids across the globe [88,89]. Additionally, the mean temperature of the coldest quarter (BIO11) exerts an influence on the distribution of *L. abortivum*. Upon examination of the BIO11 response curve (Figure S6), it can be observed that an increase in the mean temperature value during winter is associated with a net decrease in the probability value of the presence of suitable habitats, acting as a limiting factor.

The results indicate that habitats with the potential to host the studied species under future climate conditions are likely to be significantly impacted. The scenario with the greatest loss of suitable habitat, in terms of area, is the SSP585 in the 2050s, with a loss of suitable area of 288.19 km^2 in *C. rubra*, 213.89 km^2 in *E. microphylla* and 206.25 km^2 in *L. abortivum*. In all three cases, the percentage of lost area exceeded 90%. This trend has been observed worldwide and in Europe for both terrestrial and epiphytic orchids [90], as well as for other plant species [91], although in many cases it seems to have positive effects, leading to an expansion of the range suitable for the species

[92,93]. Furthermore, there is a clear distinction in the potentially suitable area of *L. abortivum*, which is the only species in which the habitats suitable for it in that climatic situation appear to shift towards the ridge areas with higher altitudes. In particular, the 98 cells (68.06 km²) gained in comparison to the current distribution are located in the ridge areas. The upward altitudinal shift of the area potentially occupied by suitable habitats for *L. abortivum* is on average 331 m compared to the mean altitude occupied by suitable areas under current climatic conditions. In this case, the suitable areas will be distributed between 939 m and 1420 m a.s.l. Altitudinal shifting is a frequent dynamic in previous literature, and a considerable number of studies have documented altitudinal shifting of suitable habitats [94–97], with some shifting to higher altitudes [90] and others to lower altitudes than the original distribution [83]. A comparison of the values of area lost and gained reveals a similar dynamic for *C. rubra* and *E. microphylla*. The scenario with the least area lost is SSP585 2030s, with 7.49% and 12.00% of cells lost, respectively. In both cases, the percentage of area gained is below 1%. Similarly, for the SSP245 2050s scenario, the values of the area lost are comparable to those observed in the SSP585 2030s scenario, although slightly higher (10.79% and 13.54%). The intermediate values of the area lost in the SSP245 2030s scenario for *C. rubra* and *E. microphylla* are 55.51% and 36.00% respectively. In contrast, the SSP245 2030s scenario for *L. abortivum* represents the optimal outcome, with the highest value of suitable habitat area gained (145.14 km²) and the lowest loss of occupied area (41.67 km²). This increase for the SSP245 scenario has also been verified in other studies [83,98,99]. In this case, the Species Range Change (SRC) is the highest (47.60) compared to all other scenarios. The SSP585 2030s and SSP245 2050s scenarios for *L. abortivum* species present an intermediate situation. In the SSP245 2050s scenario, the area of suitable habitat lost and gained in comparison to the current conditions is comparable to that of the SSP245 2030s scenario, although with a higher percentage of area lost (20.45%) in contrast to a lower value of area gained (62.62%). In the SSP585 2030s scenario, the values of lost and gained area are almost equivalent, with a negative SRC value of -6.71. In consideration of the SSP245 scenario, there is a widening of the area suitable for *L. abortivum*, accompanied by a shift towards higher altitudes for both the 2030s and 2050s. In the SSP585 scenario, there is a habitat reduction at lower altitudes in both the 2030s and 2050s that is suitable for *L. abortivum*, with a shift towards higher altitude areas. In contrast to other myxotrophic species, which appear to be less susceptible to global warming, the reduction of the suitable climatic niche for this species was also identified in other studies [100,101]. In *C. rubra* and *E. microphylla*, it is observed that the greatest stability of area occupied by suitable habitats occurs in SSP245 2050s and SSP585 2030s, while for the remaining scenarios, the area suitable for the species is intensely reduced. The expansion of the distribution range of *L. abortivum*, as observed in other Mediterranean orchid species (e.g., *Orchis*

anthropophora (L.) All., *O. purpurea* Huds. and *O. simia* Lam.), has been documented in conjunction with the contraction of the distribution range of *C. rubra* and *E. microphylla*, which are continental species (e.g., *Orchis militaris* L.) [76]. In contrast, studies have demonstrated that forest orchids do not experience a significant shift in their elevational distribution due to climate change [61,94]. The results of the present study provide partial confirmation of this hypothesis. In the continental species *C. rubra* and *E. microphylla*, there is a progressive reduction in suitable areas, rather than a shift towards higher altitudes, as is the case in *L. abortivum*. According to Jakubska-Busse et al. [102], the disappearance of occurrence sites of the genus *Cephalanthera* (including *C. rubra*) along the altitudinal gradient in Lower Silesia (SW Poland) is not due to recent climatic changes, but rather to the change in land use at the beginning of the 20th century. Similarly, for European *Epipactis* (including *E. microphylla*), environmental variables such as bedrock and land cover type appear to be more important than climatic variables alone in the prediction of distribution [103].

Habitat Suitability Models (HSMs) represent a valuable tool for species conservation, offering the potential to inform the planning of habitat and species protection actions [104,105]. Although they are typically employed to model the distribution of species at a large scale [106], the utilisation of HSMs for the conservation of threatened species is also possible at a fine scale [107], for instance, within protected areas (PAs). In the specific case of this study, the application of habitat suitability modelling in a PA in the Northern Apennines has demonstrated that fine-scale application can yield useful results for the conservation of plant species. The initial outcome demonstrates the suitability of ridge habitats for orchids in mesophilic environments (*C. rubra* and *E. microphylla*), which are already partially occupied by these species under the prevailing climatic conditions. Given the climate scenarios identified in the different cases, it is imperative that these areas are given the highest level of protection within the PA boundaries. This can be achieved through the establishment of new fully PAs or the modification of existing ones. The second result is similarly related to areas located at high altitudes, although in a different way. For thermophilic species, such as *L. abortivum*, these areas could serve as both expansion and refuge sites, where future conditions of suitability for the habitats to which the species are linked are envisaged. Consequently, these areas should be included in the planned conservation and protection plans for plant and animal species, and their protection should be a priority. The existing literature has demonstrated that climate change represents a significant threat to European conservation areas, necessitating the development of new protection policies [108]. In Italy, some studies have been conducted [35,109–111], and further analysis could be carried out in the future with the application of prioritisation

tools (e.g., Marxan tool) within the boundaries of the PAs, to identify the areas that require protection in response to the new climate challenges [112,113].

3.6. Materials and Methods

3.6.1. Study Area

The Foreste Casentinesi, Monte Falterona and Campigna National Park (Figure 1) is a protected area (PA) situated in the Northern Apennines, specifically in the Tuscan-Romagna Apennines, on the border between the regions of Emilia-Romagna and Tuscany, straddling the provinces of Forlì-Cesena, Arezzo and Firenze. The PA encompasses an area of 36,400 hectares. One of the defining characteristics of the PA is the Apennine ridge, which runs north-west to south-east and divides the territory into two main slopes. The ridge's highest altitudes are reached at the summits of Mount Falco (1657 m a.s.l.) and Mount Falterona (1654 m a.s.l.). The geology of the Romagna slope is characterised by sandstones and arenaceous marls (Middle-lower Miocene); in contrast, the Tuscan slope is dominated by sandstones and arenaceous marls (sometimes turbiditic) (Palaeogene) units [114]. A dividing feature between the two slopes is a belt of clays, limestones and clays (turbiditic) (Palaeogene) formations, which runs along the ridge in the central area [114]. Two additional areas of interest can be identified on the Tuscan slope. The first one is located at the southern border of the Park at La Verna, where skeletal limestones and calcarenites (Middle-lower Miocene) are present; the second one is situated between the localities of Moggiona and Camaldoli, where marls are found, occasionally containing pelagic facies chert (Middle-lower Miocene) [114]. The Park is situated in a temperate macrobioclimate and temperate oceanic bioclimate, exhibiting a weak Euroceanic subtype on the two sides, both the Tyrrhenian and the Adriatic; in contrast, the ridge area displays a semi-continental weak subtype [115]. The area can be divided into two different ombrotypes, namely a semi-arid lower horizon on the two sides and a semiarid upper horizon in the ridge area [115]. In terms of thermotype, three different classifications can be identified: supratemperate lower horizon for the lower areas of the two sides, supratemperate upper horizon for the central area that rises up to the ridge, and a third thermotype, orotemperate lower horizon, at the two highest peaks of the Park [115].

3.6.2. Species Occurrence Data

Target species occurrence data were obtained by the Foreste Casentinesi National Park Orchids Database [67]. Records are collected from 2000 to 2023; they include species occurrences from field research carried out in the PA territory, records collected by citizen science projects and data from bibliographic research [67]. Geographic coordinates are associated with each species

occurrence collected in the field (datum: WGS84). The datasets were analysed by QGIS 3.32.3 software [116], R software [117] and RStudio [118]. To be used in the model, occurrence points were prepared through the following steps: duplicate records were removed first; then, records falling outside the boundary of the PA were identified and removed; finally, spatial thinning (or filtering) was applied using the R package *spThin* [119] to reduce spatial autocorrelation [120,121]. Although the redundancy of records is automatically reduced by MaxEnt algorithms which remove excess occurrence points leaving only one record for every single cell [81] the reduction of autocorrelation of spatial data from sampling error through specific methodologies can significantly improve the quality of ecological distribution models [122–124]. The distance used as the thinning parameter (thin.par) is 1 km, which is larger than the reference grid cell size (≃ 1 km).

3.6.3. Environmental Variables

To develop the distribution models, the environmental variables that most influence the global distribution of plant species were considered [125]. Specifically, climatic, edaphic, topographic, anthropic and land cover variables were used. Bioclimatic variables (BIO1-BIO19) and elevation (ELV) were obtained from the WorldClim2.1 climate database [126]. The variables Slope (SLP) and Aspect (ASP) were extracted with the QGIS 3.32.3 software [116] starting from elevation data. In total, there are 3 topographic variables. The land cover variables (LC1-LC12) were obtained from the EarthEnv Global 1-km Consensus Land Cover database [127]. The anthropic impact variable (CHP) was obtained from the Last of the Wild Project, Version 3 (LWP-3): 2009 Human Footprint, 2018 Release database [128,129]. The edaphic variables (SOIL1-SOIL11) were obtained from the ISRIC SoilGrids250m 2.0 database and are referred to a depth of 0–5 cm of soil [130,131]. In total 46 ecological variables were used, at a spatial resolution of 30 arc-seconds (usually referred to as '1-km' spatial resolution) which corresponds to a surface of ≃ 0.86 km^2 at the equator [126].

One of the main problems of species distribution models is the choice of environmental variables to include in the model. This is because collinearity exists between environmental variables and this can very negatively influence the quality of the model in various ways [132,133]. As a result, it is essential to test multicollinearity between environmental variables with appropriate statistical analyses to avoid this [134,135]. In this work, the analyses were carried out using the software R [117], R studio [118] and Past 4.04 [136]. The workflow used to identify the best environmental variables among those identified was taken up and integrated based on other studies [120,137] and consists of several sequential steps listed below:

Data matrixes creation: using the QGIS 3.32.3 software [116] we combined each species occurrence record with the spatial value of the corresponding attribute for the 46 variables, i.e., the cell value of

the environmental variable in which the occurrence point falls. A matrix for all investigated species was obtained.

EV screening and ranking: A preliminary modelling exercise was initiated utilising MaxEnt to identify the number and nature of environmental variables influencing the model. The initial model was constructed by applying the default 'Auto features' setting (default FC and RM settings) and then three replicate runs were initiated. The mean value of permutation importance for each of the variables included in the model in the three runs was then obtained [138]. The jackknife test [139] was applied to assess the significance of each environmental variable in elucidating the distribution of a species within the MaxEnt model. This enables the assessment of the impact of predictors on the model performance in terms of gain. Variables that lead to a reduction in gain when excluded are considered more important during the modelling process. The light blue bars indicate the impact on the model when the single variable is not included, the dark blue bars indicate the impact with only the variable included, and the red bar indicates the inclusion of all variables. Following, a ranking of the variables was established according to their permutation importance in the model. The use of permutation importance over percent contribution is preferable because it depends on the final model, not on the path used for each run, and this is better for correctly assessing the importance of each variable [140,141]. Furthermore, we decided to directly eliminate variables with a small contribution rate to the model, as this was deemed to be too low [141–143]. Variables with a contribution rate of less than 1% were removed [144,145].

Multicollinearity test #1: Pearson correlation coefficient (r) between each pair of environmental variables was calculated using Past 4.04 software [136]. If $|r| \geq 0.8$ [135,145–148] there is a correlation between the variables and one of the two must be excluded. Based on the permutation importance rank, in the screening and ranking phase, the variable with the greatest contribution for the model was retained while the second was discarded. This operation was performed for each pair of environmental variables.

Multicollinearity test #2: to further reduce the multicollinearity between the environmental variables selected by the first multicollinearity test, Variance Inflation Factor (VIF), was calculated with the R package *usdm* [149]. A precautionary threshold was chosen at 5. Variables with VIF > 5 were excluded because they were strongly correlated with each other [84,135,150,151].

Final environmental dataset: finally, variables that respect both multicollinearity conditions tests ($|r| \leq 0.8$ and VIF < 5) were chosen as final predictors. From these, based on the ranking obtained in the screening and ranking phase, the top five variables contributing to the model were selected, sorted according to permutation importance values. These variables, five for each species, are used to build the final models.

In addition to investigating habitat suitability for current climatic conditions, the study focuses on identifying the most suitable habitats for changing climatic conditions in the near future. To do this, we used bioclimatic data (BIO1-BIO19) referring to the future, i.e., 2030s (average values from 2021 to 2040) and 2050s (average values from 2041 to 2060). These data, as for the current conditions (1970–2000), were obtained from the WorldClim2.1 climate database [126]. For each future period, we selected two Shared Socioeconomic Pathways (SSPs), SSP2-4.5 "Middle of the road", and SSP5-8.5 "Taking the Highway" developed within the Panel on Climate Change (IPCC) and used in the Coupled Model Intercomparison Project Phase 6 (CMIP6) to estimate future climate change [152]. The Global Climate Model (GCM) from which the scenarios were selected is the CMCC-ESM2 of the Euro-Mediterranean Center on Climate Change [153,154]. Each Shared Socio-economic Pathway [155] is associated with a narrative [156,157] that describes socioeconomic change for the future with demographic, economic, energy, land use and greenhouse gas and air pollutant emissions drivers, developed by models [158–160]. The SSP2-4.5 estimate is based on intermediate greenhouse gas (GHG) emissions with CO_2 emissions around current levels until 2050, after which they are projected to fall but not reach net zero by 2100 [152,161]. Conversely, SSP5-8.5 predict very high GHG emissions with CO_2 emissions tripling by 2075 [152,161]. The estimated warming for the 2041–2060 and 2081–2100 periods in these scenarios is 2.0 °C and 2.7 °C for the SSP2-4.5 scenario and 2.4 °C and 4.4 °C for SSP5-8.5, respectively, with a likely range in 2081–2100 of 2.1 °C–3.5 °C for SSP2 4.5 and 3.3 °C–5.7 °C for SSP5 8.5 [152,162]. This paper assumes that all other variables in the MaxEnt model, except the 19 climate variables, will not change in future years [137].

3.6.4. Final Model Construction, Optimization and Evaluation

MaxEnt software version 3.4.4 [163,164] was used to predict the habitat suitability of the three species reported in this work. In the models, 75% of the occurrence data was randomly selected and used as a model training set, while the remaining 25% was used as a model validation set. We have set the modelling parameters in the settings panel as follows: maximum number of iterations set to 500, 'Bootstrap' replication method and 10 model replications. Furthermore, the response curve and jackknife test parameters have been enabled to analyse the effects and contribution of each environmental variable. We left the convergence threshold to the default value (1×10^{-5}). The output format chosen is cloglog (complementary log-log). The use of default parameters in MaxEnt models, although applied in many studies, can lead to overfitting problems and the production of over-complex or over-simplistic models [165–167]. To avoid these problems, we used the R package *ENMeval* [168,169] to adjust two parameters of the MaxEnt model, namely regularization

multipliers (RM) and feature combinations (FC). By default, these parameters are set by MaxEnt as RM = 1 and as FC = LQHPT where L = linear, Q = quadratic, H = hinge, P = product and T = threshold. These parameters can be adjusted to achieve a more refined model [81,170] and this has been done through the use of ENMeval metrics. The best set of combinations of the RM and FC parameters was identified based on the Akaike information criterion correction (AICc). The lowest value of the AICc delta (ΔAICc = 0) calculated by *ENMeval* identifies better parameters value [82,145,171] and corresponds to the best model in terms of goodness-of-fit and complexity [168,172]. The degree of overfitting of the model can be effectively quantified through the comparison of two other ENMeval metrics: the difference between the AUC training and AUC testing value ($AUC_{DIFF} = AUC_{TRAIN}—AUC_{TEST}$) and the 10% training omission rate (OR_{10}) [82,83,168]. High values of AUC_{DIFF} and $OR_{10} > 0.1$ indicate overfitting of the models [80,81]. Finally, the accuracy of the model was evaluated using the Receiver Operating Characteristic (ROC) curves and the area under the ROC curve or AUC values (Area Under Curve), a method widely used in predicting habitat suitability using the MaxEnt algorithm [173,174]. The AUC value has a range from 0.5 to 1, where 0.5 indicates that the model does not predict better than a random distribution. The higher the value, the better the model prediction and the greater the correlation between the presence of the species and the environmental characteristics. Based on the AUC value, the forecast is classified as fail or inadequate (0.5–0.6), poor (0.6–0.7), reasonable or fair (0.7–0.8), good (0.8–0.9), perfect or excellent (0.9–1.0) [82–84].

3.6.5. Habitat Suitability Analysis and Visualization

MaxEnt model chosen for each of the analysed species, under current and future conditions were imported into QGIS [116], R [117] and Rstudio [118]. MaxEnt generates cartography where each cell is associated with a suitability index that ranges from 0 to 1. For low values, there are minimal probabilities of finding suitable habitats, while for high values, the probabilities increase [40,175]. In order to effectively discriminate the areas classifiable as unsuitable and suitable, the average value of the Maximum Test Sensitivity Plus Specificity (MTSPS) was applied as a threshold [120,176–178]. It has been demonstrated that this threshold leads to effective results in models based on presence data only [179–181]. The MaxEnt outputs were therefore reclassified based on the probability (p) of habitat suitability occurrence. For probability values below the MTSPS threshold ($p <$ MTSPS), the output was classified as unsuitable for the species. Conversely, for probability values above the MTSPS threshold ($p >$ MTSPS), the output was further classified into three suitability classes at equal size intervals [144,182,183]: low suitability, moderate suitability and high suitability [120,147,171]. Furthermore, the outputs were reclassified using the

presence/absence (1/0) format of suitable habitats using the MTSPS threshold. With the R package *biomod2* [184,185] the range change between current and future models was calculated [171,186].

Author Contributions

Conceptualization, A.P.; methodology, A.P.; software, A.P.; validation, A.P., D.V. and S.M.; formal analysis, A.P.; investigation, A.P.; data curation, A.P. and D.V.; writing—original draft preparation, A.P.; writing—review and editing, A.P., D.V. and S.M.; visualization, A.P. and D.V.; supervision, S.M. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement

All data necessary to replicate this study's results are included in this published article (and its Supplementary Materials). Raw data are available upon request.

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Conflicts of Interest

The authors declare no conflicts of interest.

3.7. Supplementary materials

	Cephalanthera rubra		*Epipactis microphylla*		*Limodorum abortivum*	
ID	**Long**	**Lat**	**Long**	**Lat**	**Long**	**Lat**
1	11,708245	43,891257	11,708245	43,891257	11,795190	43,925821
2	11,747015	43,958646	11,687583	43,927517	11,755750	43,961867
3	11,721036	43,964506	11,932549	43,710116	11,926903	43,746414
4	11,724476	43,977175	11,797805	43,879971	11,691217	43,928833
5	11,735129	43,966953	11,733523	43,943719	11,757908	43,899523
6	11,672503	44,012987	11,726421	43,935071	11,782292	43,938181
7	11,698705	43,958796	11,798249	43,852197	11,837736	43,836313
8	11,734158	43,993957	11,701975	43,961639	11,769201	43,944752
9	11,790129	43,957477	11,659354	43,963103	11,739502	43,963928
10	11,728818	43,891687	11,793537	43,870236	11,830902	43,850867
11	11,712980	44,023697	11,947150	43,720962	11,671432	43,967220
12	11,894184	43,793517	11,895576	43,775788	11,659354	43,963103
13	11,778444	43,849949	11,817802	43,944259	11,646492	43,975745
14	11,792455	43,844193	11,766917	43,852401	11,770328	43,881569
15	11,817958	43,832035	11,700175	43,880697	11,795925	43,885671
16	11,700737	44,014178	11,743009	43,855058	11,915014	43,822815
17	11,740448	43,944024	11,730194	43,870261	11,707978	43,943418
18	11,700454	43,935107	11,914269	43,798465	11,796876	43,782154
19	11,745160	43,929236	11,744017	43,872968	11,809918	43,781624
20	11,723726	43,950008	11,813887	43,783705	11,806134	43,761452
21	11,722180	43,940710	11,822124	43,809628	11,745853	43,951137
22	11,879272	43,799553			11,895902	43,830788
23	11,874381	43,791283			11,756317	43,929869
24	11,857986	43,773533			11,864007	43,874880
25	11,790587	43,792330			11,761446	43,985699
26	11,836357	43,882975			11,708834	44,013064
27	11,807958	43,881555			11,666022	44,005749
28	11,760176	43,926697			11,725375	43,996809
29	11,738715	43,916607			11,774878	43,892883
30	11,804132	43,922076			11,819183	43,927148
31	11,802380	43,934235			11,720545	43,938856
32	11,941453	43,714527			11,706727	44,029894
33	11,700364	43,922457			11,836357	43,882975
34	11,932537	43,707686			11,807958	43,881555
35	11,683389	43,931597			11,769354	43,922946
36	11,744017	43,872968			11,738715	43,916607
37	11,813887	43,783705			11,700364	43,922457
38					11,697832	43,953852
39					11,938167	43,701045

Table S1: Reduced occurence points of *C. rubra*, *E. microphylla* and *L. abortivum*

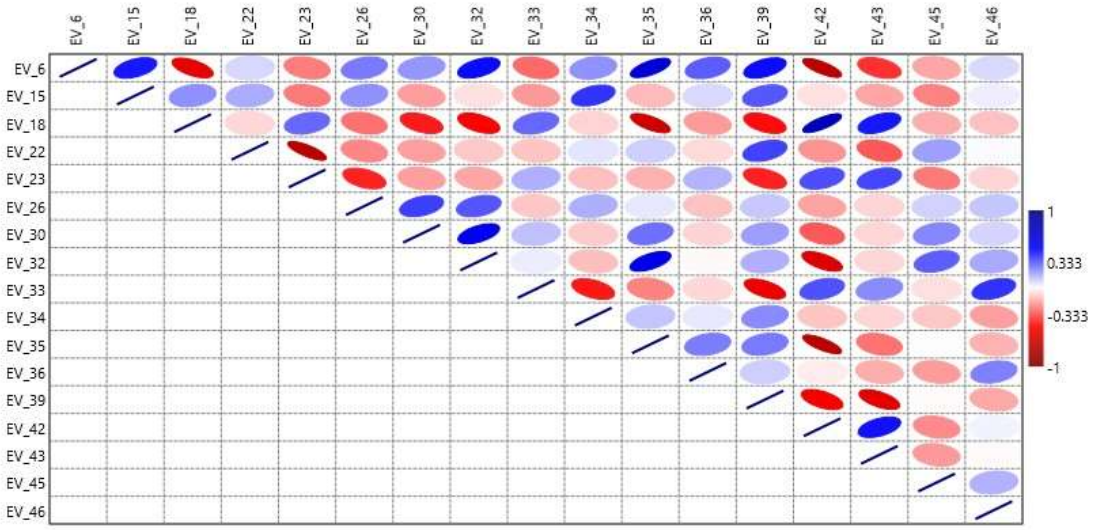

Figure S1: Pearson's correlation table of *C. rubra*

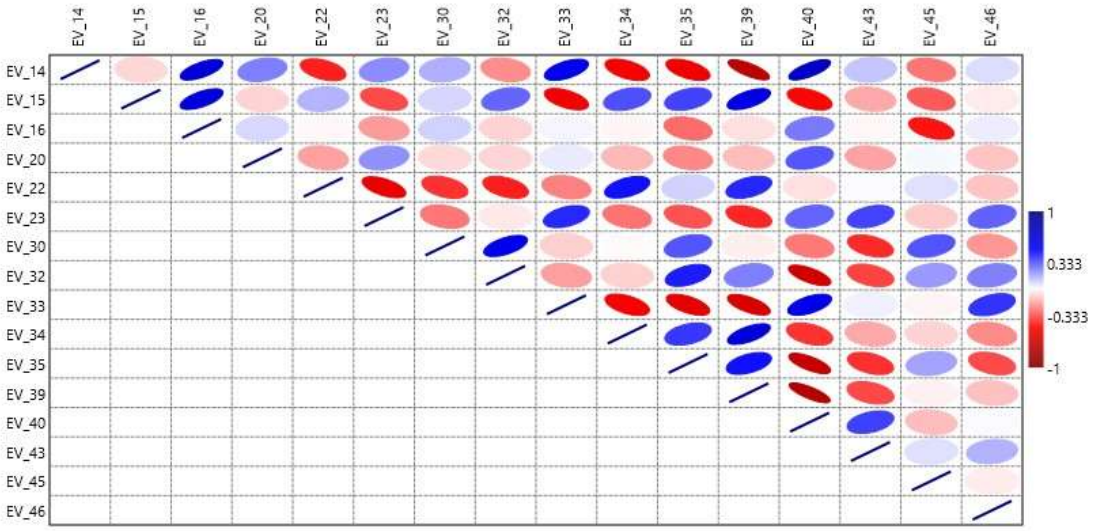

Figure S2: Pearson's correlation table of *E. microphylla*

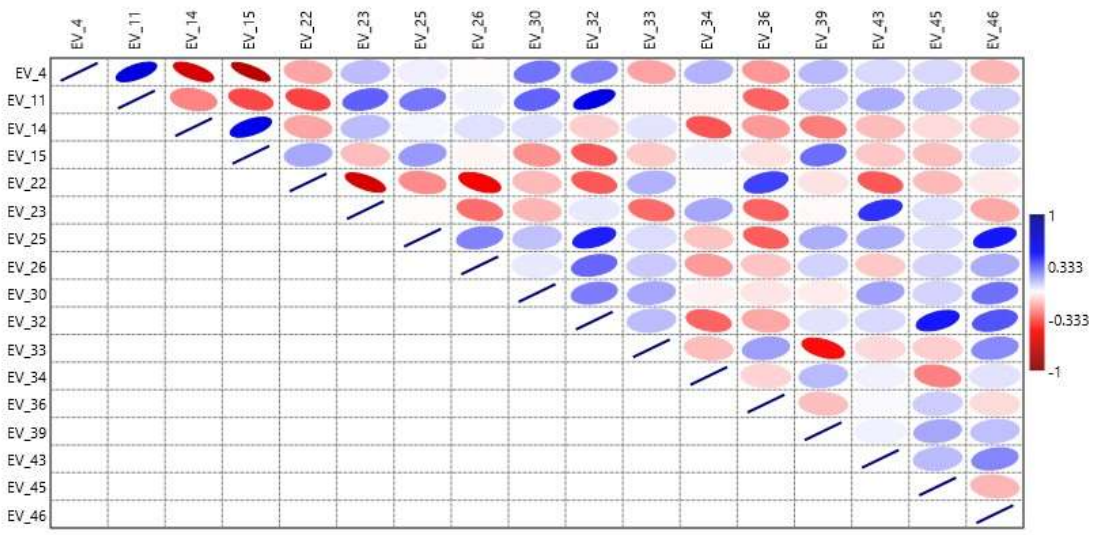

Figure S3: Pearson's correlation table of *L. abortivum*

Cephalanthera rubra		*Epipactis microphylla*		*Limodorum abortivum*	
EVs	**VIF**	**EVs**	**VIF**	**EVs**	**VIF**
BIO15	2,3	BIO14	2,94	BIO4	4,63
BIO18	4,78	BIO15	1,74	BIO11	2,91
LC04	1,62	LC03	2,52	BIO14	4,77
LC07	2,05	SOIL1	2,84	LC03	3,21
LC11	1,99	SOIL3	1,95	LC06	1,53
SOIL1	2,53	SOIL4	2,12	LC07	2,19
SOIL2	2,44	SLP	1,41	LC11	1,54
SOIL3	1,61			SOIL1	2,95
SOIL4	3,4			SOIL3	1,74
SOIL8	3,72			SOIL5	1,79
SLP	1,9			SOIL8	1,23
CHP	1,74			SLP	1,77
				ASP	1,55

Table S2: Variance Inflation Factors

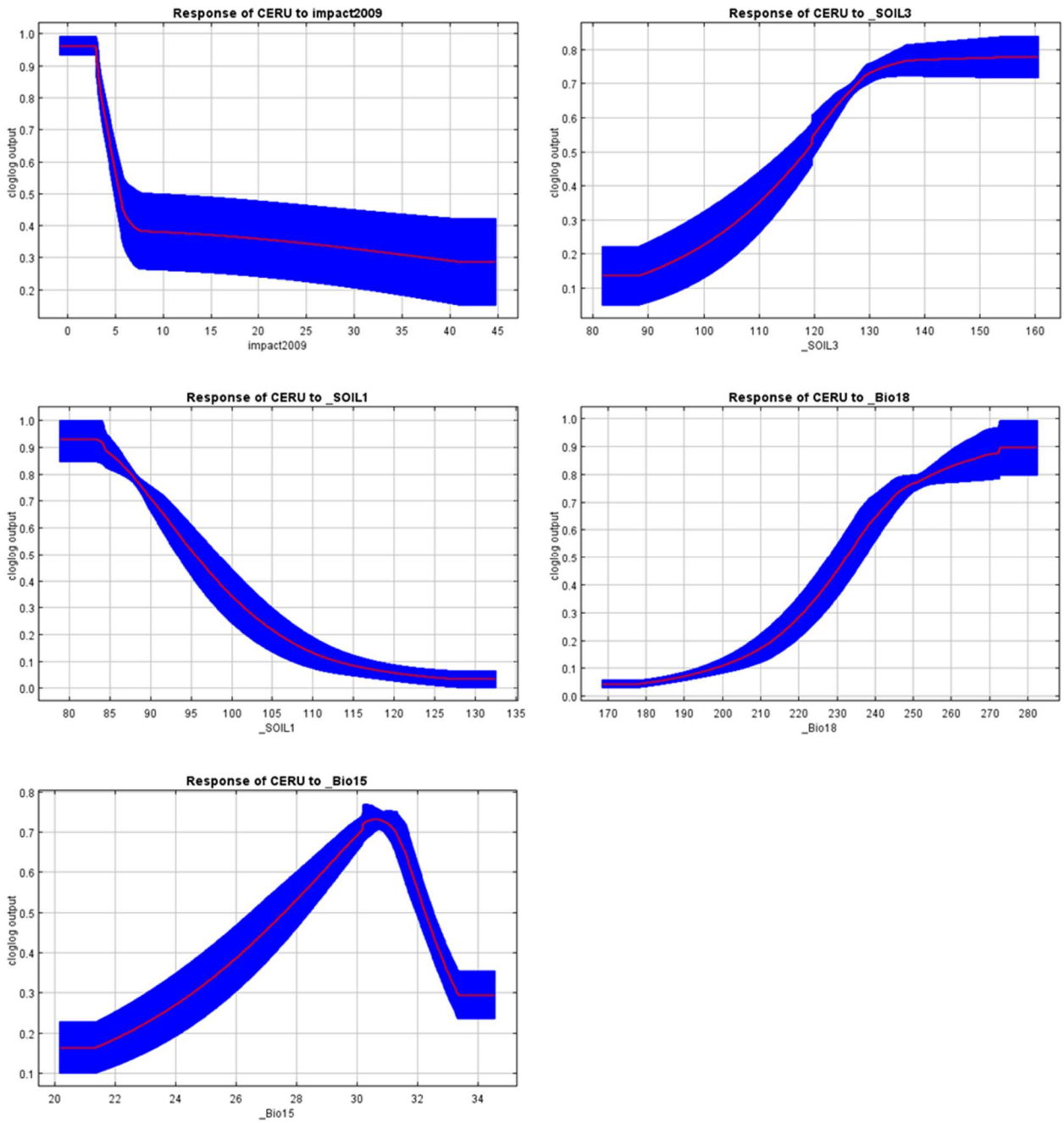

Figure S4: Response curve of environmental factors of *C. rubra*

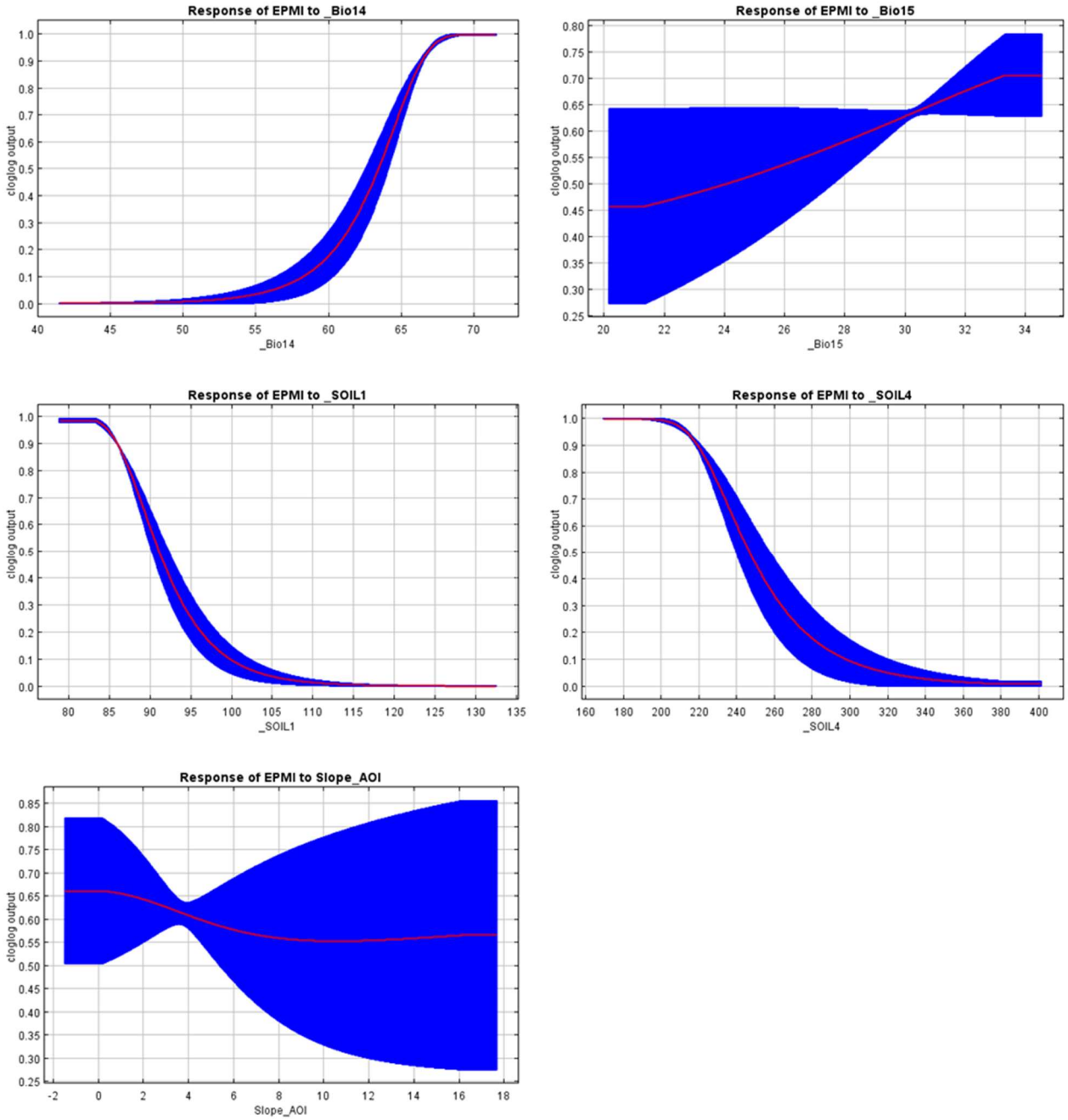

Figure S5: Response curve of environmental factors of *E. microphylla*

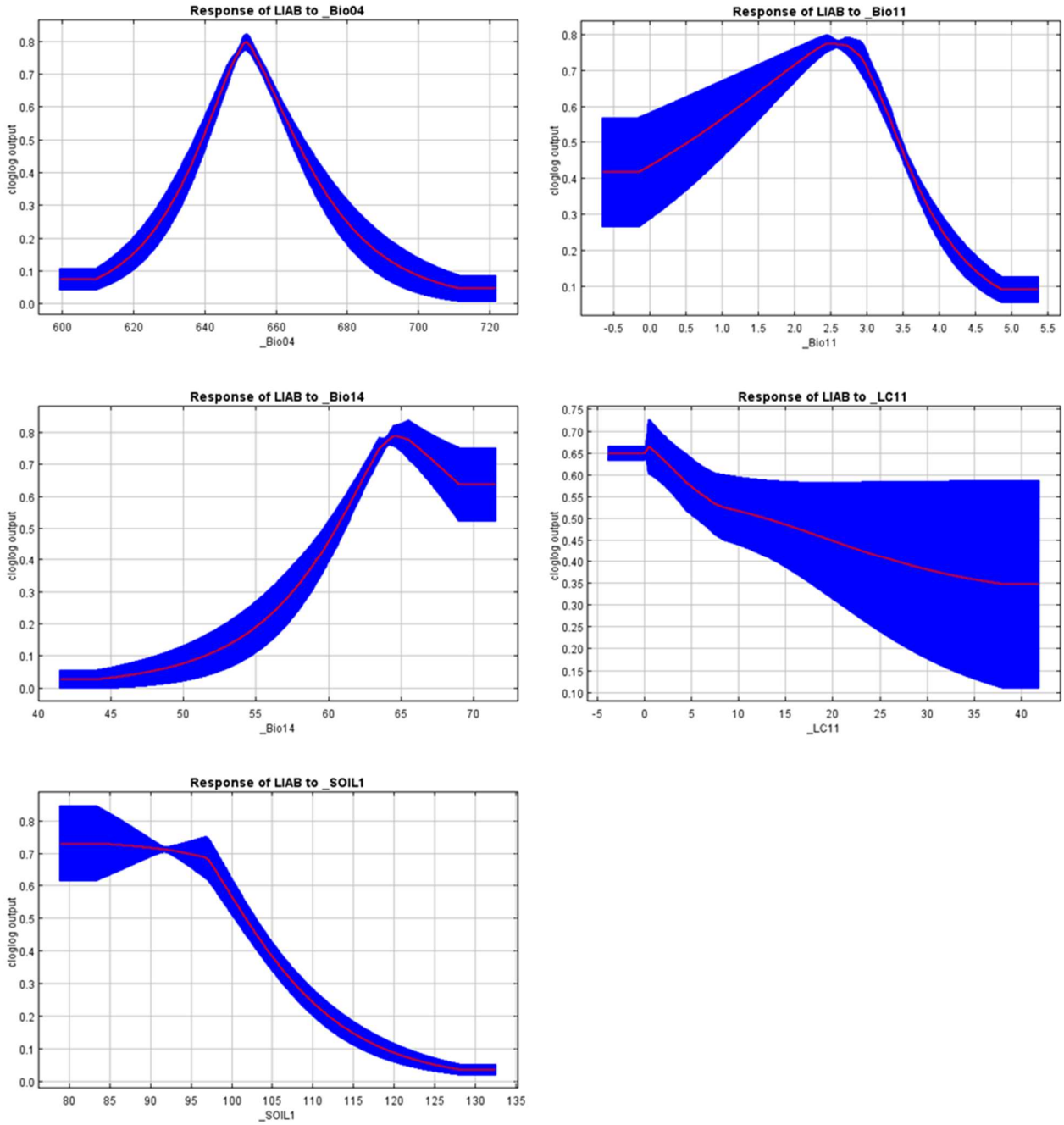

Figure S6: Response curve of environmental factors of *L. abortivum*

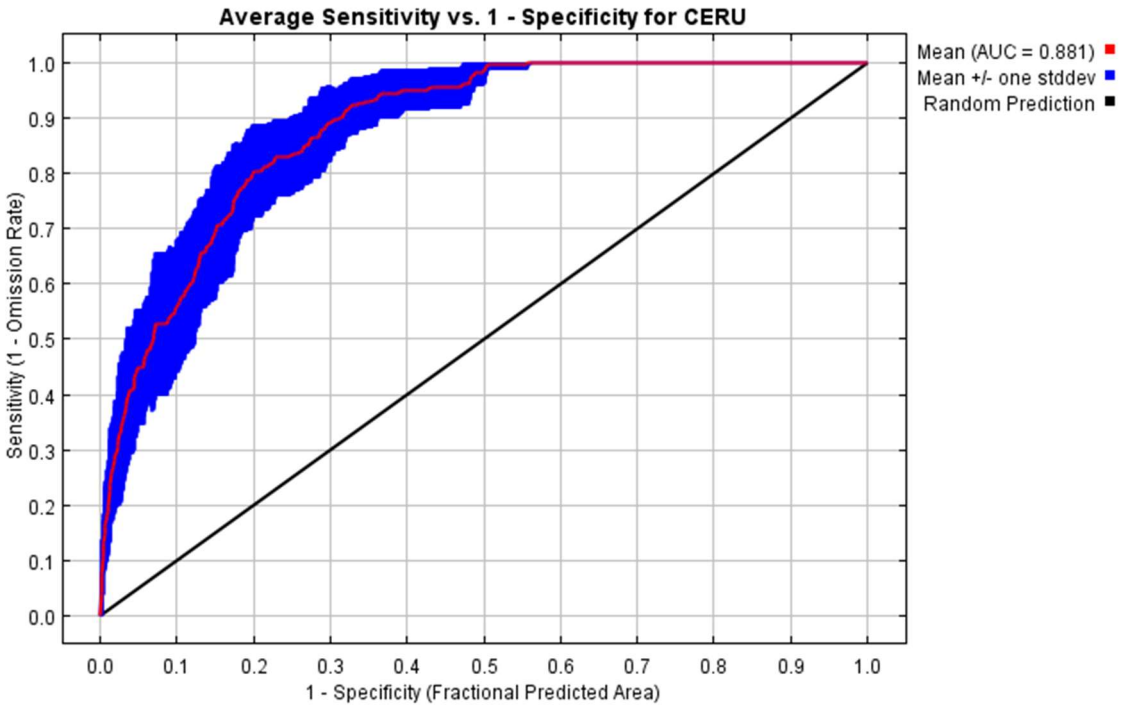

Figure S7: Goodness-of-fit test of the distribution model created for *C. rubra*

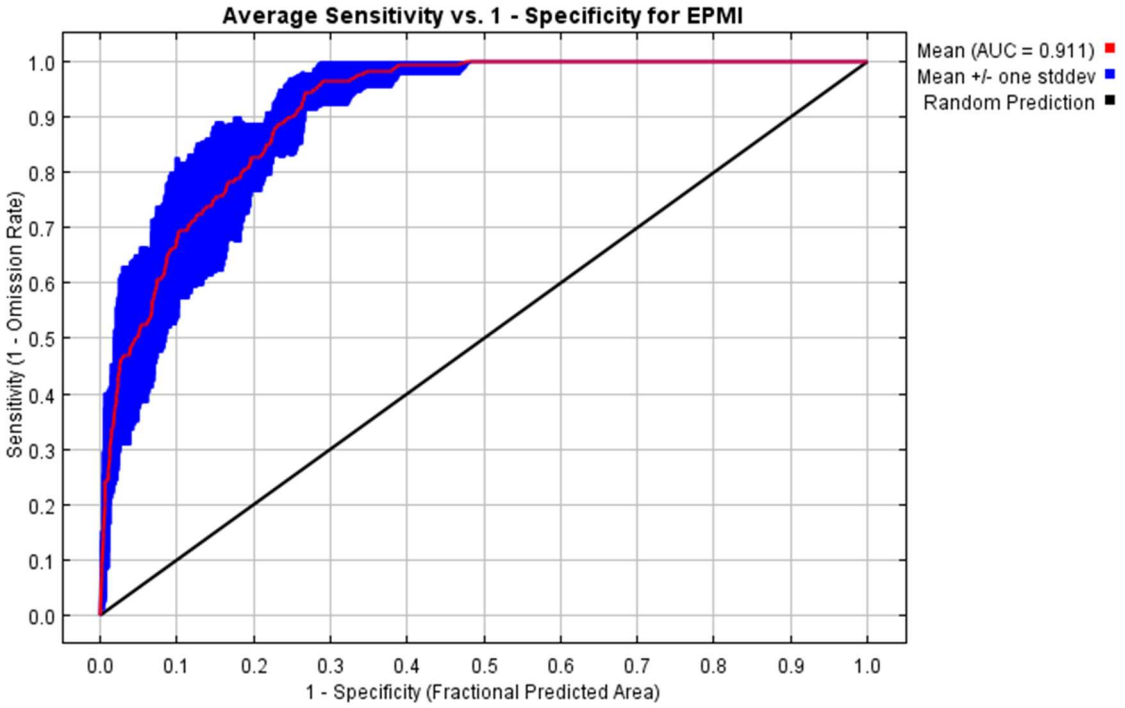

Figure S8: Goodness-of-fit test of the distribution model created for *E. microphylla*

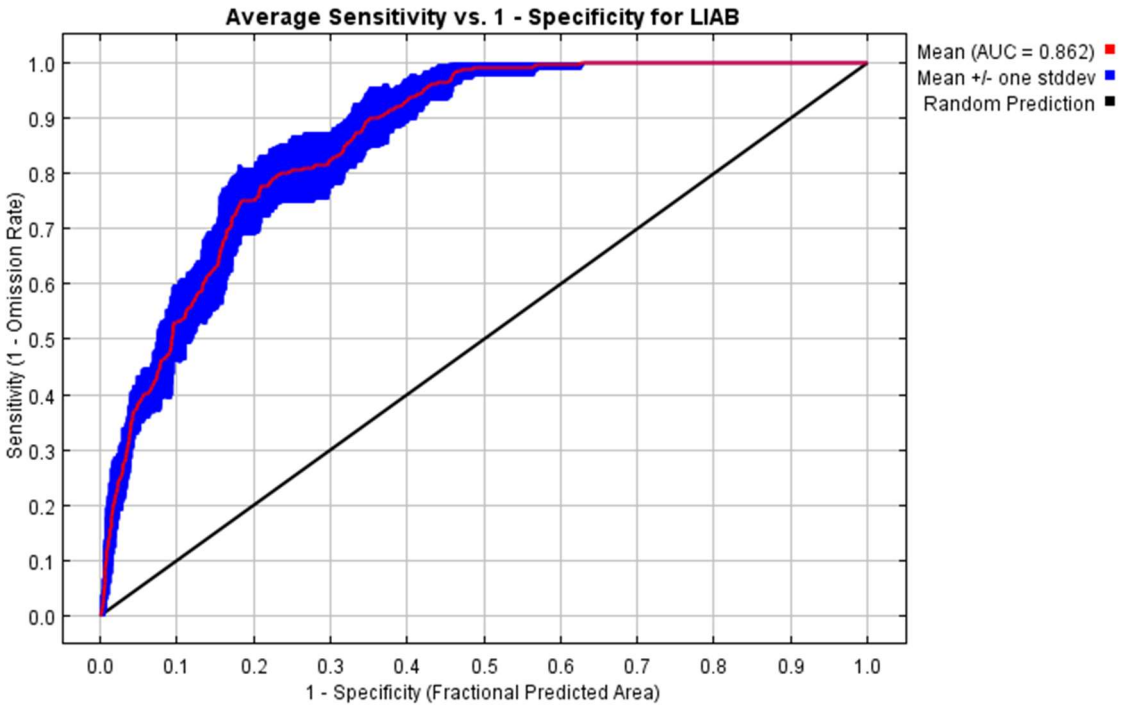

Figure S9: Goodness-of-fit test of the distribution model created for *L. abortivum*

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4. Naturalness and tree composition determine the abundance of rare and threatened orchids in mature and old-growth *Abies alba* forests in the Northern Apennines (Italy)

Research paper

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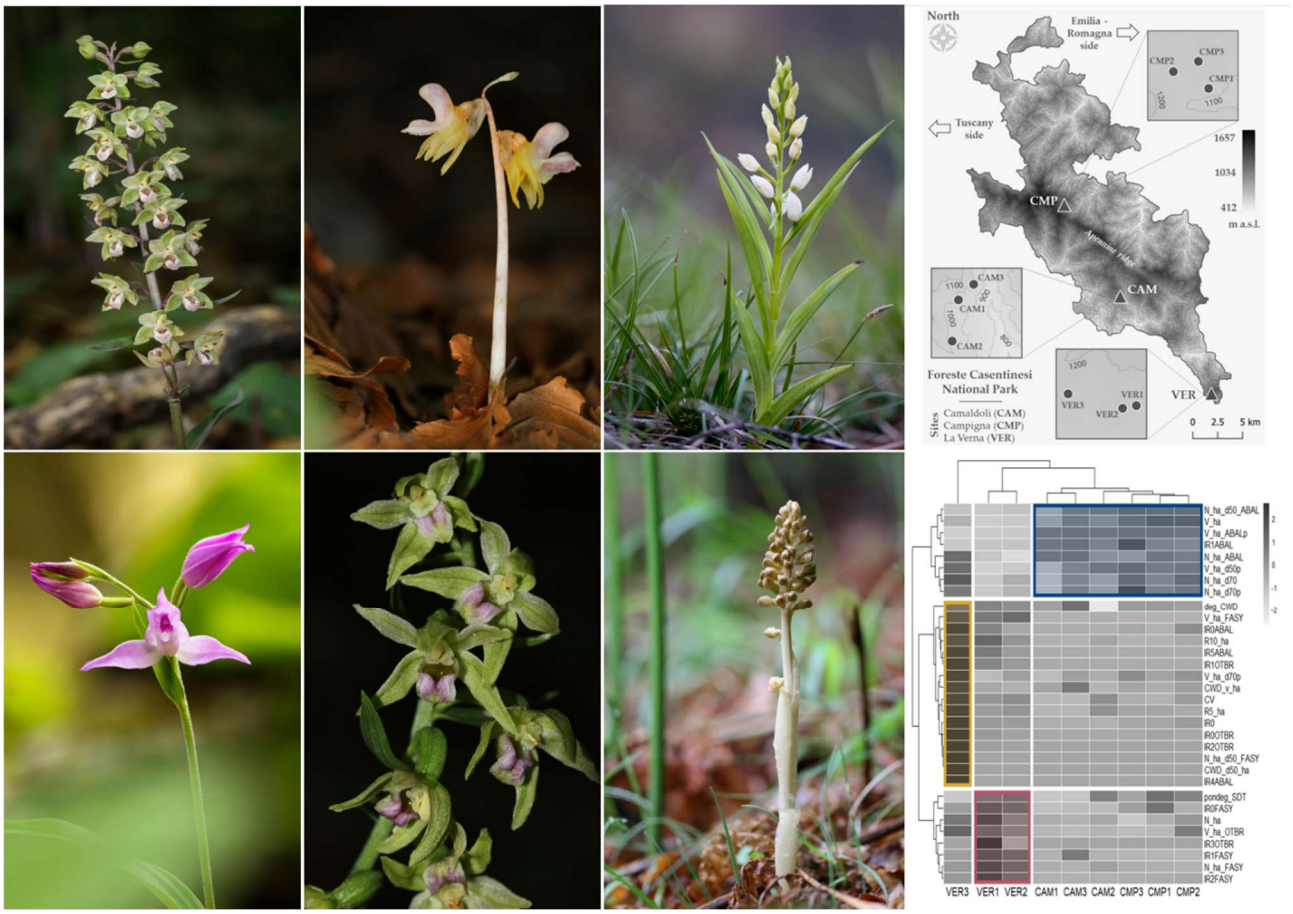
4.1. Graphical abstract



4.2. Abstract

Forest *Orchidaceae* are important for European temperate forests, yet their distribution and abundance have so far interested limited research. In three pure or mixed silver fir stands in the Foreste Casentinesi National Park (NP) (Northern Apennines, Italy) we analysed how structural traits in mature and old-growth forests affected orchid communities in terms of abundance of the main genera, trophic strategy and rarity in the NP. We established three 20 × 60 m plots to quantify the structure of living and dead tree community, including a set of old-growth attributes connected to large trees, deadwood, and established regeneration. In each plot, we measured the abundance of all orchid species and explored their behaviour according to the trophic strategy (autotrophy/mixotrophy, obligate mycoheterotrophy), rarity within the NP, and threatened status according to the IUCN Red List. We used multivariate ordination and classification techniques to assess plot similarities according to forest structure and Orchid Community and identify the main structural factors related to orchid features. The main structural factors were used as predictors of community traits. Forest composition (i.e., the dominance/abundance of silver fir) affected the presence of the main orchid genera: *Epipactis* were abundant in silver fir-dominated forests,

Cephalanthera in mixed beech and fir forests. Interestingly, *Cephalanthera* could become limited even in beech-dominated conditions if fir regeneration was abundant and established. Old-growth attributes like the density of deadwood and large tree volume were important determinants of the presence of rare and mycoheterotrophic species. Our results provided a first quantitative description of forest reference conditions to be used in the protection and restoration of threatened and rare orchid species.

Keywords: terrestrial orchids; mycoheterotrophic orchids; mixotrophic orchids; necromass (dead biomass); primary forest; mature and old-growth; naturalness; forest restoration; conservation

4.3. Introduction

The *Orchidaceae* is one of the largest plant families globally, with approximately 25,000 to 33,000 species [1,2] distributed across diverse environments worldwide [3]. It is the second-largest plant family in terms of species count, after the *Asteraceae* [4]. This family includes a significant number of endangered species, particularly among terrestrial orchids [5,6]. Human activities, such as habitat destruction and direct harm to populations, represent a major threat [7,8], while climate change will affect local species distribution [9,10]. Consequently, the conservation of these species and their habitats has become a global priority [11,12].

Forest biodiversity is widely recognised as being shaped by forest structure and management practices [13,14], which are often influenced by varying degrees of human intervention in forest ecosystems [15]. The relationships between forests and orchids have increasingly drawn the attention of researchers, who have explored various ecological aspects of these interactions [16–20]. In the case of temperate terrestrial forest orchids, their growth is known to depend not only on climatic factors and edaphic factors, but also on biotic interactions [21–23]. These species depend on mutualistic mycorrhizal associations with fungi to absorb carbon from nearby trees, a process that is essential for their survival [24]. These interactions, whether obligatory or not, play a pivotal role in completing their life cycles and for some species, fungi are indispensable partners throughout all life stages [25,26]. The germination of orchid seeds, due to their lack of reserves, is entirely dependent on the establishment of mycorrhizal associations, which can range from highly specific to less [27]. Subsequently, during growth, plant carbon supplies may rely entirely on mycorrhizae (fully or obligate mycoheterotrophic species) or only partially by combining it with photosynthesis (partially mycoheterotrophic or mixotrophic species) [28]. Furthermore, the degree of mixotrophy can reduce to minimum and definitely shift towards autotrophy under certain conditions [29]. It can therefore be assumed that the more orchids rely on mycorrhizae to

compensate carbon deficiencies (e.g., by establishing links with saprotrophic fungi) [30], the more they may be adapted, co-evolved, and specialised for forest ecosystems (e.g., non-photosynthetic orchid species). This underscores the intricate ecological interdependence of orchids within forest ecosystems, as well as the inherent challenges associated with studying these complex relationships.

It is well established that forest orchids are closely linked to light availability within forest ecosystems. Light is one of the primary physical factors influencing orchid distribution and abundance [3,31]. In forests, the amount of light reaching the ground can determine the presence of certain *Orchidaceae* species over others, depending on their ecology [32]. This phenomenon is linked to the ecological valence of each species with respect to the light factor [33–35]. Forest management practices often modify the canopy structure, thereby altering the amount of light that reaches the forest floor. Research indicates that human-induced disturbances, such as selective logging, can positively influence the growth of some forest orchids [36–38]. Conversely, studies have shown that practices like clear-cutting can negatively impact shade-tolerant species, potentially leading to their decline [39]. For strictly nemoral species, maintaining a closed canopy is essential for their survival [40]. Natural disturbance and the ecological processes connected to forest succession play a pivotal role in the survival of certain orchid species, yet these dynamics remain insufficiently explored [41,42]. Additionally, forest edge effects have been identified as significant factors influencing orchid distribution and occurrence [43]. Research on the ecology of orchids in complex habitats, such as old-growth forests, has seen some advancement in tropical regions [44,45]. However, this remains a largely underexplored area for terrestrial forest orchids in temperate climates [46].

In the forest ecosystem, other factors can be crucial. Soil characteristics play a fundamental role in influencing the abundance and distribution of *Orchidaceae* [3,23]. The type of geological substrate is important at both regional and local levels. Changes in the availability of soil resources (like water and nutrients) across different substrates led to variations in the richness and composition of orchid species [47,48]. Soil physical and chemical properties are essential, as well [3,49], e.g., soil moisture and pH at the microsite scale, are of great interest as they not only affect the species composition of orchids, but also their abundance [48]. Furthermore, the organic matter in the soil represents the main source of carbon and nutrients transferred to orchids through their mycorrhizal fungi [50]. It has been observed that the germination rate of orchids is positively correlated with the soil organic matter content [51]. The influence of these and other factors on population dynamics of forest orchids and their potential conservation implications has been only partially explored [21], leaving significant knowledge gaps.

Temperate orchids of open habitats have historically attracted greater attention from researchers, while forest orchids have remained relatively understudied. Genera such as *Ophrys* and *Orchis* have been extensively studied, particularly from systematic and ecological perspectives [52–54], even at a very fine taxonomic scale to the point of describing several possible hybrids [55–57]. Certain forest-specific orchids, especially those that are highly protected and threatened, like *Cypripedium calceolus* L. [58], have been the focus of numerous studies examining the impact of forest cover on their fitness and population dynamics [38,59,60]. However, other temperate forest orchid species, which face fewer threats, lack legal protection or fall outside designated protected areas, have generally been less studied concerning the effects of changes in forest cover. This trend partly reflects a global research bias favouring open and semi-natural ecosystems [61] and favouring "charismatic" and visually appealing flowering plants, which tend to attract more attention and funding in conservation science [62]. Some European forest orchid species exhibit a paucity of visually appealing morphological and chromatic characteristics, which often leads to their inadvertent neglect by researchers. These observations underscore the necessity for further investigation into this group of species.

In the last decade, a growing interest has focused on Mature and Old-Growth (MOG) forests to identify their potential for biodiversity conservation as well as climate change mitigation [63,64]. Besides primary forests, i.e., naturally-developing ecosystems representing undiscussed biodiversity sanctuaries [65], studying MOG naturalness-related attributes is crucial to better understand the long-term development of forests and highlight pathways to ecological restoration in the so-called proforestation approaches [66]. The old-growth forest status provides unique features in terms of large tree dominance [67] and lifespan [68], deadwood and microhabitats [69], as well as structural complexity [70]. Furthermore, the development of MOG into more advanced structural stages implies the onset of rare and complex patterns [71] and processes [72], favouring habitat conditions fundamental for the survival of highly specialised taxa [73,74]. Again, more research is still needed to fully describe and understand the casual relationships sustaining the presence of highly specialised forest species and the most advanced structural traits.

This research focused on orchid communities in pure and mixed forests with silver fir (*Abies alba* Mill.) at three sites within the "Parco Nazionale delle Foreste Casentinesi, Monte Falterona e Campigna" (National Park, NP) in the Northern Apennines (Italy). The study aimed to: (i) assess how forest structure, in particular old-growth features, influenced the prevailing traits of the Orchid Community in terms of dominant genera and trophic strategy; (ii) evaluate the ability of selected forest structure indicators to predict the selected traits of the Orchid Community; (iii) provide a first

description of the potential reference values of forest structural attributes to be used in species conservation and forest restoration.

4.4. Materials and Methods

4.4.1. Study area

The “Parco Nazionale delle Foreste Casentinesi, Monte Falterona e Campigna” (hereafter referred to as the National Park or NP) is an Italian protected area located in the Northern Apennines, specifically in the “Tosco-Romagnolo” Apennine, in Central Italy (Figure 1). It spans the border between the Emilia-Romagna and Toscana regions, covering parts of the provinces of Forlì-Cesena, Arezzo, and Firenze. The NP encompasses a total area of 36,400 ha. A key feature of the NP is the Apennine ridge, which runs from northwest to southeast, dividing the landscape into two main slopes. The highest points along this ridge are “Monte Falco” Mt. (1657 m a.s.l.) and “Monte Falterona” Mt. (1654 m a.s.l.). The three study sites are situated within the boundaries of the NP (Figure 1, Table 1). The first site, called Campigna (CMP), is located within the province of Forlì-Cesena and represents the northernmost site. Moving to the south, the other two sites are Camaldoli (CAM) and La Verna (VER), in the province of Arezzo. The geology of Campigna and Camaldoli is comparable, characterised by sandstones and arenaceous marls (Middle-Lower Miocene and Palaeogene age, respectively), while La Verna can be distinguished by the presence of Middle-Lower Miocene skeletal limestones and calcarenites [75]. Soil texture and organic matter were, in general, comparable among the sites (Table S1). In all cases, soil texture included mostly sand and, only in CMP, clay content was half of the other sites (Table S1). All soils contained calcium carbonate [75] and had similar amounts of organic matter (Table S1).

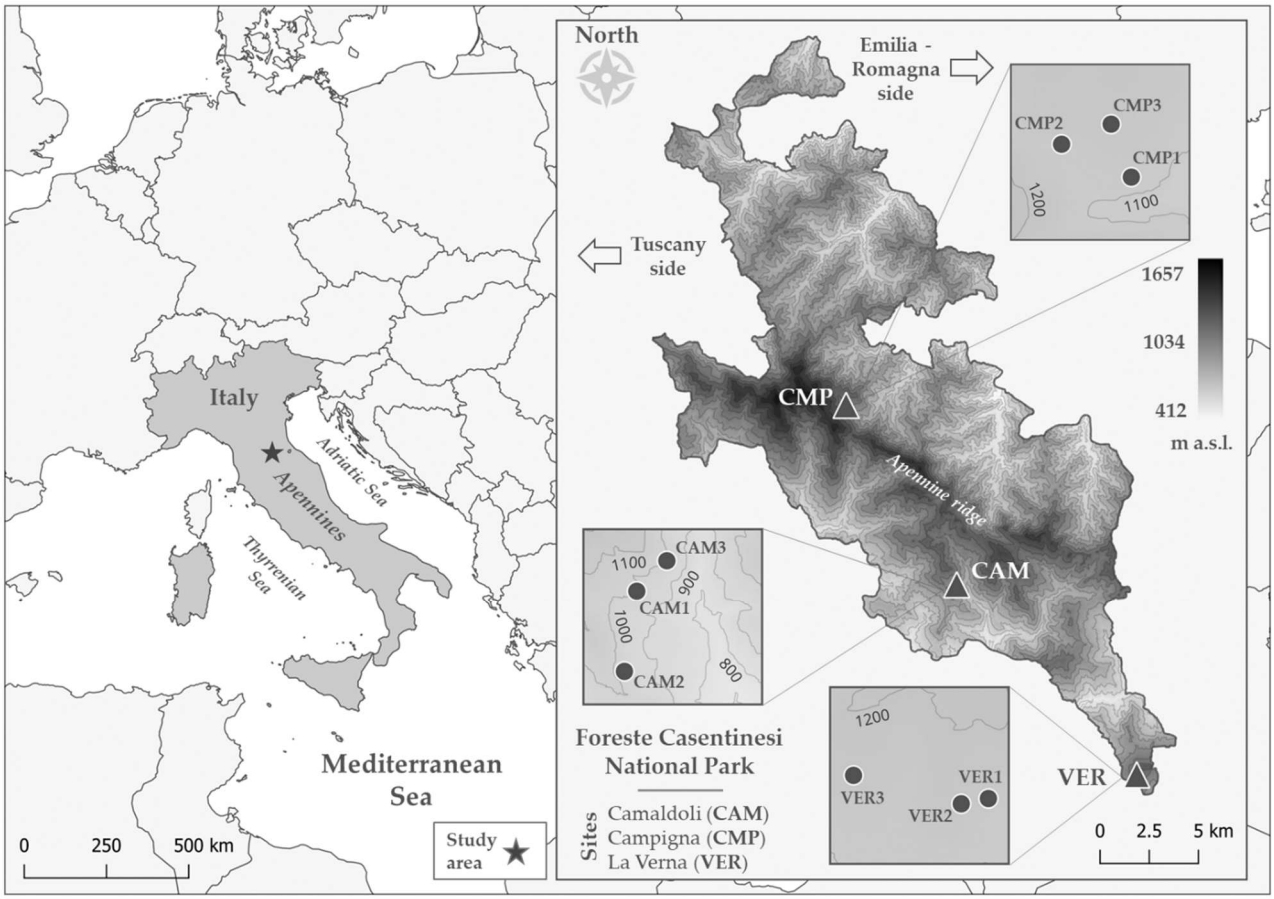


Figure 1. The location of (left) the study area and (right) the three study sites (triangles; CAM, CMP, VER) with each plot (circles) within the boundary of the National Park.

According to Pesaresi et al. [76], the areas fell within the temperate macrobioclimate and the temperate oceanic bioclimate, with a slightly semicontinental subtype. The three sites exhibit a humid ombrotype and a supratemperate upper horizon [76]. At the average plot elevation (c. 1090 m a.s.l.), the mean annual precipitation is 1625 mm, and the mean annual temperature is 8.3 °C. From an ecological perspective, Campigna is mainly characterised by a semi-natural forest of fir and beech, interspersed with small areas of conifer reforestations, Camaldoli is dominated by old coniferous reforestations undergoing spontaneous dynamics with patches of semi-natural fir or pure or mixed beech forests, and La Verna is characterised by beech and fir mixed stands [77]. A common feature of the three sites is their status as well-preserved forest which host high levels of specific diversity, comprising taxa often unique to the study areas and rarely found elsewhere in the NP [78–85]. In particular, our study sites fell within or were contiguous to habitats of interest to the Natura 2000 Network, classified under codes 9130 (*Asperulo-Fagetum* beech forests), 91M0 (Pannonian-Balkanic turkey oak-sessile oak forests), 9220 * (Apennine beech forests with *Abies alba* and beech forests with *Abies nebrodensis*), and 9210 * (Apennine beech forests with *Taxus* and

Ilex) [86]. Additionally, these localities host numerous species of community interest, including the beetles *Rosalia alpina* Linnaeus and *Osmoderma eremita* Scopoli, restricted to the old-growth forest [87].

Fifty-one species of *Orchidaceae*, grouped into 17 genera [83,88], are included among the 1172 native taxa recorded in the NP [85]. As a result of the extensive forested area covered by woods and forests in the NP (over 80%), many of the existing orchid species are typical plants of forest environments. For example, species such as *Neottia nidus-avis* (L.) Rich., *Cephalanthera damasonium* (Mill.) Druce, and *Epipactis helleborine* (L.) Crantz occur in over 60% of the NP territory, divided into equal-sized 2 km cells [83]. Some species are even rarer, such as *Epipogium aphyllum* Sw., *Epipactis placentina* Bongiorni & Grünanger, and *E. greuteri* H. Baumann & Künkele [85].

Table 1. Summary of site features. Coordinates refer to the WGS84 system. Mean (min – max) values of elevation, slope and aspect were provided.

Site	Code	Latitude (°N)	Longitude (°E)	Elevation (m a.s.l.)	Slope (%)	Aspect (°)
Camaldoli	CAM	43.79151	11.81329	982 (956 – 1000)	14 (9 - 20)	125 (81 - 185)
Campigna	CMP	43.87225	11.74016	1135 (1118 – 1159)	22 (15 - 30)	172 (152 - 195)
La Verna	VER	43.70830	11.93217	1153 (1144 – 1161)	19 (17 – 28)	130 (100 - 180)

4.4.2. Field Sampling of Forest Structure and Orchid Species Diversity

The study forests were selected as the best examples of stands with large old fir trees and mature or old-growth structure within the National Park. Once chosen, forest areas were scouted in spring–summer 2024 for the presence of orchid populations. Plot locations were randomly selected among areas within each forest hosting orchid populations with at least 2 stems. This approach was adopted because forest orchid species have a spotted and non-homogeneous distribution, often with only a few individuals. At each site, three replicated 20 m × 60 m plots (1200 m^2) were established in forest ecosystems at a comparable elevation (Table 1). Three plots were set as the minimum number of replicates achievable in the three study forests. The number was deemed representative considering the patchy distribution and limited occurrence of *Orchidaceae* populations. Each plot was set with a short side on the forest margin and then developed with its long side into the forest,

parallel to the main slope. Plot coordinate endpoints were collected using a Garmin GPSMAP 66i (Garmin Ltd., Olathe, Kansas). In each plot, we quantified living and dead tree structures. For all living trees with height > 1.3 m and Diameter at Breast Height (DBH) ≥ 2.5 cm, we recorded the species and measured DBH using a caliper. Height (H) was measured with a Haglof Vertex IV on trees sampled to represent 20 cm DBH classes. To quantify the establishment of tree regeneration, we counted the number of all trees with DBH < 12.4 cm and falling in one of the following height (H) classes: 1. <10 cm; 2. 11–50 cm; 3. 51–150 cm; 4. 151–300 cm; 5. >300 cm.

The presence and absolute abundance (i.e., number of stems) of orchid species were recorded for each plot. When it was not possible to identify a specimen at the species or subspecies level (especially in plants without flowers of *Cephalanthera* and *Epipactis*), it was assigned to the appropriate higher taxonomic group and labelled as not classified species (NC). The taxonomic nomenclature follows Bartolucci et al. [89].

4.4.3. Quantifying Forest and Orchid Community Traits

Site-level H-DBH curves were calculated by merging data from the three plots using the Naslund equation [90]. Tree volume was calculated using measured DBH and predicted H according to species allometries available in Tabacchi et al. [91]. The necromass components were divided into Standing Dead Trees (SDTs; DBH ≥ 10 cm) and Coarse Woody Debris (CWD; median diameter $D_{0.5}$ ≥ 10 cm and length ≥ 1 m). On each SDT, we measured DBH and H, and calculated the volume using the cylinder formula. On each CWD, $D_{0.5}$ and length served to calculate the volume according to the cylinder formula. Each deadwood piece was assigned to a decomposition stage on a scale from 1 (with intact shape and consistency) to 5 (advanced decomposition with loss of original shape and consistency) according to Rubino and McCarthy [92].

To quantify the degree of old-growthness of each forest plot, we calculated a set of Structural Indicators (SIs) [70,72]: stand structural complexity, measured with the DBH coefficient of variation (CV_{DBH}); established regeneration (frequency of trees with DBH < 12.5 cm); the density of large trees (DBH > 50 cm and DBH > 70 cm), large CWD ($D_{0.5}$ > 50 or 70 cm), and large SDT (DBH > 50 or 70 cm). Additionally, the mean and density-weighted decay values were calculated for both CWD and SDT.

The Index of Regeneration (IR) was calculated as the weighted sum of regeneration density multiplied by the mean height value of each class (1–5). All indicators were also calculated separately for ABAL (*Abies alba*), FASY (*Fagus sylvatica* L.), and OTBR (other broadleaves). All SI values were reported in Table S2.

The forest Orchid Community (OC) dataset comprises 119 records collected across all plots. Orchids were grouped by genus and species. Specific codes were assigned and their main features were synthesised in Table 2. Based on the existing literature, genera and species were classified into two distinct categories according to their primary trophic regime: fully mycoheterotrophic species (code MH) and autotrophic/mixotrophic species (code AUMX). The species classified as fully mycoheterotrophic include *Epipogium aphyllum* and *Neottia nidus-avis* [93–95]. The species belonging to the genera *Cephalanthera*, *Epipactis*, and *Dactylorhiza* exhibit a more complex situation. These genera include both species in which mixotrophy, to varying degrees, is well documented [26,28,96–98], and species that occupy a trophic continuum between autotrophy and mixotrophy, which are still under investigation [99–101]. From a distributional perspective, orchid species were classified as widespread (code WIDE) or narrow range and rare (code NARROW) within the study area, according to Pica and Laghi [83]. Additionally, we included the IUCN Red List category assigned to each species according to the global assessment (*Epipactis greuteri*, *E. leptochila*, *E. purpurata*, *Neottia nidus-avis*), European assessment (*Cephalanthera rubra*, *C. longifolia*, *C. damasonium*, *Epipactis helleborine*, *E. microphylla*, *Dactylorhiza maculata* s.l., *Epipogium aphyllum*), and Mediterranean assessment (*Epipactis exilis*) [102]. Finally, the Ellenberg indicator values for each species, as derived from Pignatti et al. [103] and Tichý et al. [104], were also reported (Table 2).

Table 2. *Orchidaceae* species recorded in all sites, classified by: genus, trophism (MH, Fully Mycoheterotrophs; AUMX, Autotrophs/Mixotrophs), distribution within the National Park (WIDE, Widespread Species; NARROW, Narrow Range and Rare Species), IUCN Red List assessment (LC, Least Concern; NT, Near Threatened; EN, Endangered), Ellenberg indicator values (L, Light; T, Temperature; K, Continentality; F, Moisture; R, Soil Reaction; N, Nutrients). Codes corresponding to genera and species are provided.

Genus	**Code**	**Trophism**	**Species**	**Code**	**NP distribution**	**Red List**	**Ellenberg Indicator Values**					
							L	T	K	F	R	N
Cephalanthera	CEPHA	AUMX	*C. rubra* (L.) Rich.	CERU	WIDE	LC	3.0	5.0	5.0	4.0	8.0	3.0
			C. longifolia (L.) Fritsch	CELO	WIDE	LC	4.0	5.0	5.0	3.0	8.0	3.0
			C. damasonium (Mill.) Druce	CEDA	WIDE	LC	2.0	5.0	4.0	4.0	7.0	4.0
						Mean	**3.0**	**5.0**	**4.7**	**3.7**	**7.7**	**3.3**
Epipactis	EPIPA	AUMX	*E. helleborine* (L.) Crantz	EPHE	WIDE	LC	3.0	5.0	5.0	5.0	7.0	5.0

			E. greuteri H.Baumann & Künkele	EPGR	NARROW	EN	2.0	6.0	-	7.0	7.0	6.0
			E. microphylla (Ehrh.) Sw.	EPMI	WIDE	NT	7.0	7.0	4.0	3.0	6.0	2.0
			E. leptochila (Godfery) Godfery	EPLE	NARROW	LC	3.0	6.0	3.0	4.0	9.0	4.0
			E. purpurata Sm.	EPPU	NARROW	LC	2.8	5.8	-	5.5	7.3	5.3
			E. exilis P.Delforge	EPEX	NARROW	LC	-	-	-	-	-	-
						Mean	**3.6**	**6.0**	**4.0**	**4.9**	**7.3**	**4.5**
Neottia	NEOTT	MH	*N. nidus-avis* (L.) Rich.	NENA	WIDE	LC	2.0	5.0	5.0	5.0	7.0	5.0
Dactylorhiza	DACTY	AUMX	*D. maculata* (L.) Soó s.l.	DAMA	WIDE	LC	7.0	5.0	5.0	5.0	-	4.0
Epipogium	EPIPO	MH	*E. aphyllum* Sw.	EPAP	NARROW	LC	1.0	4.0	5.0	5.0	3.0	9.0

To quantify the Orchid Community features and compare plots, we chose the following indicators: genera and species number; genera and species absolute abundance; genera and species relative abundance; trophic group relative abundance; and distribution range relative abundance. Statistical analyses were performed using the relative abundances of the taxonomic (genus), trophic, and distributional levels, indicated by the letter "p" following the variable (CEPHAp, EPIPAp, NEOTTp; MHp, AUMXp; WIDEp, NARROWp). The relative abundance was calculated as the percentage of the total absolute abundance. Species grouping was necessary due to the frequent zero or low values of some species in several plots. Scarcely represented genera (*Epipogium* and *Dactylorhiza*) were included only in trophism and distribution analysis.

4.4.4. The Relationships Between the Orchid Community and Forest Structure

A Principal Component Analysis (PCA) was used to identify the main Structural Indicators to describe stand/plot differences and identify the candidate predictors for the Orchid Community. The initial set of 102 variables was divided into thematic groups describing tree composition, regeneration, large trees, standing, and lying deadwood (Table S2).

To remove redundant or ineffective variables, we proceed with a two-step method [72]: (i) with the first PCA, we filtered out variables with loading <50% of the absolute maximum axis loading [105,106]; (ii) the remaining variables were passed again through a PCA, to select the best ones per each group/subgroup, i.e., those with the highest loading (satisfying the 50% threshold). In both PCAs, we retained the minimum number of axes explaining ≥2/3 of the overall variance (i.e., 2 [105,106]). The initial set of 102 Structural Indicators was first reduced to 77 and then to 32.

To further illustrate how the plots were grouped according to similarities in either structural or Orchid Community features, we classified them using Ward's clustering algorithm and Pearson's distance [72].

To identify potential predictors for orchids, we ran a final PCA incorporating both the selected Structural Indicators (SIs) and Orchid Community descriptors to highlight correlations between the two datasets. The best SIs, i.e., 2–3 per group (Table S2) with the highest loading, were retained as candidate predictors for modelling Orchid Community variables. The selected SIs were used to model their univariate relationship with the Orchid Community variables using linear models (LMs), second-degree polynomial models (Poly2), and nonlinear least-squares models (NLS). The lowest Akaike Information Criterion (AIC) was used for model selection. AIC was also used to explore possible improvements deriving from using a bivariate rather than a univariate model. To avoid multicollinearity among predictors, in bivariate models, we used only variables from orthogonal PCA groups. The goodness-of-fit metrics were reported for the final model, which was also checked for residual analysis [107,108]. Data were analysed and processed using the QGIS 3.32.3 software [109] and R 4.4.1 software [110].

4.5. Results

4.5.1. Analysis of Forest Structure, Living and Dead Biomass

According to their DBH distributions, Campigna (CMP) and Camaldoli (CAM) hosted mainly pure even-aged silver fir stands, with angiosperms locally established in smaller size classes, while La Verna (VER) was an uneven-aged beech-dominated stand with fir and minor presence of other angiosperms (Figure 2, Table 3). Despite its lower stature (35 m compared to 40 m in CAM and CMP), VER had the largest trees (Table 3), either silver fir or beech (Figure 2). Pure forests (CAM and CMP) showed a cathedral-like canopy of silver fir, but locally (i.e., CMP2 and CAM2) plots exhibited a two-layered structure with an understory layer dominated by beech and other angiosperms. In the regeneration layer, the most established species was fir, especially at CAM, while at CMP both the establishment and the presence of beech were higher (Figures 3 and S1). In VER, the multilayered structure of the mixed stand was accompanied by higher values of the regeneration index, with half of IR made of fir and the other half made of angiosperms (Figures 3 and S1). VER3 had the most complex structure, with higher density of both very large and small trees, especially fir (Figure 2), and the highest IR values detected (Figures 3 and S1).

Figure 2. DBH distribution (relative frequency) by site/plot. The bar colour represents the tree composition (ABAL, *Abies alba*; FASY, *Fagus sylvatica*; OTBR, other broadleaves). Next to each site's code, the numbers indicate the corresponding plots.

Table 3. Summary of the structural characteristics, Index of Regeneration, deadwood and species composition (ABAL, Abies alba; FASY, Fagus sylvatica; OTBR, other broadleaves) for each site. Values indicate the site mean and, when the parentheses are present, the plot's minimum and maximum.

		CAM	CMP	VER
Forest type		Pure silver fir	Pure silver fir	Mixed beech
Living Trees	Stature (m)	33.4	37.2	30.9
	DBH (cm)	38.7 (34.9 – 44.3)	45 (39.5 - 49)	22.1 (19.6 – 25.1)
	Density (stem ha^{-1})	483 (458 – 508)	469 (358 – 583)	772 (666 – 933)
	Basal Area (m^2 ha^{-1})	65 (55.4 – 75.4)	83.4 (75.6 – 87.3)	45.2 (43.3 – 48.6)
	Tree Volume (m^3 ha^{-1})	958.9 (772 – 1137.6)	1,345 (1246 – 1404.8)	584 (481.1 – 726.5)
	Large Tree Volume (%)*	5.5	14.4	21.1
Tree Species composition (% Volume)	ABAL	98.8	98.7	24.7
	FASY	1	0	63.7
	OTBR	0.2	1.3	11.6
Tree Index of Regeneration (%)	Small (IR1-2)	96.5	64.6	34.8
	Intermediate (IR3)	0	4.1	0.2
	Established (IR4-5)	3.5	31.3	65
Total Deadwood	Density (stem ha^{-1})	202.8 (108.3 – 391.7)	166.7 (75 – 283.3)	83.3 (33.3 – 158.3)
	Volume (m^3 ha^{-1})	76.6 (10.6 – 172.4)	24.6 (14.4 – 36.5)	42.2 (4.4 – 93.5)
Coarse Woody Debris (CWD)	Density (stem ha^{-1})	166.7 (0 – 391.7)	136.1 (66.7 – 100)	50 (33.3 – 75)
	Volume (m^3 ha^{-1})	19.1 (0 – 46.7)	10.1 (5.1 – 15.1)	34.8 (3.4 – 93.5)
Standing Dead Tree (SDT)	Density (stem ha^{-1})	36.1 (0 – 108.3)	30.6 (8.3 – 41.7)	33.3 (0 – 83.3)
	Volume (m^3 ha^{-1})	57.5 (0 – 172.4)	14.5 (4.2 – 31.4)	7.3 (0 – 20.9)

*DBH > 70 cm

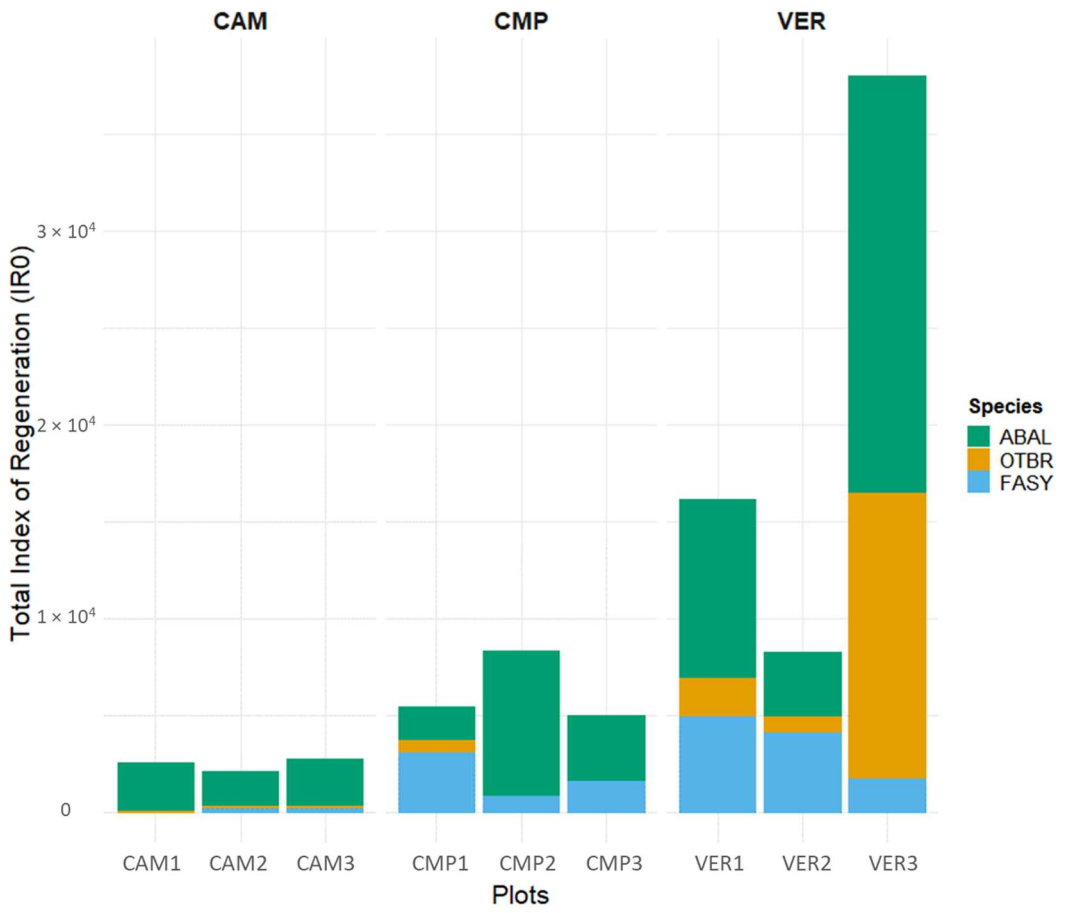


Figure 3. Total Index of Regeneration (IR0) for different tree compositions (ABAL, *Abies alba*; FASY, *Fagus sylvatica*; OTBR, other broadleaves). IR1-5 is separately reported in Figure S1.

Deadwood presence was highly variable in terms of density and volume between- and within-sites (Figure 4). Deadwood density was on average around 150 elements per ha and less than 48 m^3 ha^{-1}, and originated mainly from silver fir at CAM and CMP and beech at VER. CMP showed a high density, but low volume of deadwood (particularly in CMP2), especially CWD. CAM had comparable patterns but can be distinguished for an exceptionally high SDT volume in CAM2, characterised by many large standing dead fir trees. VER3, instead, was distinguished for having a few but large CWD.

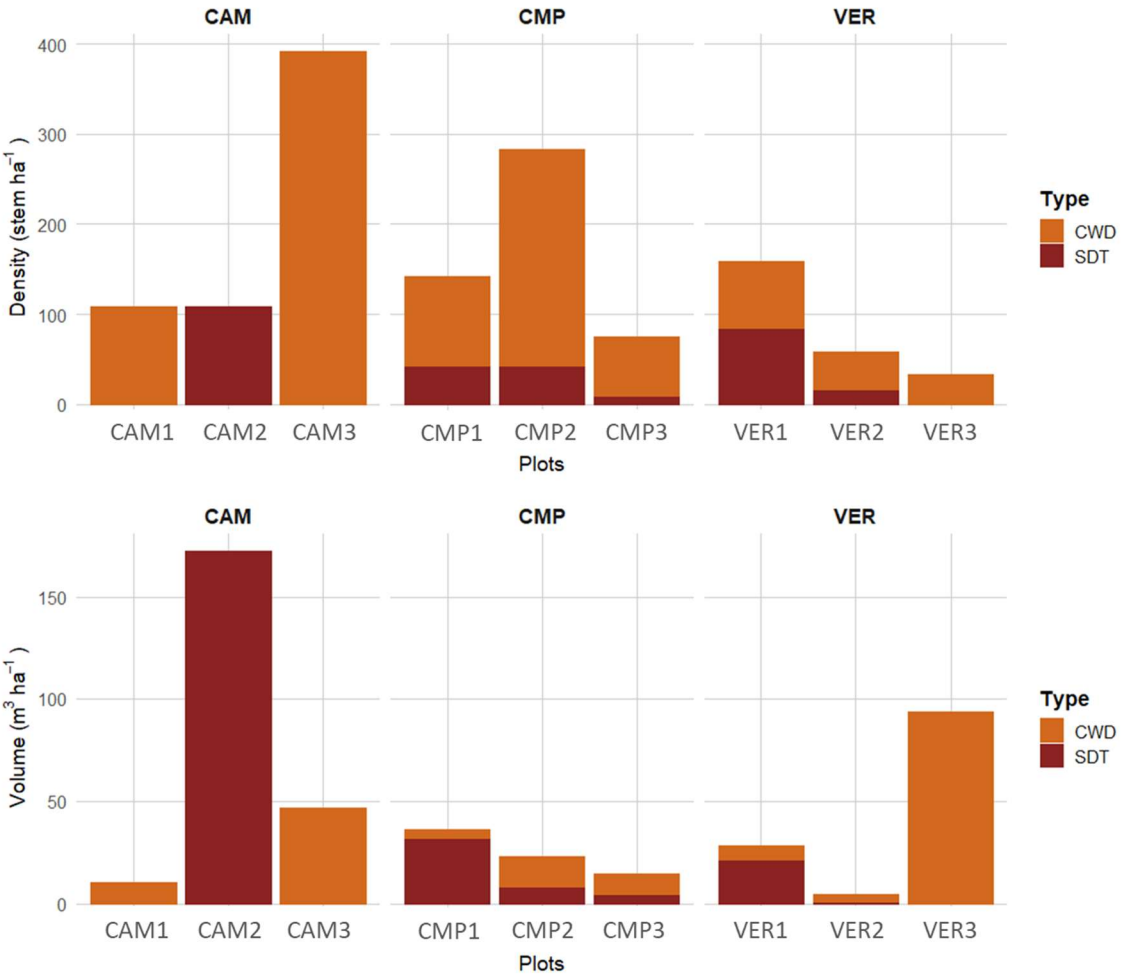


Figure 4. Deadwood density (stem ha^{-1}) and volume (m^3 ha^{-1}) across sites and individual plots (CWD, Coarse Woody Debris; SDTs, Standing Dead Trees).

Among all the 102 Structural Indicators (SIs) initially calculated to describe forest structure and their old-growthness, a final set of 32 SIs were selected through the PCA screening (Figure S2) to group plots in terms of similarity in structural features (Figure 5).

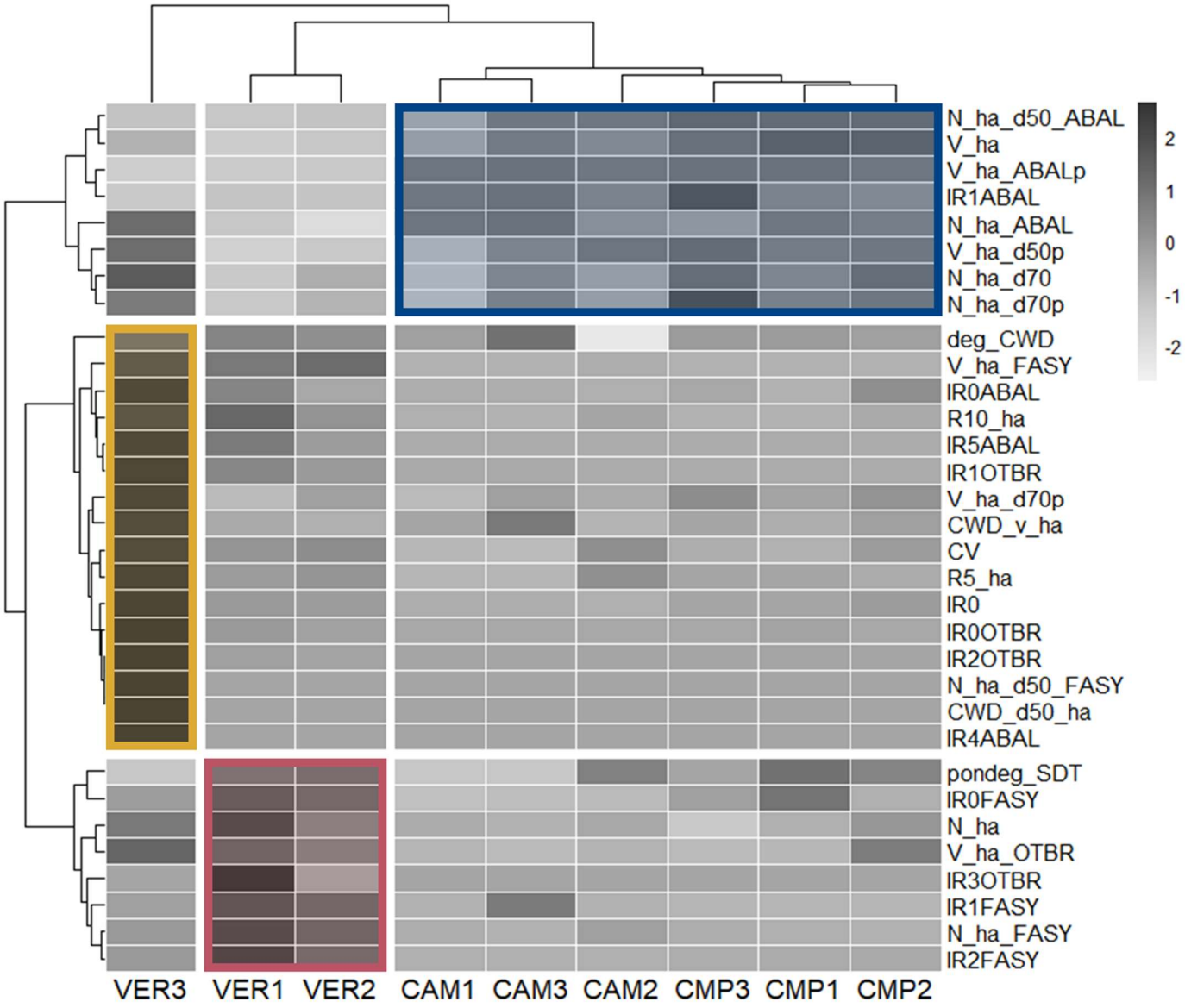


Figure 5. Correlation matrix ordered according to the hierarchical clustering of plots based on selected Structural Indicators (SIs). Boxes delineated the main three clusters grouping the plots: higher old-growthness (yellow; VER3); cathedral-like fir forest (blue; CAM 1-3 and CMP 1-3); mixed beech stands (red; VER 1-2).

One group (yellow), including only VER3, was characterised by beech dominance and the highest levels of structural complexity and old-growthness comprising the DBH coefficient of variation (CV); volume and density of large trees (DBH > 70 cm, FASY with DBH > 50 cm); and CWD volume with advanced decomposition stages. Furthermore, there was a substantial established regeneration of silver fir (IR4 and IR5, R5 and R10) and smaller cohorts of other broadleaf species (IR0OTBR). Plots VER1 and VER2 (red) were characterised by beech abundance (N_ha_FASY) and high biomass of other broadleaves (V_ha_OTBR), alongside younger (IR1 and IR2FASY) and

intermediate (IR3FASY) regeneration often dominated by beech. Lastly (blue), all CMP and CAM plots were dominated by silver fir with a cathedral-like structure, i.e., high density of large trees, associated with small silver fir regeneration (IR1ABAL).

4.5.2. Analysis of Forest Orchid Community

The forest Orchid Community showed that, in terms of relative abundance, the genera *Epipactis* and *Neottia* are ubiquitous and the genus *Epipogium* is exclusive of a single site (CMP1; Figure 6). In terms of species, some are rare and exclusively located in individual plots, i.e., *Epipactis microphylla* at CAM3; *E. leptochila*, *E. purpurata*, *Cephalanthera damasonium,* and *Epipogium aphyllum* at CMP1; *E. exilis* at VER1 (Figure S3). Each plot contained an average of three species, with CMP1 reaching a maximum of eight species. On average, there were two genera per plot, with a maximum of four genera coexisting. The average absolute abundance was around 13 individuals per plot, ranging from 54 individuals (CMP1) to 2 (CMP3).

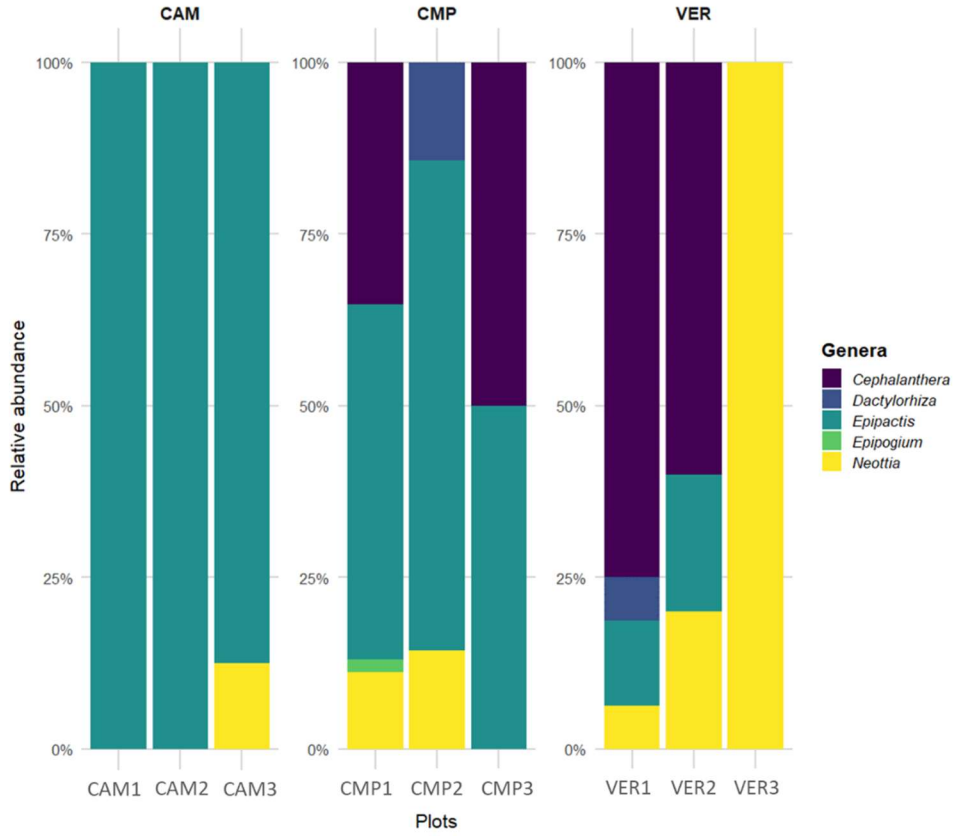


Figure 6. Relative abundance and distribution of *Orchidaceae* genera across sites and plots.

The analysis of the Orchid Community in terms of trophic strategy (Figure S4) or distribution range (Figure S5) revealed that the most abundant species were mixotrophic and with a wide range.

Mycoheterotrophic and narrow distribution species were present at all sites, often with lower abundance (except for VER3). A correlation matrix, ordered according to hierarchical clustering, was conducted to better understand the grouping of the Orchid Community and plots (Figure 7).

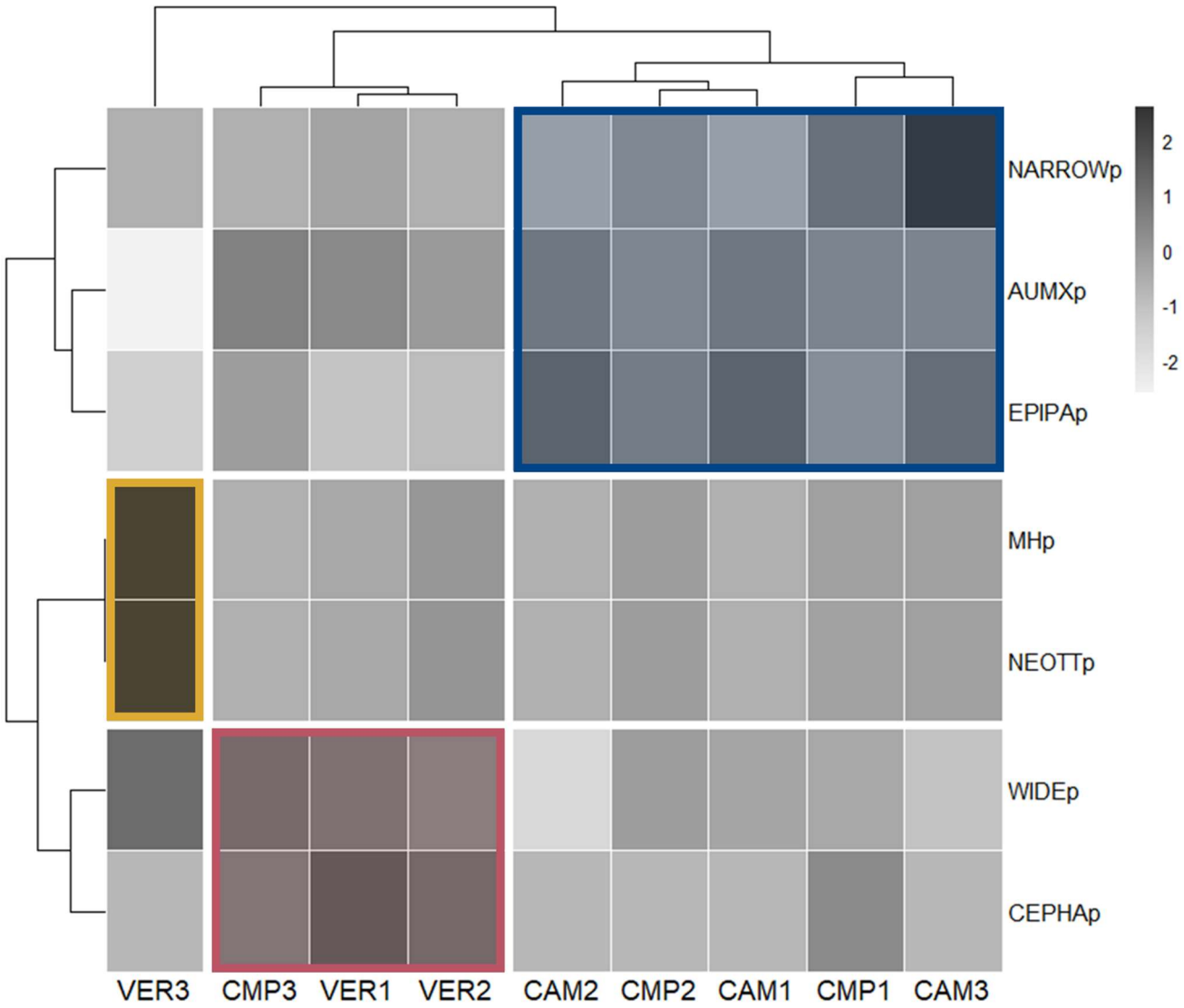


Figure 7. Correlation matrix ordered according to the hierarchical clustering of plots based on the Orchid Community. All orchid variables were calculated as percentage *p*-values.

Interestingly, plot clustering according to similarity in the Orchid Community well reflected the classification made with the Structural Indicators (SIs; Figure 5). The cluster with VER3 (yellow; old-growthness, beech dominance) had a higher presence of mycoheterotrophs (MHps), all represented by the genus *Neottia* (NEOTTp). Most plots (blue; CMP 1-2 and CAM 1-3), including cathedral-like silver fir stands, were characterised by a high abundance of the genus *Epipactis* (EPIPAp) and, only in some plots (especially CAM3), by a higher percentage of narrow range

species (NARROWp). In contrast to the SI classification, Orchid Community clustering associated CMP3 (cathedral-like silver fir stands) to VER 1-2 (red; mixed forests with high beech density and regeneration), due to the presence of widely distributed orchids (WIDEp) and the abundance of the genus *Cephalanthera* (CEPHAp). The last two clusters shared also the highest frequency of autotrophic/mixotrophic species (AUMXp).

4.5.3. Forest Structure and Orchid Community Relations

The joint PCA analysis (Figure 8) made on selected Structural Indicators and Orchid Community metrics arranged plots primarily along an increasing gradient of old-growthness (PC1, 64.5% total variance) and then along species composition (PC2, 23.8% total variance). The composition varied from mixed forests dominated by beech to pure silver fir forests. Along the PC1 axis, positive PC1 loadings (VER3) featured higher values of structural complexity and old-growth attributes (e.g., coefficient of variation, deadwood volume, large tree volume) where mycoheterotrophic species (MH), i.e., *Neottia* (NEOTTp), prevailed. Under these conditions, high broadleaved regeneration was accompanied by advanced silver fir regeneration (Figures 2 and 3), whose shadow depressed the establishment of autotrophic-mixotrophic species (AUMXp). Negative PC1 loadings characterised even-aged, biostatic forests with low regeneration (CMP and CAM plots). On the PC2, these plots with negative loadings were dominated by silver fir with a higher frequency of *Epipactis* (EPIPAp) and narrow range species (NARROWp). These were juxtaposed to mixed forests with abundant beech and high beech regeneration (positive loadings, VER 1-2), where the genus *Cephalanthera* (CEPHAp) is widely distributed (WIDEp).

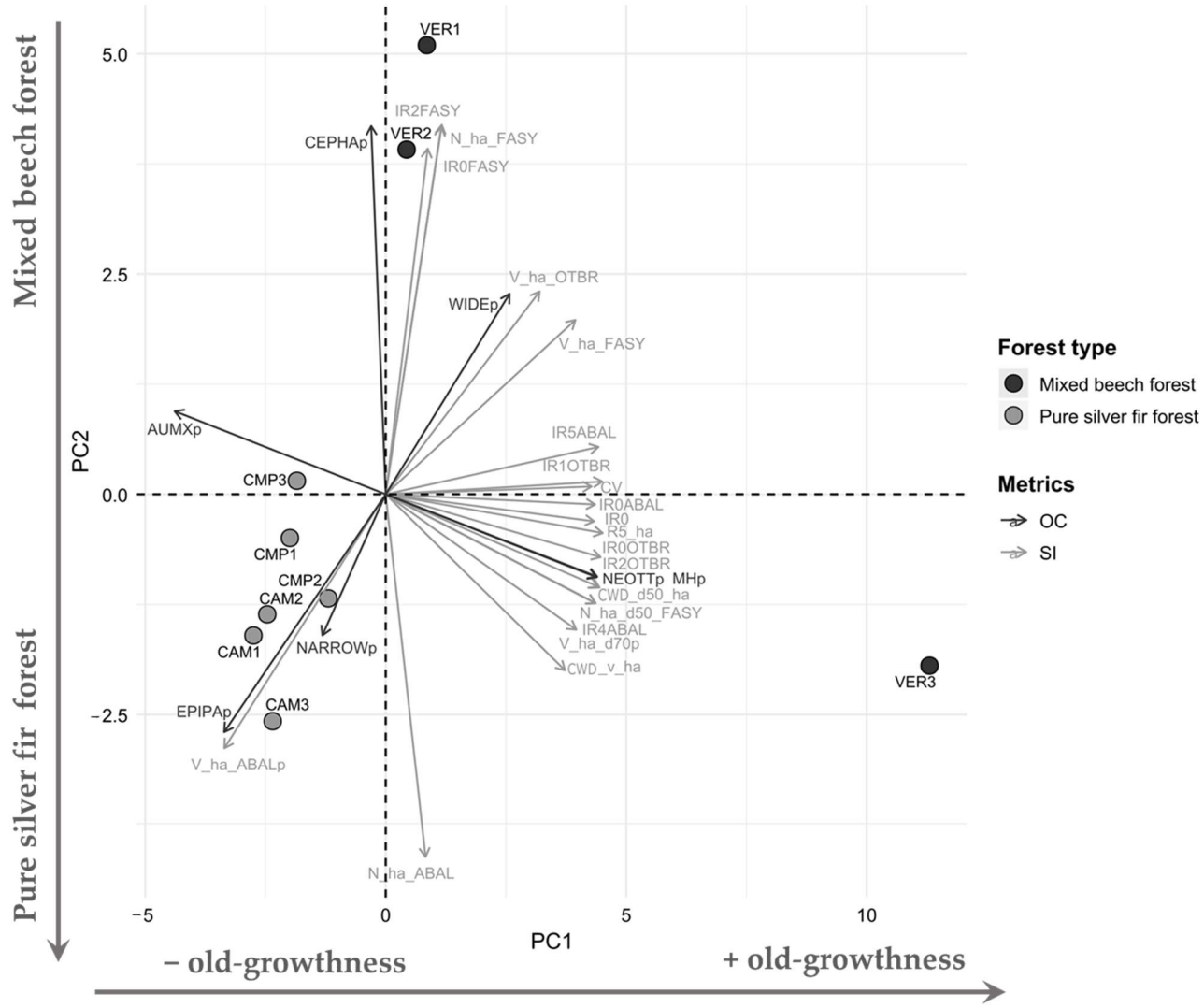


Figure 8. PCA loadings biplot illustrating the relationship between Structural Indicators (SIs, grey arrows) and Orchid Community (OC, black arrows) metrics. Dots indicate the plots coloured according to the forest type. The PCA explained 88.3% of total variance.

4.5.4. Modelling the Orchid Community According to Forest Features

Among the Orchid Community descriptors, we focused the modelling on those showing good correlations: (1) plot abundance of genus *Epipactis* (six species; four with narrow distribution; one endangered and one nearly-threatened species); (2) plot abundance of genus *Cephalanthera* (three species); (3) plot abundance of mycoheterotrophs (two species, one with narrow distribution); (4) plot abundance of narrow distributed species (five species). Widespread and autotrophic/mixotrophic species showed low correlation and were therefore not considered.

The best models between Orchid Community features and forest structure were reported in Table 4, alongside with their goodness-of-fit metrics, while the analysis of regression residuals was reported in Table S3. To predict the relative abundance of *Epipactis* sp.pl. (Table 4, Model 1) and

Cephalanthera sp.pl. (Table 4, Model 2), the best model based on the AIC value was the linear model (LM); to predict the relative abundance of mycoheterotrophic species (Table 4, Model 3), the best model was the nonlinear least-squares regression (NLS); to predict the relative abundance of narrow range species (Table 4, Model 4), the best model was the second-degree polynomial (Poly2). All univariate models performed better than bivariate ones in terms of AIC values, avoiding collinearity among predictors (Table 4).

Table 4. AIC values of the univariate and multivariate models. Selected models (bold) are linear model (LM), second-degree polynomial model (Poly2), and nonlinear least-squares model (NLS) with the lowest AIC. NA indicates the lack of fit for NLS.

	AIC Values						Goodness-of-Fit	
	LM		Poly2		NLS		Final Model	
	Univariate	Bivariate	Univariate	Bivariate	Univariate	Bivariate	R^2	*p*-value
Model 1 (*Epipactis* sp.pl.)	**83.19**	84.03	83.59	-	83.87	-	0.76	0.0023
Model 2 (*Cephalanthera* sp.pl.)	**82.42**	84.39	84.41	-	NA	-	0.66	0.0077
Model 3 (Mycoheterotrophic species)	75.48	-	69.46	-	**66.15**	NA	0.95	0.0002
Model 4 (Narrow range species)	74.09	-	**74.03**	76.54	NA	-	0.78	0.0046

The relative abundance of *Epipactis* was mainly predicted by silver fir dominance (Table 4, Model 1; Figure 9), confirming the strong dependency of the species of this genus on the conditions found in pure and mature fir stands, where their average abundance was 75% compared to 12% in mixed stands, with less than 30% biomass made of fir (t-test: *p*-value = 0.002).

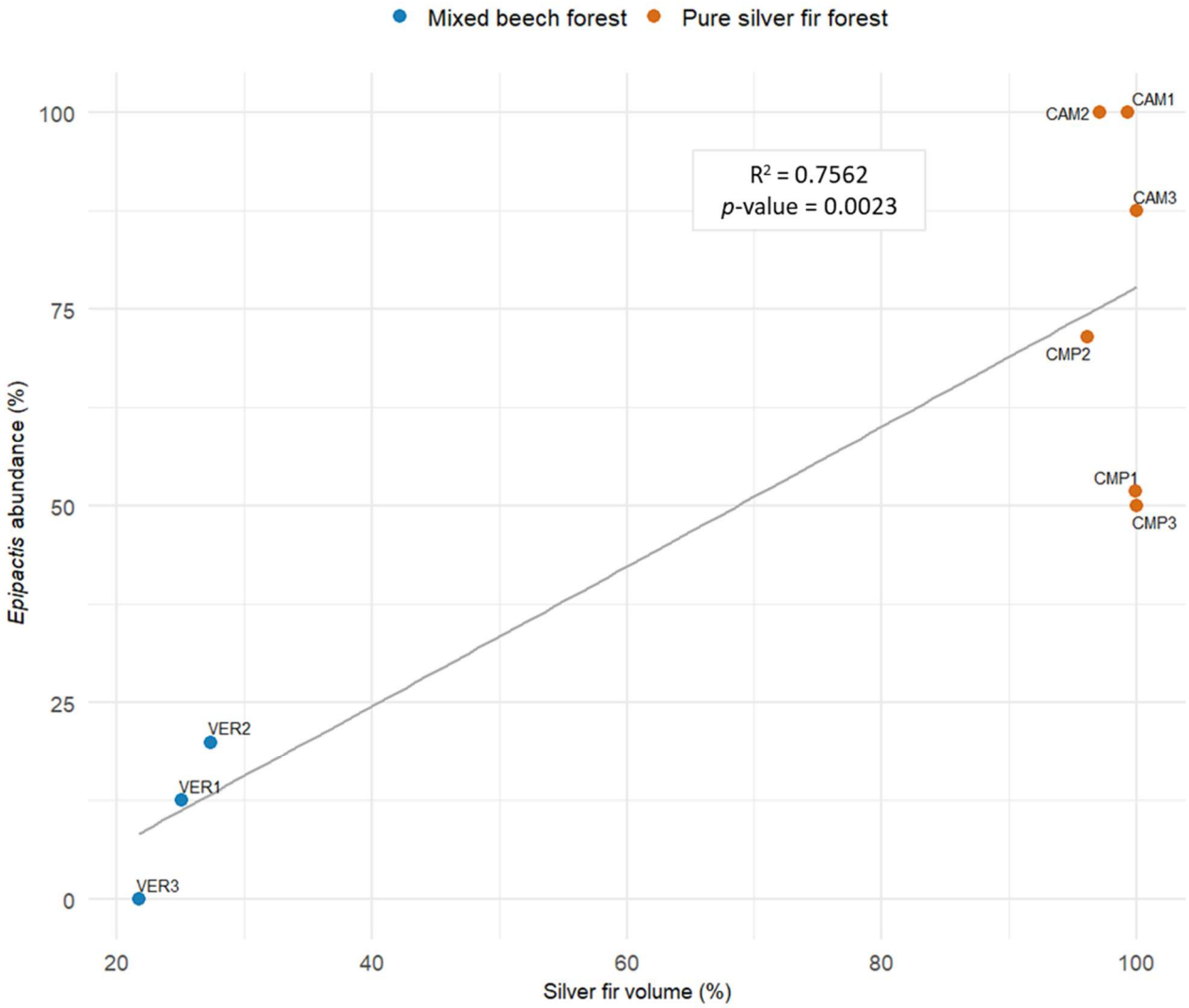


Figure 9. Linear regression (LM) modelling the relative abundance of the genus *Epipactis* with silver fir volume at the plot level (Model 1, Table 4).

Conversely, the genus *Cephalanthera* was negatively affected by the density of silver fir (Figure 10). Fir density below 250 stem ha^{-1} provided increases in *Cephalanthera* up to 50% of the overall diversity, while values exceeding 350 stem ha^{-1} *Cephalanthera* declined below 30%. This pattern held both for mixed forests (VER 1-2) and low-density fir stands (CMP3). Among the mixed forest plot, VER3 was the only one without *Cephalanthera*; this plot had the highest density of established silver fir regeneration (Figures 2 and 3).

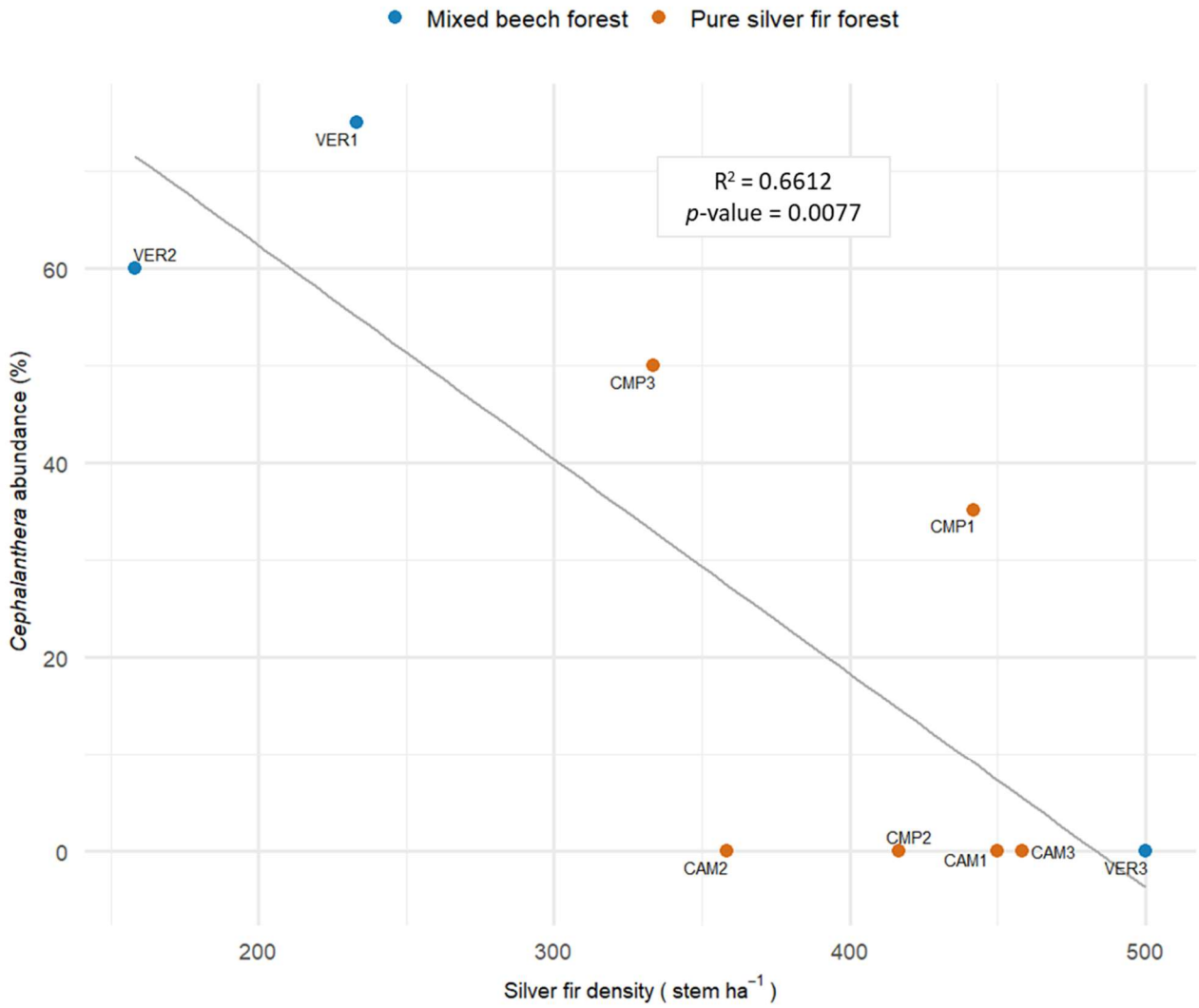


Figure 10. Linear regression (LM) modelling the relative abundance of genus *Cephalanthera* and the density of silver fir at the plot level (Model 2, Table 4).

The abundance of fully mycoheterotrophic species (*Neottia nidus-avis* and *Epipogium aphyllum*, MH) was directly predicted by the percentage of volume in large trees (DBH > 70 cm) (Figure 11). Mycoheterotrophic species accounted for 0 to 15% of the Orchid Community if the large tree volume was less than 20%, and increased to 100% in the case with the largest shares (50%). Furthermore, their relative abundance is directly related to the coefficient of variation (CV) and the CWD volume (Figure S6).

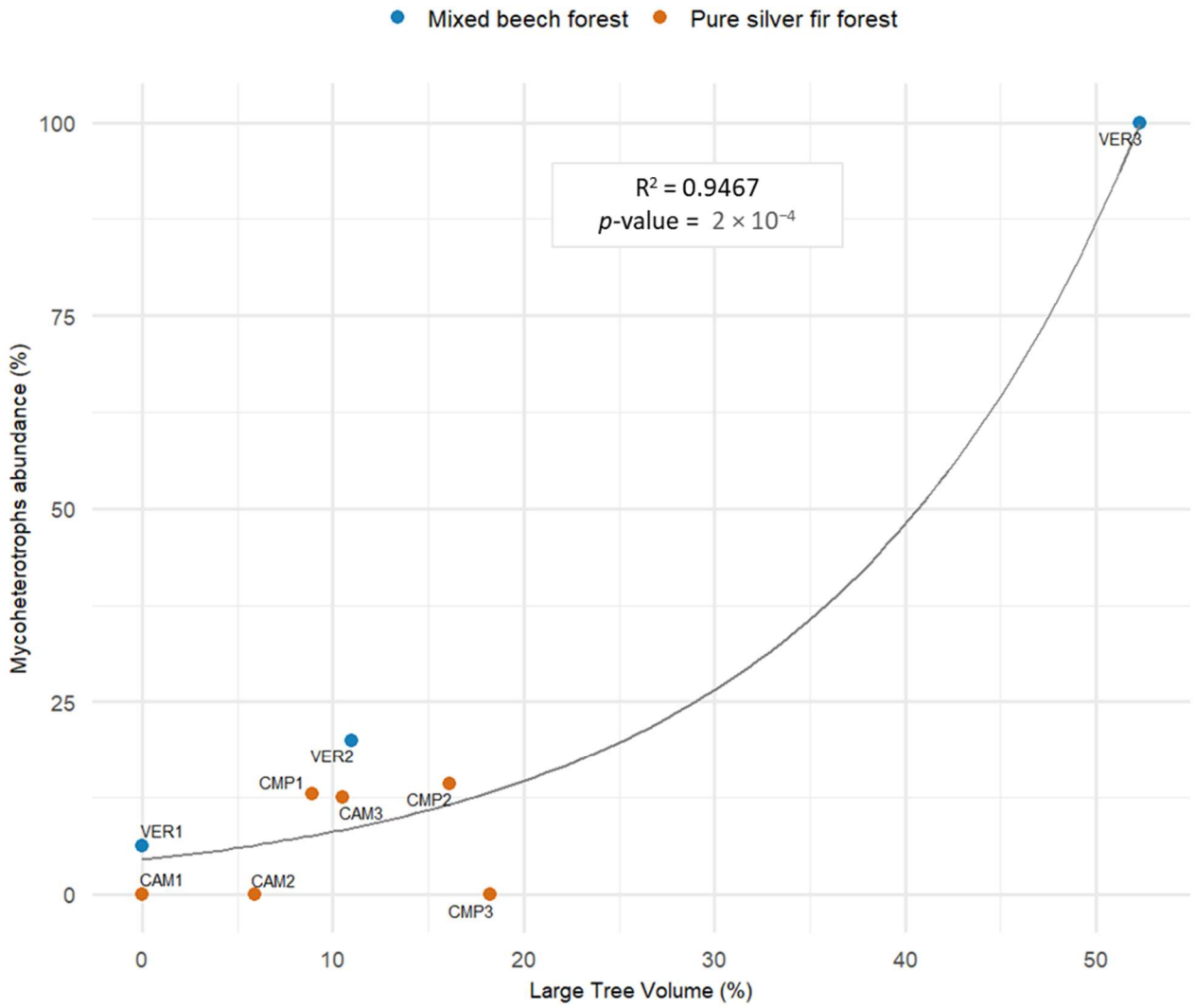


Figure 11. Nonlinear least-squares regression (NLS) modelling the relative abundance of fully mycoheterotrophic species (*Neottia nidus-avis* and *Epipogium aphyllum*) and the volume of large trees (DBH > 70 cm) (Model 3, Table 4).

Orchid species with limited distribution (*Epipactis exilis*, *E. greuteri*, *E. leptochila*, *E. purpurata,* and *Epipogium aphyllum*) were directly related to the cumulative deadwood density (CWD + SDT; Figure 12). The highest values were reached in pure silver fir forest plots, with the maximum in CAM3.

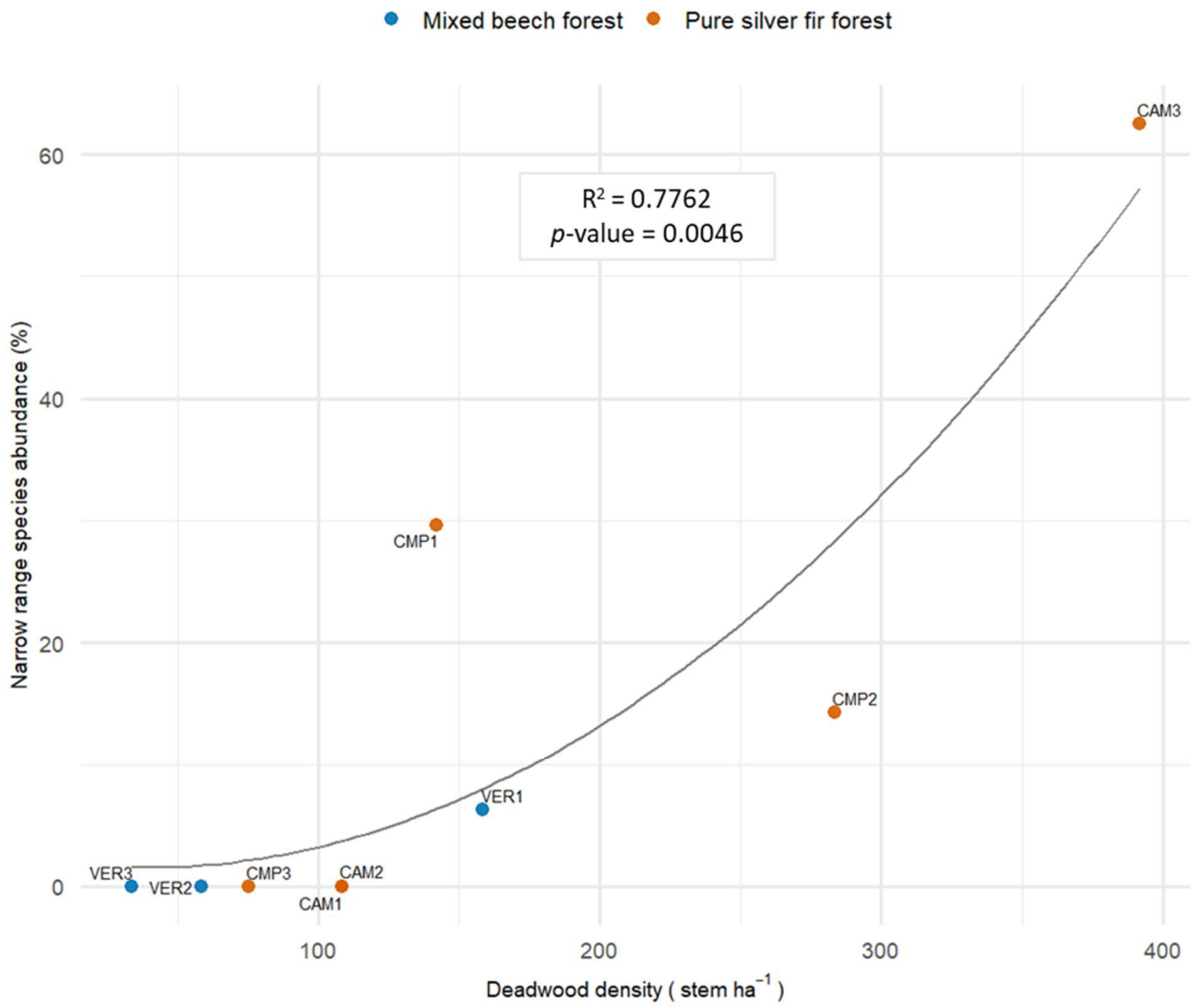


Figure 12. Second-degree polynomial (Poly2) regression modelling the relative abundance of narrow range species and the density of total deadwood (CWD + SDT) (Model 4, Table 4).

4.6. Discussion

Forest structure could be related to the presence of orchid species in various ways, which must be considered individually. The structure of the stands can be broken down and analysed into two main components: species composition and old-growthness. The relations between forest orchids and plots should be examined by comparing structural metrics with the groups of species associated with them.

For soil aspects, although partly comparable among the study sites, local differences in lithology and soil properties may additionally affect the presence of orchids either directly (e.g., pH, Cation Exchange Capacity, nutrients, etc.) [23] or indirectly (e.g., tree height, forest composition) [3]. However, we acknowledge that the lack of enough replications in our study does not allow for fully disentangling the relative effects of tree community vs. soil features on the presence of orchids.

Forest structure could be related the presence of orchid species in various ways, which must be considered individually. The structure of the stands can be broken down and analyzed into two main components: species composition and old-growthness. The relations between forest orchids and transects should be examined by comparing structural metrics with the groups of species associated with them.

4.6.1. Tree Composition and Orchid Diversity

Orchid species diversity was highly variable among the plots (one to eight species) but reached high values both in pure and mixed silver fir forests. In particular, one pure silver fir plot (CMP1) hosted the highest number of orchid species found (8). In general, beech forests host most of the European forest orchid species [3,111], but a significant number can also be present in conifer forests [3]. It has been observed that, in contexts dominated by broadleaf trees, forest orchids avoid conifer-dominated zones [112], attributing their absence to substrate acidification caused by needle litter [112,113]. The high widespread presence especially of *Epipactis* sp.pl. in our silver fir-dominated sites is therefore noteworthy.

The abundance of the main genera of our Orchid Community (*Epipactis* and *Cephalanthera*, 9/12 species found) was anticorrelated and highly dependent on tree composition and light availability. *Epipactis* was the main genus in silver fir-dominated cathedral-like forests, reaching 100% when fir exceeded 90% dominance and preferring even-aged, biostatic tree communities without established regeneration and relatively scarce light conditions. Similar to other forest orchid species, *Epipactis* responds differently to light conditions [3]. Canopy closure has been observed to reduce the reproductive success of *E. helleborine* [114], even if it is possible that shaded conditions promote the production of heavier seeds, and therefore higher seedling survival rates [115]. *Epipactis* species are also associated with a wide range of fungal species [26,29,98,116–118]. The initial germination process of *Epipactis* does not necessarily depend on the presence of specific symbionts, and *Epipactis* species with different ecological requirements share similar mycorrhizal partners during germination [119]. A high presence of ectomycorrhizal symbionts associated with silver fir has been confirmed, even in very small areas [120]. Furthermore, large, mature plants of different species can promote high diversity in fungal communities associated with their roots [121], even if simply co-occurring in nearby habitats [119].

Cephalanthera species responded positively to conditions characterised by greater light availability associated to structural heterogeneity and the dominance of beech both in the dominant and regeneration layer, with scarce fir regeneration. In southeastern England, *C. damasonium* was able

to colonize rapidly young beech plantations [122]. *C. longifolia* has high photosynthetic efficiency and can benefit from higher light intensity conditions [123]. In *C. damasonium*, carbon gain can increase by 52% when transitioning from a more illuminated forest habitat (open pine forest) to a darker one (dark beech forest) [124–126]. Increased light exposure can lead *Cephalanthera* species (*C. damasonium* and C. *longifolia*) to transition from partially mycoheterotrophy to autotrophy, thereby balancing the use of naturally available carbon [127]. Light response can also affect physiological and reproductive efficiency [3], i.e., reductions in dormancy and the number of flowers due to low light conditions (*C. longifolia* [128,129]) or the reduced fruit set rates caused by dense tree and shrub cover (*C. rubra* [130]).

4.6.2. Trophic Strategies in Orchids and Old-Growth Attributes

Fully mycoheterotrophic species increased with old-growth features, i.e., higher dominance of large trees (DBH > 70 cm), deadwood (CWD) volume, and structural complexity. One of the best predictive factors was the amount of downed deadwood, confirming that these orchids depend on ground deadwood for carbon [30,117,131], differing in their life cycle from orchids associated with leaf-litter-decaying fungi [132]. Mycoheterotrophs were favoured by deadwood in the form of large logs with advanced decomposition stages (Table 5), which confirmed their preference for habitat integrity [133]. Their presence in several pure fir plots and their prevalence in multilayered forests with established fir regeneration and lower light availability at the ground (i.e., VER3) confirmed the shade tolerance of mycoheterotrophic species [134]. VER3 differed in many aspects from all other plots. However, we primarily interpreted its features to the structural variability associated to old-growth forests and their mosaic-like, multilayered structure and, therefore, we did not consider it as an outlier to be excluded from the analyses.

Rare species within the NP responded positively to the overall deadwood density (CWD + SDT), with substantial increases when the density was > 200 elements per ha. The total deadwood counted per ha includes both downed deadwood (CWD) and standing deadwood (SDT) at various decay stages. Contrarily to mycoheterotrophs, rare species were more related to medium/small size deadwood (no need of large, decomposed logs). Almost all rare orchids were autotrophic/mixotrophic *Epipactis*, but included also the mycoheterotroph *Epipogium aphyllum* (only at CMP1). Overall, rare species are present in cathedral-like even-aged silver fir forests (promoting *Epipactis*) with prevailing self-thinning/self-pruning producing small deadwood (promoting *Epipogium aphyllum*). Mycorrhizal formation within specific microhabitats may be difficult and influence orchid abundance [135] and the rarity of terrestrial orchids is both the cause and consequence of high mycorrhizal specialisation [136]. Nevertheless, the biological differences

of our rare taxa demonstrated the need for further research to investigate separately and with more detail the ecology of rare species.

According to the variety of the ecology and the trophic strategies possessed by orchid species in forests with silver fir in the National Park, an ensemble of approaches must be implemented to maximize the conservation and promote the restoration of orchid diversity. Specifically, maintaining or restoring tree communities with mixed rather than pure silver fir, with even-aged or complex structure, and with different degrees of old-growth attributes may lead to the presence and abundance of some taxa rather than others (Table 5).

The presence of mycoheterotrophs (MHs) may be promoted by allowing for the development of old-growth conditions that generate large trees (>stems ha^{-1}), a tree community with high coefficient of variation (>) and, especially, substantial deadwood accumulation (>m^3 ha^{-1}) (Table 5). Rare species (localised distribution within the NP) are mainly represented by *Epipactis* sp.pl. and are, therefore, favoured in cathedral-like pure silver fir forests (770–1140 m^3 ha^{-1}, 90–100% silver fir). These conditions were also associated to a high density of small deadwood (medium/small size CWD and SDT, c. 200–400 per ha), a factor probably favouring the mycoheterotroph *Epipogium aphyllum*. Such conditions also allowed for hosting the only two globally threatened (e.g., *Epipactis microphylla*, *E. greuteri*) orchids in our dataset, stressing once again the importance of conserving pure mature fir stands.

As a preferential habitat for *Epipactis* sp.pl., which comprised 50% of the orchid species found in this study, pure silver fir mature forests conservation is key in the area. The other main genus, *Cephalanthera*, needed instead opposite conditions, i.e., lower silver fir density (<350 stems ha^{-1} focus on composition), as well as a significant proportion of beech in the canopy and in the regeneration layer. Forests with a more complex, multilayered structure with sufficient light availability would promote the presence of *Cephalanthera*, especially in areas where *Cephalanthera* species are threatened [137,138].

Table 5. Reference values of forest attributes (rounded) related to the occurrence and relative abundance of the studied Orchid Community.

Forest Features	**Large Trees**	**CWD**	**Deadwood**	**Silver Fir**		**Preferred Forest Structure**
Values	% Volume	Volume (m^3 ha^{-1})	Density (stem ha^{-1})	% Volume	Density (stem ha^{-1})	
Mycoheterotrophic species (abundance > 25%)	>30	>55	-	-	-	Complex, old-growth structure with decaying CWD

Narrow range species (abundance > 25%)	-	-	>270	-	-	Mature, self-thinning/self-pruning pure fir
Cephalanthera (abundance > 50%)	-	-	-	-	<250	Angiosperm dominant, scarce fir regeneration
Epipactis (abundance > 50%)	-	-	-	>70	-	Mature, pure fir

4.6.3. Recommendations

To maximize the overall biodiversity of the Orchid Community, both in terms of abundance and dominance, the forest structure should include a mosaic of different structural phases. In fact, fir-dominated mature patches favour *Epipactis*, self-thinning forest patches with small deadwood favour *Epipogium*, uneven-aged patches dominated by angiosperms favour *Cephalanthera* and, finally, degradation patches with dominant tree mortality and large deadwood favour *Neottia*. Such a structure characterizes natural temperate forests with a mixed disturbance regime characterised by gap-dynamics, that could ideally benefit the entire ecological spectrum of the orchid diversity described [139]. In any case, the conservation of orchid communities is closely tied to natural forest processes and the preservation of older forest areas, and the attributes associated to forest age both in mature and old-growth tree communities, such as self-thinning or snag/log abundance [41].

In summary, localised changes in the vertical structure and texture of forests can profoundly impact the presence of certain orchid species. Implementing targeted management practices may facilitate the abundance of specific forest orchid taxa, depending on conservation goals. This highlights valuable opportunities for future research that could refine forest management practices, emphasising the preservation of species that are critically threatened at both European and global scales.

However, it must be considered that the study of forest orchids is highly limited by their rarity and spotty distribution. Moreover, forests left to regenerate naturally are increasingly threatened by human intervention, making it difficult to understand their dynamics [61]. Further in-depth case studies from different environments are highly required to adequately document the effects of forest structure on orchid communities [38,39]. The availability of larger samples exploring wider environmental gradients will help in addressing with more confidence the interplay among forest structure and site factors (such as soil, temperature, light, etc.) [21,23] and providing our results with more generality. In particular, the use of quantitative results in ecological restoration projects as the one reported here must carefully assess possible alterations by silvicultural activities to the

forest microclimate and soil and, consequently, to the Orchid Community. Providing recommendations in these cases is challenging because they must be based on the most objective criteria. Also, the risks connected to future climate change impacts must be monitored in situ to determine the long-term efficacy of any action [17]. In this context, given their unique trophic role within ecosystems and their sensitivity to drought, orchid taxa may represent important indicators of climate change impacts on forest ecosystems.

Supplementary Materials: The following supporting information can be downloaded at: www.mdpi.com/xxx/s1. Figure S1: Indices of Regeneration (IR1-5); Figure S2: PCA of Structural Indicators (SIs); Figure S3: Orchid species abundance; Figure S4: Trophic regime abundance; Figure S5: NP distribution abundance; Figure S6: Mycoheterotrophs model regressions; Table S1: Soil texture and carbon content; Table S2: List of Structural Indicators (SIs); Table S3: Residual validation tests.

Author Contributions: Conceptualization, A.D.F. and A.P.; methodology, A.D.F. and A.P.; formal analysis, A.P.; writing—original draft preparation, A.D.F. and A.P.; writing—review and editing, A.D.F., A.P., S.M., K.C., B.S. and P.L.; supervision, B.S. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The original contributions presented in this study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

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Conflicts of Interest: The authors declare no conflicts of interest.

4.7. Supplementary materials

Table S1. Soil texture values (percentage of sand, silt, and clay), and total percentage of carbon (TOC, SOM) for each site.

		Value (%)		
	Site	**CMP**	**CAM**	**VER**
Soil texture	Sand	72.9	82.1	80.1
	Silt	21.9	7.1	8.5
	Clay	5.3	10.8	11.4
Carbon	Total organic carbon (TOC)	2.7	3.8	2.4
	Soil organic matter (SOM)	4.7	6.5	4.2

Table S2. Structural Indicators (SI): variables highlighted in gray were selected through PCA screenings. Final variables used are shown in bold. Variables are categorized by type: live biomass (LIVING), deadwood (DEAD) and forest regeneration (REGEN). The sub-type indicates whether the variable relates to old-growth characteristics (OG). The group identifies similar variables from which a selection was made.

ID	**Metric**	**Unit**	**Description**	**Type**	**Sub-type**	**Group**
1	N_ha	stem ha^{-1}	Total number of stems per ha	LIVING		a
2	**N_ha_ABAL**	**stem ha^{-1}**	**Number of *A. alba* stems per ha**	**LIVING**		**a**
3	N_ha_OTBR	stem ha^{-1}	Number of other broadleaves stems per ha	LIVING		
4	**N_ha_FASY**	**stem ha^{-1}**	**Number of *F. sylvatica* stems per ha**	**LIVING**		**a**
5	BA_ha	m^2 ha^{-1}	Total Basal Area per ha	LIVING		b
6	BA_ha_ABAL	m^2 ha^{-1}	Basal Area of *A. alba* per ha	LIVING		b
7	BA_ha_OTBR	m^2 ha^{-1}	Basal Area of other broadleaves per ha	LIVING		b
8	BA_ha_FASY	m^2 ha^{-1}	Basal Area of *F. sylvatica* per ha	LIVING		b
9	V_ha	m^3 ha^{-1}	Total volume per ha	LIVING		b
10	V_ha_ABAL	m^3 ha^{-1}	Volume of *A. alba* per ha	LIVING		b
11	**V_ha_OTBR**	**m^3 ha^{-1}**	**Volume of other broadleaves per ha**	**LIVING**		**b**
12	**V_ha_FASY**	**m^3 ha^{-1}**	**Volume of *F. sylvatica* per ha**	**LIVING**		**b**
13	**V_ha_ABALp**	**%**	**Percentage of volume per ha of A. alba**	**LIVING**		**b**
14	V_ha_OTBRp	%	Percentage of volume per ha of other broadleaves	LIVING		b
15	V_ha_FASYp	%	Percentage of volume per ha of *F. sylvatica*	LIVING		b

16	N_ha_d50	stem ha^{-1}	Total number of stems per ha of large trees with DBH> 50 cm	LIVING	OG	ao
17	N_ha_d70	stem ha^{-1}	Total number of stems per ha of large trees with DBH> 70 cm	LIVING	OG	ao
18	N_ha_d50p	%	Percentage of number of stems per ha of large trees with DBH> 50 cm	LIVING	OG	ao
19	N_ha_d70p	%	Percentage of number of stems per ha of large trees with DBH> 70 cm	LIVING	OG	ao
20	N_ha_d50_ABAL	stem ha^{-1}	Percentage of number of stems per ha of *A. alba* large trees with DBH> 50 cm	LIVING	OG	ao
21	N_ha_d70_ABAL	stem ha^{-1}	Percentage of number of stems per ha of *A. alba* large trees with DBH> 70 cm	LIVING	OG	ao
22	N_ha_d50_OTBR	stem ha^{-1}	Percentage of number of stems per ha of other broadleaves large trees with DBH> 50 cm	LIVING	OG	ao
23	N_ha_d70_OTBR	stem ha^{-1}	Percentage of number of stems per ha of other broadleaves large trees with DBH> 70 cm	LIVING	OG	
24	**N_ha_d50_FASY**	**stem ha^{-1}**	**Percentage of number of stems per ha of *F. sylvatica* large trees with DBH> 50 cm**	**LIVING**	**OG**	**ao**
25	N_ha_d70_FASY	stem ha^{-1}	Percentage of number of stems per ha of *F. sylvatica* large trees with DBH> 70 cm	LIVING	OG	ao
26	BA_ha_d50	m^2 ha^{-1}	Basal Area per ha of large trees with DBH> 50 cm	LIVING	OG	bo
27	BA_ha_d70	m^2 ha^{-1}	Basal Area per ha of large trees with DBH> 70 cm	LIVING	OG	bo
28	V_ha_d50	m^3 ha^{-1}	Volume per ha of large trees with DBH> 50 cm	LIVING	OG	bo
29	V_ha_d70	m^3 ha^{-1}	Volume per ha of large trees with DBH> 70 cm	LIVING	OG	bo
30	V_ha_d50p	%	Percentage of volume per ha of large trees with DBH> 50 cm	LIVING	OG	bo
31	**V_ha_d70p**	**%**	**Percentage of volume per ha of large trees with DBH> 70 cm**	**LIVING**	**OG**	**bo**
32	**CV**	**%**	**DBH coefficient of variation**	**LIVING**		**c**
33	CWD		Coarse Woody Debris	DEAD		
34	SDT		Standing Dead Trees	DEAD		
35	CWD_ha	N ha^{-1}	Number of CWD per ha	DEAD		
36	SDT_ha	N ha^{-1}	Number of SDT per ha	DEAD		
37	**CWD_v_ha**	**m^3 ha^{-1}**	**Volume per ha of CWD**	**DEAD**		**d**
38	SDT_v_ha	m^3 ha^{-1}	Volume per ha of SDT	DEAD		
39	deg_CWD		Decay class of CWD	DEAD		d
40	deg_SDT		Decay class of SDT	DEAD		
41	pondeg_CWD		Weighted value of decay class of CWD	DEAD		
42	pondeg_SDT		Weighted value of decay class of SDT	DEAD		d
43	CWD_d50		Number of CWD with diameter > 50 cm	DEAD	OG	do
44	CWD_d70		Number of CWD with diameter > 70 cm	DEAD	OG	do
45	SDT_d50		Number of SDT with DBH > 50 cm	DEAD	OG	
46	SDT_d70		Number of SDT with DBH > 70 cm	DEAD	OG	
47	**CWD_d50_ha**	**N ha^{-1}**	**Number of CWD per ha with diameter > 50 cm**	**DEAD**	**OG**	**do**
48	CWD_d70_ha	N ha^{-1}	Number of CWD per ha with diameter > 70 cm	DEAD	OG	do
49	SDT_d50_ha	N ha^{-1}	Number of SDT per ha with DBH > 50 cm	DEAD	OG	
50	SDT_d70_ha	N ha^{-1}	Number of SDT per ha with DBH > 70 cm	DEAD	OG	
51	TOT		Total number of regeneration	REGEN		et
52	tot1		Regeneration of height class 1	REGEN		e1
53	tot2		Regeneration of height class 2	REGEN		e2
54	tot3		Regeneration of height class 3	REGEN		e3
55	tot4		Regeneration of height class 4	REGEN		e4

56	tot5	Regeneration of height class 5	REGEN	e5
57	**IR0**	**Total regeneration index**	**REGEN**	**et**
58	IR1	Index of Regeneration of height class 1	REGEN	e1
59	IR2	Index of Regeneration of height class 2	REGEN	e2
60	IR3	Index of Regeneration of height class 3	REGEN	e3
61	IR4	Index of Regeneration of height class 4	REGEN	e4
62	IR5	Index of Regeneration of height class 5	REGEN	e5
63	TOT_ABAL	Regeneration of *A. alba*	REGEN	et
64	tot1_ABAL	Regeneration of *A. alba* of height class 1	REGEN	e1
65	tot2_ABAL	Regeneration of *A. alba* of height class 2	REGEN	
66	tot3_ABAL	Regeneration of *A. alba* of height class 3	REGEN	
67	tot4_ABAL	Regeneration of *A. alba* of height class 4	REGEN	e4
68	tot5_ABAL	Regeneration of *A. alba* of height class 5	REGEN	e5
69	**IR0ABAL**	**Index of Regeneration of *A. alba***	**REGEN**	**et**
70	IR1ABAL	Index of Regeneration of *A. alba* of height class 1	REGEN	e1
71	IR2ABAL	Index of Regeneration of *A. alba* of height class 2	REGEN	
72	IR3ABAL	Index of Regeneration of *A. alba* of height class 3	REGEN	
73	**IR4ABAL**	**Index of Regeneration of *A. alba* of height class 4**	**REGEN**	**e4**
74	**IR5ABAL**	**Index of Regeneration of *A. alba* of height class 5**	**REGEN**	**e5**
75	TOT_FASY	Regeneration of *F. sylvatica*	REGEN	et
76	tot1_FASY	Regeneration of *F. sylvatica* of height class 1	REGEN	e1
77	tot2_FASY	Regeneration of *F. sylvatica* of height class 2	REGEN	e2
78	tot3_FASY	Regeneration of *F. sylvatica* of height class 3	REGEN	e3
79	tot4_FASY	Regeneration of *F. sylvatica* of height class 4	REGEN	
80	tot5_FASY	Regeneration of *F. sylvatica* of height class 5	REGEN	
81	**IR0FASY**	**Index of Regeneration of *F. sylvatica***	**REGEN**	**et**
82	IR1FASY	Index of Regeneration of *F. sylvatica* of height class 1	REGEN	e1
83	**IR2FASY**	**Index of Regeneration of *F. sylvatica* of height class 2**	**REGEN**	**e2**
84	IR3FASY	Index of Regeneration of *F. sylvatica* of height class 3	REGEN	e3
85	IR4FASY	Index of Regeneration of *F. sylvatica* of height class 4	REGEN	
86	IR5FASY	Index of Regeneration of *F. sylvatica* of height class 5	REGEN	
87	TOT_OTBR	Regeneration of other broadleaves	REGEN	et
88	tot1_OTBR	Regeneration of other broadleaves of height class 1	REGEN	e1
89	tot2_OTBR	Regeneration of other broadleaves of height class 2	REGEN	e2
90	tot3_OTBR	Regeneration of other broadleaves of height class 3	REGEN	e3
91	tot4_OTBR	Regeneration of other broadleaves of height class 4	REGEN	
92	tot5_OTBR	Regeneration of other broadleaves of height class 5	REGEN	
93	IR0OTBR	Index of Regeneration of other broadleaves	REGEN	et
94	**IR1OTBR**	**Index of Regeneration of other broadleaves of height class 1**	**REGEN**	**e1**
95	**IR2OTBR**	**Index of Regeneration of other broadleaves of height class 2**	**REGEN**	**e2**
96	IR3OTBR	Index of Regeneration of other broadleaves of height class 3	REGEN	e3
97	IR4OTBR	Index of Regeneration of other broadleaves of height class 4	REGEN	
98	IR5OTBR	Index of Regeneration of other broadleaves of height class 5	REGEN	

99	R5	Established regeneration of DBH class 5 cm	REGEN	f
100	R10	Established regeneration of DBH class 10 cm	REGEN	f
101	**R5_ha**	**Established regeneration per ha of DBH class 5 cm**	**REGEN**	**f**
102	R10_ha	Established regeneration per ha of DBH class 10 cm	REGEN	f

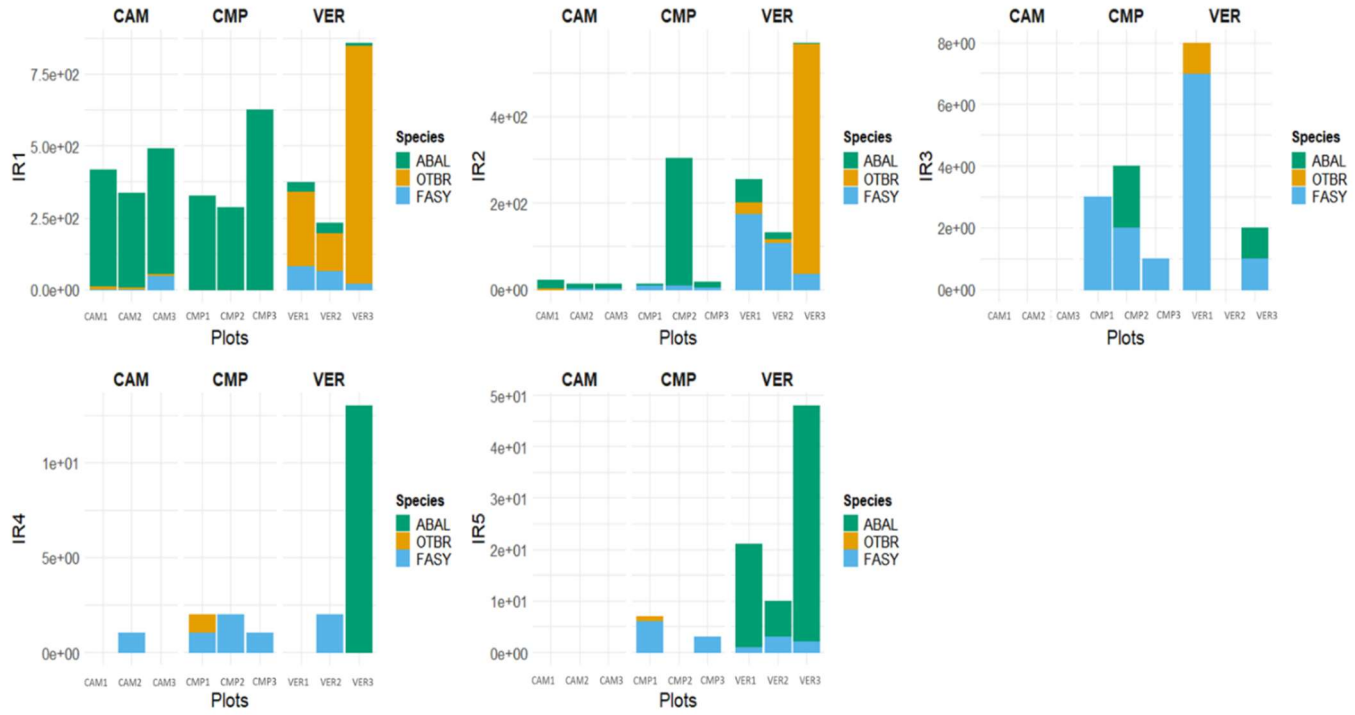


Figure S1. Indices of Regeneration according to tree composition (ABAL, *Abies alba*; FASY, *Fagus sylvatica*; OTBR, other broadleaves) and height classes (IR1: <10 cm; IR2: 11–50 cm; IR3: 51–150 cm; IR4: 151–300 cm; IR5: >300 cm).

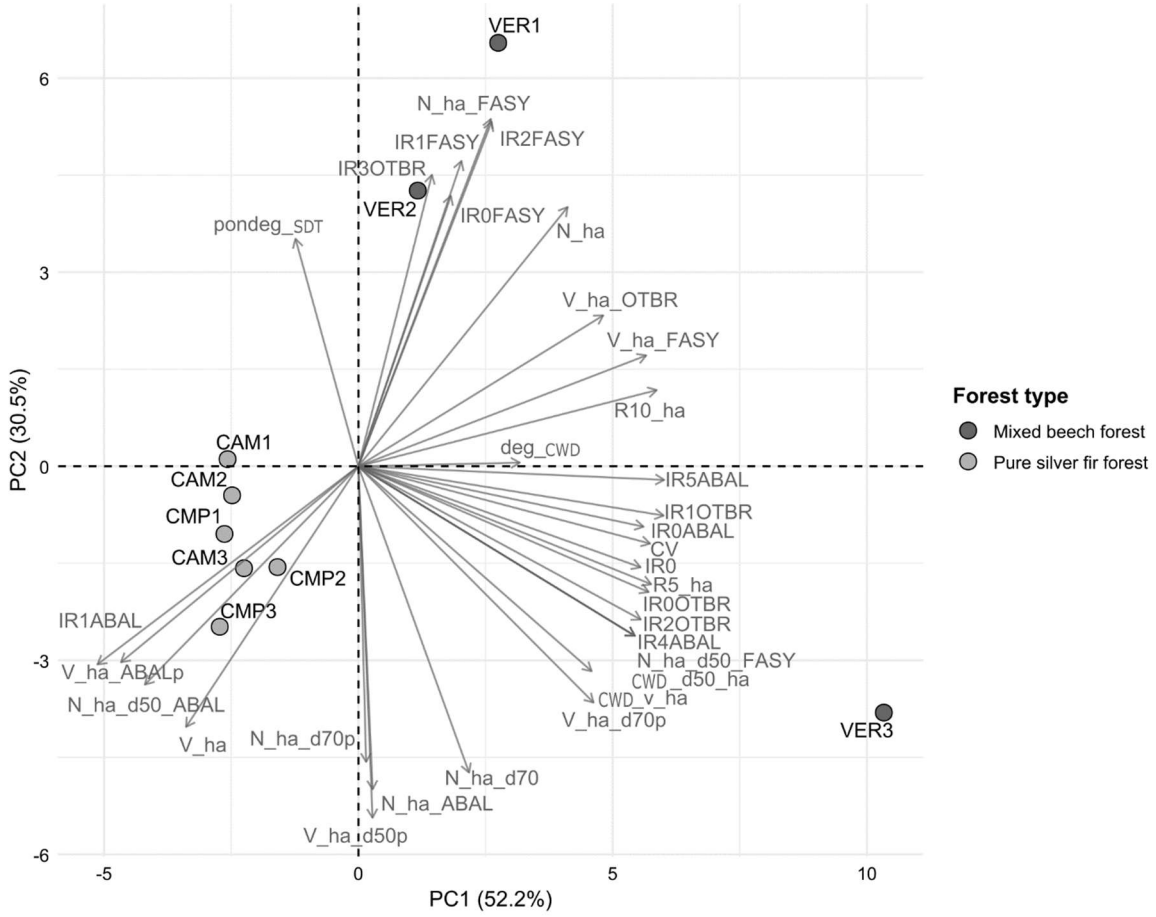


Figure S2. PCA loadings biplot illustrating the relationship among structural indicators (SI) and plots. Dots: plots coloured according to forest type. The PCA explained 82.7% of total variance.

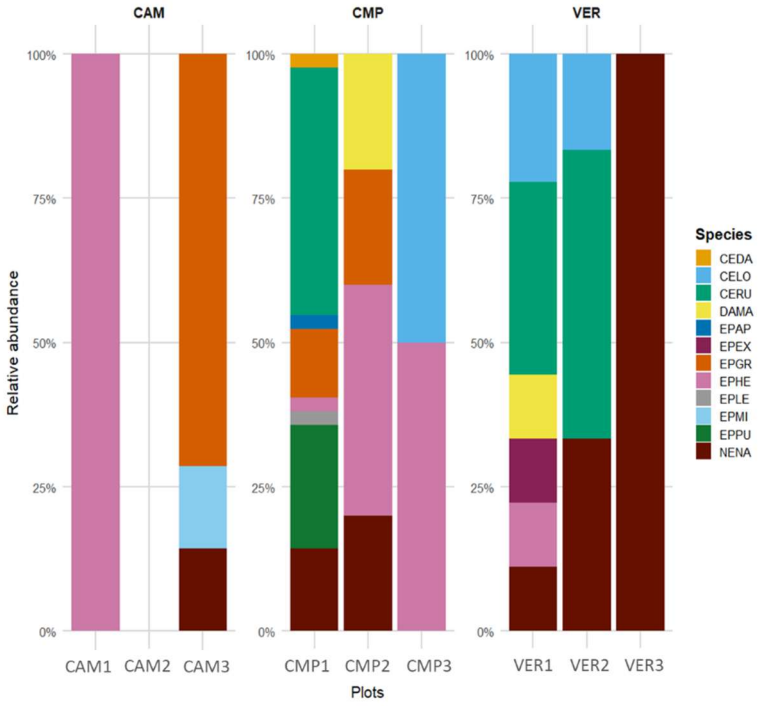


Figure S3. Relative abundance and distribution of *Orchidaceae* species across sites and plots. Bars were coloured according to orchid species (CEDA: *Cephalanthera damasonium*; CELO: *C. longifolia*; CERU: *C. rubra*; DAMA: *Dactylorhiza maculata* s.l.; EPAP: *Epipogium aphyllum*; EPEX: *Epipactis exilis*; EPGR: *E. greuteri*; EPHE: *E. helleborine*; EPLE: *E. leptochila*; EPMI: *E. microphylla*; EPPU: *E. purpurata*; NENA: *Neottia nidus-avis*).

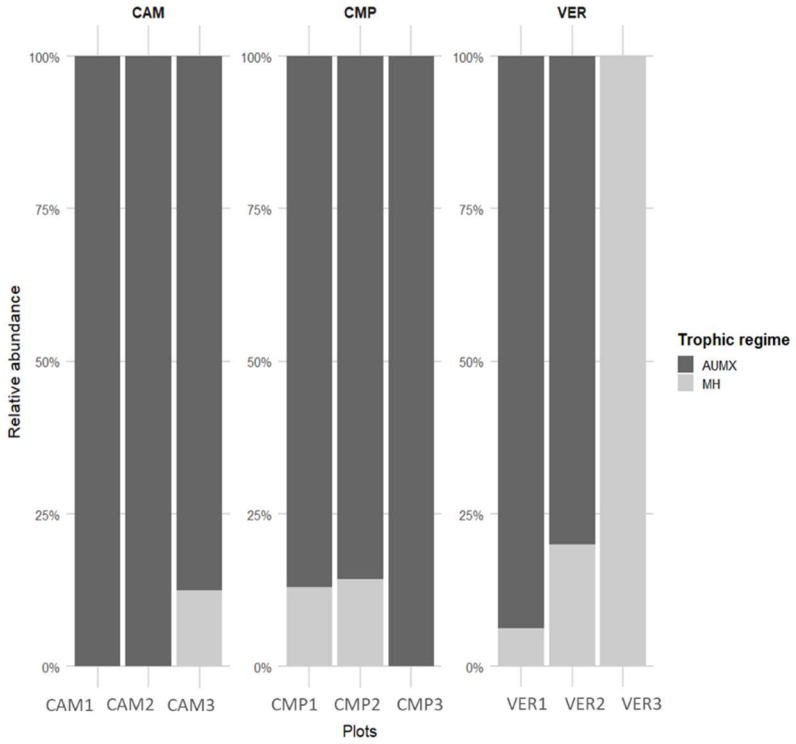


Figure S4. Relative abundance of orchid species classified according to their trophic regime across sites and plots (AUMX: Autotrophs/Mixotrophs; MH: Fully Mycoheterotrophs).

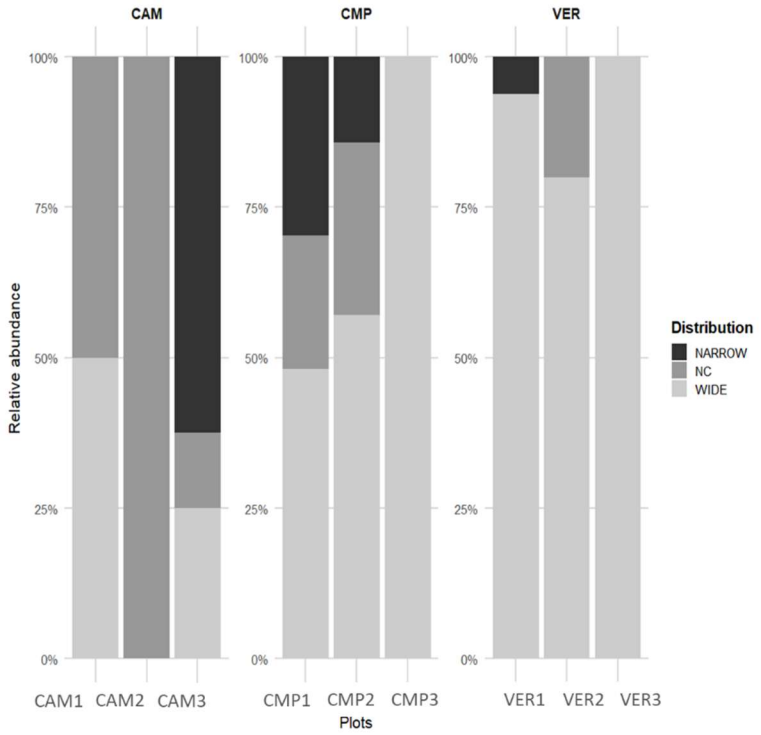
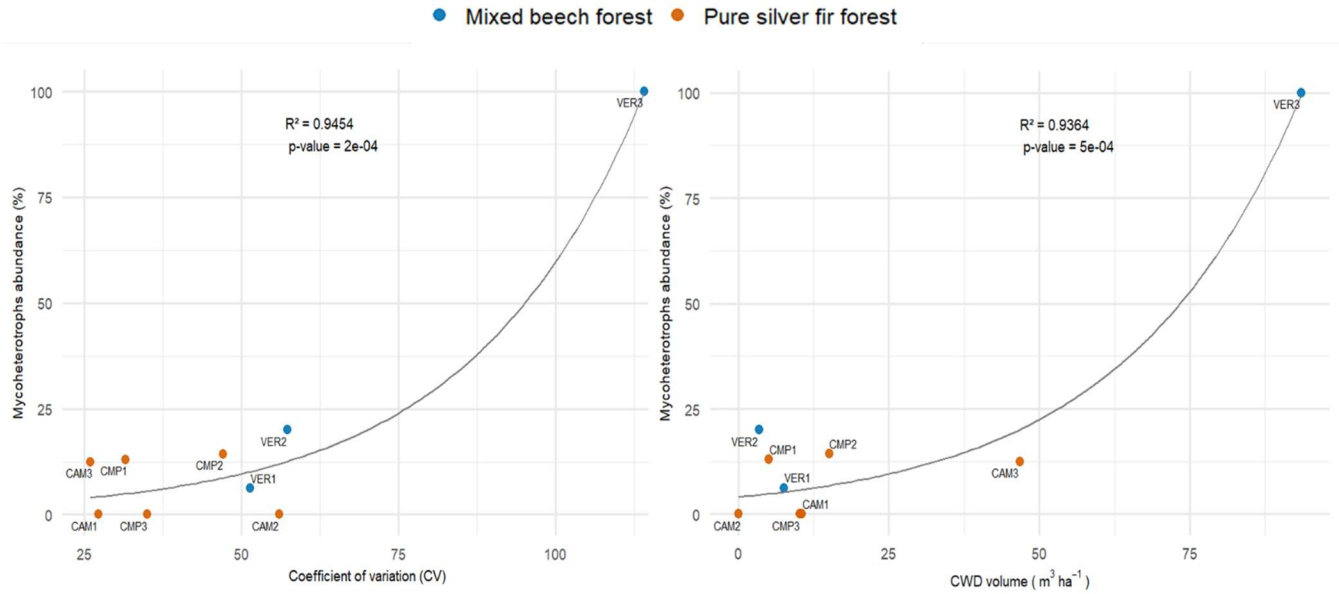


Figure S5. Relative abundance of orchid species classified according to their distribution in the study area across sites and plots (NARROW: Narrow range species; NC: Not-Classified species; WIDE: Widespread species).

Table S3. Residual validation tests confirmed the absence of violations of model assumptions, i.e. in terms of residuals normality (Kolmogorov-Smirnov test), homoscedasticity (Breusch-Pagan test), no autocorrelation in residuals (Durbin-Watson test).

Assumption	Residual normality		Homoscedasticity	Autocorrelation	
Test	*Kolmogorov -Smirnov*		*Breusch-Pagan*	*Durbin-Watson*	
	D	p-value	p-value	DW	p-value
Model 1 (*Epipactis* sp.pl.)	0.21	0.76	0.86	1.21	0.06
Model 2 (*Cephalanthera* sp.pl.)	0.19	0.83	0.46	2.33	0.69
Model 3 (Mycoheterotrophic species)	0.17	0.93	0.60	1.58	0.19
Model 4 (Narrow range species)	0.34	0.25	0.35	2.06	0.52



Assumption	Residual normality		Homoscedasticity	Autocorrelation	
Test	*Kolmogorov -Smirnov*		*Breusch-Pagan*	*Durbin-Watson*	
	D	p-value	p-value	DW	p-value
Model 5 (left)	0.20	0.78	0.67	2.17	0.51
Model 6 (right)	0.19	0.85	0.55	1.28	0.09

Figure S6. Nonlinear least-squares (NLS) regression modeling the relative abundance of fully mycoheterotrophic species (MH) with the Coefficient of Variation (left, Model 5) and CWD volume (right, Model 6). Residual validation tests confirmed the absence of violations of model assumptions, i.e. in terms of residual normality (Kolmogorov-Smirnov test), homoscedasticity (Breusch-Pagan test), no autocorrelation (Durbin-Watson test).

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5. Conclusion

The *Orchidaceae* family represents a key component of global biodiversity. These plants have gained significance not only from a purely cognitive perspective—driven by the human impulse to understand the world around us—but also for their medicinal, ornamental, and historical importance, among others. Their complexity makes them inherently fascinating, with their peculiar forms, vivid colors, fragrances, intricate pollination mechanisms, and distribution across the most diverse habitats worldwide. In this study, we decided to investigate some lesser-known aspects of this group, focusing particularly on orchids inhabiting European temperate forests. Our research is concentrated within one of the best-preserved protected areas in Italy: the "Parco Nazionale delle Foreste Casentinesi, Monte Falterona e Campigna" National Park (PNFC).

To achieve a comprehensive understanding of the ecological aspects of such a complex plant group, it is essential to conduct research at multiple levels. For this reason, our investigation followed a stratified approach, moving from general to specific. We examined the responses of *Orchidaceae* to various factors, both macro and micro, across spatial and temporal scales. The PNFC emerges as an area rich in diversity, not only in terms of the number of *Orchidaceae* species (51 species recorded) but also in terms of their ecological and conservation value. Within its forest formations are some of the rarest and most protected species in Europe. This underscores the importance of preserving the quality of these habitats and their dynamic interconnections.

Identifying sites that should be prioritized for conservation and understanding the key factors that enhance the naturalness of these habitats remain critical challenges. Effective protection of these ecosystems and their biodiversity demands both strategic management approaches and a deeper comprehension of the ecological processes that sustain them. Tools such as Habitat Suitability Models (HSMs) are invaluable for species conservation, providing critical insights to guide the planning of habitat and species protection strategies. The application of HSMs can also be effectively tailored to fine-scale conservation efforts, particularly within the boundaries of protected areas (PAs). The modeling was conducted using climate data and future scenarios while keeping current forest conditions unchanged (i.e., same cover and soil indices). This ensures simple, comparable models that highlight climate change effects. However, forest dynamics over time should also be considered for greater accuracy. This requires integrating more variables and tracking their evolution—at the cost of increased complexity and the need for more advanced training and refinement. Future studies should aim to model climate impacts and the adaptive response of soil and forest cover to changing conditions.

Preliminary findings highlight the importance of ridge habitats for orchids in mesophilic environments, which are already partially occupied by these species under current climatic conditions. Considering the future projected climate scenarios, it is essential to assign the highest conservation priority to these areas within the boundaries of the protected area (PA). This could involve the creation of new fully protected zones or the adjustment of existing ones. Another significant finding relates to high-altitude areas, albeit in a different context. For thermophilic species, these zones could serve as both expansion and refuge sites, providing future habitat suitability as conditions evolve. As a result, these areas should be incorporated into planned conservation and protection strategies for both plant and animal species, with their preservation becoming a key priority. Existing research has shown that climate change poses a considerable threat to European conservation areas, emphasizing the need for new protection policies. Further research could be conducted using prioritization tools within PA boundaries to identify zones requiring protection in response to emerging climate challenges.

Changes in the vertical structure and texture of forests, particularly at a localized level, can significantly affect the presence of certain species. For instance, the density of total deadwood and volume of coarse woody debris, as well as the degree of old-growth characteristics in a forest stand, can substantially influence the presence of mycoheterotrophic and/or rare species. In contrast, the dominance of a particular tree species appears to have a different impact on the composition of the orchid community. Implementing targeted management practices could support the conservation of specific forest orchid species or groups, depending on the conservation objectives. This need underscores the potential for future research that could refine forest management strategies, focusing on the preservation of species that are critically endangered both in Europe and globally. However, additional comprehensive studies are necessary to further understand the ecology of *Orchidaceae* within forest ecosystems.

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