www.nature.com/scientificreports

scientific reports

OPEN

# Climate change will decrease the coverage of suitable niches for Asian medicinal orchid (*Bulbophyllum odoratissimum*) and its main phorophyte (*Pistacia weinmannifolia*)

**Marta Kolanowska**

**Considering the global biodiversity crisis and the growing demand for medicinal plants, it is crucial to preserve therapeutically useful herbs. From a conservation management perspective under climate change, identifying areas that enable valuable natural resources to persist in the future is crucial. Machine learning-based models are commonly used to estimate the locations of climate refugia, which are critical for the effective species conservation. The aim of this study was to assess the impact of global warming on the epiphytic medicinal orchid—*Bulbophyllum odoratissimum*. Given how the long-term survival of plants inhabiting shrubs and trees depends on the availability of suitable phorophyets, in this research potential range changes in reported orchid plant hosts were evaluated. According to conducted analyses, global warming will cause a decline in the coverage of the suitable niches for *B. odoratissimum* and its main phorophyte. The most significant habitat loss in the case of the studied orchid and *Pistacia weinmannifolia* will be observed in the southern part of their geographical ranges and some new niches will simultaneously become available for these plants in the northern part. Climate change will significantly increase the overlap of geographical ranges of *P. weinmannifolia* and the orchid. In the SSP5-8.5 scenario trees will be available for more than 56% of the orchid population. Other analyzed phorophytes, will be available for *B. odoratissimum* to a very reduced extent, as orchids will only utilize these species as habitats only occasionally. This study provides data on the distribution of climatic refugia of *B. odoratissimum* under global warming. Moreover, this is the first evaluation of the future geographical ranges for its phorophytes. According to the conducted analyses, only one of the previously reported tree species which are inhabited by *B. odoratissimum*, *P. weinmannifolia*, can serve as a phorophyte for this orchid in the future. In this study, the areas designated as suitable for the occurrence of both orchids and their phorophytes should be considered priority conservation areas for the studied medicinal plants.**

**Keywords** Climate projection, Medicinal plant, Niche modelling, Shared Socioeconomic Pathways

Orchidaceae is the second largest family of flowering plants with more than 31,000 recognized species[1]. Representatives of this group are found around the world, with the exception of polar regions and deserts[2]. The highest diversity of orchids is observed in the tropics[3]. These plants are known for their horticultural importance, as they are among the most popular plants in the global potted plant trade[4]. Orchid flowers are also used for cultural purposes[5] and as edible food products[4,6,7]. Orchidaceae are also widely used in traditional medicine[8–10], including ayurveda and traditional Chinese medicine[11].

One of the most interesting taxa in Orchidaceae is *Bulbophyllum* Thouars which encompasses approximately 2200 species occurring in Africa and Asia[12–14]. Among the numerous representatives of this genus, *Bulbophyllum odoratissimum* (Sm.) Lindl. *ex* Wall. is an economically and medicinally important species. It is native to

Faculty of Biology and Environmental Protection, Department of Geobotany and Plant Ecology, University of Lodz, ul. Banacha 12/16, 90-237 Lodz, Poland. email: marta.a.kolanowska@gmail.com

Southeast Asia occurring from India and Vietnam to China, Thailand and Myanmar. This orchid is not only valued by the horticulturists for its charming white and orange-tip flowers with a pleasant, sweet fragrance, but it is also among the most popular Asian therapeutic orchids. *Bulbophyllum odoratissimum* was reported to treat tuberculosis and chronic inflammation as well as fracture in Bhutan, China, India, Laos, Nepal, Thailand and Vietnam[15]. It is also used to cure cough, rheumatism and toothache in China[15–17]. As proved via biochemical analyses *B. odoratissimum* is a source of numerous biologically active compounds (e.g. phenanthraquinone, biphenanthrenes and dihydrostilbenes), which can potentially be useful in the treatment of cancers such as leukemia, lung adenocarcinoma, human hepatoma and stomach cancer[18,19].

Like numerous other tropical and subtropical orchids, *B. odoratissimum* is also threatened by anthropogenic factors, especially over-exploitation as well as habitat alterations and destruction[20]. The survival of this species is also endangered by climate change. Human-induced increases in global temperature and modifications in precipitation patterns[21] are more damaging to tropical ecosystems than to temperate ecosystems[22].

Epiphytes like *B. odoratissimum*, are considered to be more threatened than terrestrial species[23] in the context of long-term shifts in temperatures and weather patterns. Moreover, a negative effect of changes in precipitation and moisture is expected to have a more intense effect on habitats with less pronounced seasonality[23], which are common near the equator. The increased frequency of hurricanes predicted to occur as a result of global warming can also seriously damage epiphytic plant populations[24], which can be removed from their hosts by wind force or fall to the forest floor with tree branches and trunks[25]. The occurrence of approximately 70% of orchids is closely related to the availability of suitable phorophytes[26], as the host tree specificity influences the distribution and abundance of epiphytic Orchidaceae in numerous cases[26,27].

As reported in previous studies, the distribution of *B. odoratissimum* is related to the occurrence of *Pistacia weinmannifolia* J. Poisson *ex* Franch[28] (Anacardiaceae), native to northern Myanmar and southwestern China. The orchid was also reportedly growing on the branches of *Rhizophora apiculata* Blume (Rhizophoraceae), *Terminalia procera* Roxb. (Combretaceae), *Pterocarpus dalbergioides* (Baker) Kuntze (Fabaceae) and *Lagerstroemia hypoleuca* Kurz[29] (Lythraceae). While *Rhizophora apiculata* is a mangrove species broadly distributed in tropical Asia and northern Australia, the native geographical ranges of *L. hypoleuca* and *P. dalbergioides* are restricted to the Andaman Islands. The latter plant was also introduced into Bangladesh, Jawa, Madagascar, and Myanmar. *Terminalia procera* occurs only within the southern edge of *B. odoratissimum* geographical range.

Considering the global biodiversity crisis and usefulness of medicinal plants, preserving these valuable herbs it is crucial[30]. In addition to direct human activities that disturb ecosystems, such as changes in land use, overexploitation, pollution and the introduction of invasive organisms[31], climate change is considered the main factor causing biodiversity loss[32]. Machine learning-based models are commonly used to estimate the locations of climate refugia, which are essential for effective biodiversity conservation under global warming[33]. However, the usefulness of modeling depends on the incorporation of ecological factors in the analyses. Effective modeling is especially important for organisms whose long-term survival depends on specific infraspecific relationships[34].

The aim of this study was to estimate the impact of global warming on B. odoratissimum and its phorophytes, and to evaluate the future overlap of the geographical ranges of the epiphyte and its hosts in order to identify areas that can constitute climatic refugia for the studied medicinal orchid.

## Methods

### List of localities

Databases of localities of *B. odoratissimum* and its five reported phorophytes were compiled from the Global Biodiversity Information Facility[35–40]. Only records that could be georeferenced with a precision of 1 km were used in the ecological niche modelling (ENM) analyses. The duplicate presence records (records within the same grid cell) were removed using MaxEnt application. To further reduce sampling bias, the localities were rarified using 5 classes of topographic heterogeneity[41]. Species records were reduced to a minimum distance of 25 km in areas of low topographic heterogeneity and 5 km in highly heterogeneous areas). The complete list of localities used in this study is available in Table S1 and datasets are presented in Table S2.

### Climatic niche modelling

The modelling of the current and future distributions of the studied species was performed using the maximum entropy method implemented in MaxEnt version 3.3.2[42–44], which is based on presence-only observations. Bioclimatic variables which are derived from the monthly temperature and rainfall values in order to generate more biologically meaningful indicators in 30 arc-seconds of interpolated climate surface data downloaded from WorldClim v. 2.1 were used for the modelling[45]. The study area was reduced to (49.12°N-11.13°S, 64.19–131.44°E) in order to improve the models[46,47].

Pearsons' correlation coefficient was computed using SDMtoolbox 2.3 for ArcGIS[48,49] (Table S3) and highly correlated ($>0.8$) variables were removed from the ENM analyses to prevent problems associated with autocorrelation. The final list of bioclimatic variables used in the analyses is provided in Table 1.

The future extent of orchid and its phorophyte climatic niches for 2080–2100 was predicted using four projections for three Shared Socio-economic Pathways (SSPs): 1–2.6, 3–7.0 and 5–8.5[50–52], developed in the 3rd generation of Earth System Model (EC-Earth3-Veg) climate simulation[53], as this simulation works well in the analyzed geographical area[54].

SSPs are trajectories adopted by the Intergovernmental Panel on Climate Change (IPCC), comprising narrative descriptions of future world development[55]. The proposed storylines describe contrasting predictions of future society and future climate change challenges, with global warming in 2100 ranging from 3.1 to 5.1˚C above preindustrial levels in various scenarios[56].

In all analyses, the maximum number of iterations was set to 10,000 with the convergence threshold set to 0.00001. The neutral ($=1$) regularization multiplier value and auto features were used. The "random seed" option

| Code | Variable description | Used in ENM |
|---|---|---|
| bio1 | annual mean temperature | + |
| bio2 | mean diurnal range [mean of monthly (max temp—min temp)] | + |
| bio3 | isothermality (bio2/bio7) (× 100) | + |
| bio4 | temperature seasonality (standard deviation × 100) | |
| bio5 | max temperature of warmest month | |
| bio6 | min temperature of coldest month | |
| bio7 | temperature annual range (bio5-bio6) | |
| bio8 | mean temperature of wettest quarter | + |
| bio9 | mean temperature of driest quarter | |
| bio10 | mean temperature of warmest quarter | |
| bio11 | mean temperature of coldest quarter | |
| bio12 | annual precipitation | + |
| bio13 | precipitation of wettest month | |
| bio14 | precipitation of driest month | + |
| bio15 | precipitation seasonality (coefficient of variation) | + |
| bio16 | precipitation of wettest quarter | |
| bio17 | precipitation of driest quarter | |
| bio18 | precipitation of warmest quarter | + |
| bio19 | precipitation of coldest quarter | |

**Table 1.** Climatic variables used in ENM analyses (marked with + ).

| Species | AUC (standard deviation) | TSS | MaxKappa | Specificity | Sensitivity |
|---|---|---|---|---|---|
| *Bulbophyllum odoratissimum* | 0.949 (0.009) | 0.735 | 0.414 | 0.768 | 0.967 |
| *Lagerstroemia hypoleuca* | 1.000 (0.000) | 0.997 | 0.461 | 1.000 | 0.997 |
| *Pistacia weinmannifolia* | 0.959 (0.005) | 0.777 | 0.424 | 0.828 | 0.949 |
| *Pterocarpus dalbergioides* | 0.980 (0.011) | 0.830 | 0.440 | 0.830 | 1.000 |
| *Rhizophora apiculata* | 0.971 (0.005) | 0.865 | 0.455 | 0.909 | 0.966 |
| *Terminalia procera* | 0.982 (0.010) | 0.913 | 0.468 | 0.913 | 1.000 |

**Table 2.** Scores of model reliability tests and value of minimum training presence.

provided a random test partition and background subset for each run, with 40% of the samples were used as test points. The run was performed as a bootstrap with 100 replicates. The output was set to logistic. The "fade by clamping" function in MaxEnt was used to prevent extrapolations outside the environmental range of the training data[57]. All analyses of GIS data were carried out using ArcGIS 10.6 (Esri, Redlands, CA, USA). The accuracy of the models was evaluated using the area under the curve (AUC)[58] and True Skill Statistic (TSS)[59,60].

To compare the bioclimatic preferences of the orchid and its phorophytes, predicted niche occupancy (PNO) profiles for each species and environmental variable were created[61]. PNO integrates species probability distributions (derived with MaxEnt) with respect to each environmental variable.

To visualize changes in the distribution of suitable niches of the orchid, SDMtoolbox 2.3 for ArcGIS[48,49] was used. To compare the distribution model created for current climatic conditions with future predictions, all the SDMs were converted into binary rasters and analyzed using the Goode homolosine as a projection. The presence thresholds used in the analyses equaled the calculated max Kappa value[62].

## Results

### Model evaluation and limiting factors

All created models received high AUC scores (0.949–1.000) and mostly high TSS scores (0.735–0.997) tests. Both sensitivity and specificity were also generally high indicating good reliability of the presented modelling results (Table 2).

According to the jackknife test of *B. odoratissimum* models, used to evaluate the relative importance of single explanatory variables included in the analyses, bio1 was the variable with the most useful information by itself while bio3 had the most information that was not present in the other variables. Considering the relative contributions of the environmental variables to the phorophyte models, the most important variable shaping model of *P dalbergioides* and *Rhizophora apiculata* was bio1 (49.8% and 33.2%, respectively). Bio2 was crucial in *L. hypoleuca* (61.9%), bio3 was critical *T. procera* (82.6%), and bio18 was vital in *P. weinmannifolia* (31.7%) model.

The PNO profiles (Fig. 1) for *B. odoratissimum* and its phorophytes, indicated that the orchid has bioclimatic preferences similar to those of *P. weinmannifolia* with respect to all the analyzed bioclimatic factors. On the other hand, the bioclimatic tolerance of *L. hypoleuca* is the most distinctive, especially for bio2, bio3, bio12, and bio15.

## Current potential orchid and its phorophytes range

The models created for all studied species for the near-present time are presented in Fig. 2. The potential geographical range of *B. odoratissimum* is generally congruent with the known distribution of this orchid. Only some regions of except for South Korea which was indicated in the analyses as suitable for this plant, have the species not been recorded thus far.

The model of *L. hypoleuca* indicated that the Andaman Islands and southern Vietnam are areas suitable for this species. There are some discrepancies in the projected and actual distributions of *P. weinmannifolia*, however, some records of this species could be derived from cultivated material outside its natural range. The generated distribution of Pistachio's suitable niches is congruent with data presented by previous authors[63] except for South Korea and the North China Plane. According to the conducted analyses, the habitats suitable for *P. dalbergioides* are also located outside its current range, such as in the Philippines and Indonesia. Within the study area, the models of *R. apiculata* and *T. procera* are generally congruent with the known distributions of these species. In the case of the latter plant, Malaysia, which is outside the known geographic range of the species, was indicated as a suitable region for its occurrence.

## Changes in the distributions of suitable niches for orchid and its phorophytes

The calculations of future changes in the coverage of suitable niches of the studied orchid and its hosts are presented in Table 3 and visualized in Fig. 3 and Figs. S1-S5.

As a result of global warming, *B. odoratissimum* will face significant habitat loss (Fig. 3). In the SSP1-2.6 scenario, it is estimated that the species will lose 20% of currently suitable niches within its geographical range. Even more significant range contraction is predicted to occur in the SSP3-7.0 (59%) and SSP5-8.5 (64%) scenarios. Generally, poleward orchid range shift are observed, with the most stable niches located in the eastern Himalayas.

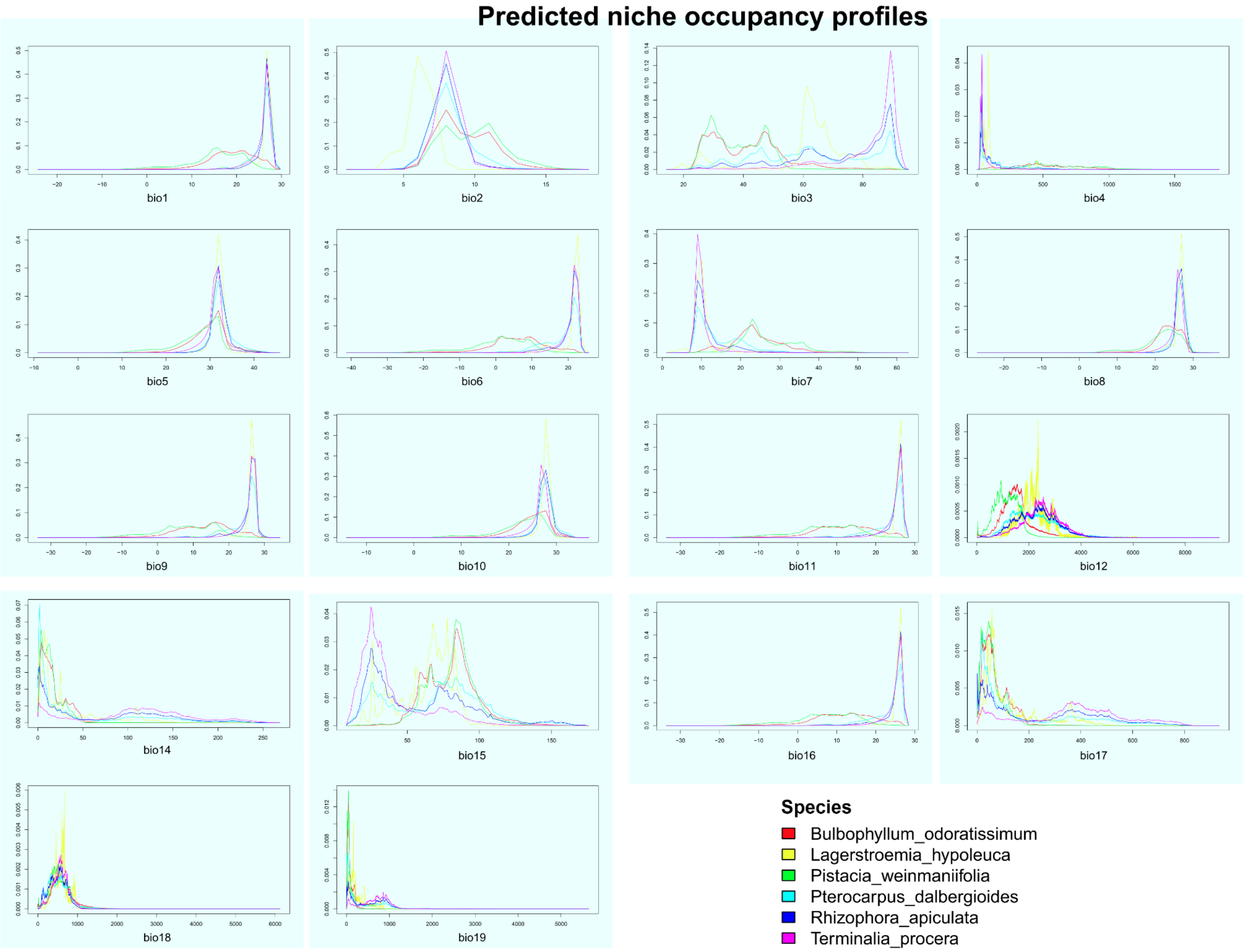

**Fig. 1**. Predicted niche occupancy (PNO) profiles created for studied species and 19 bioclimatic variables.

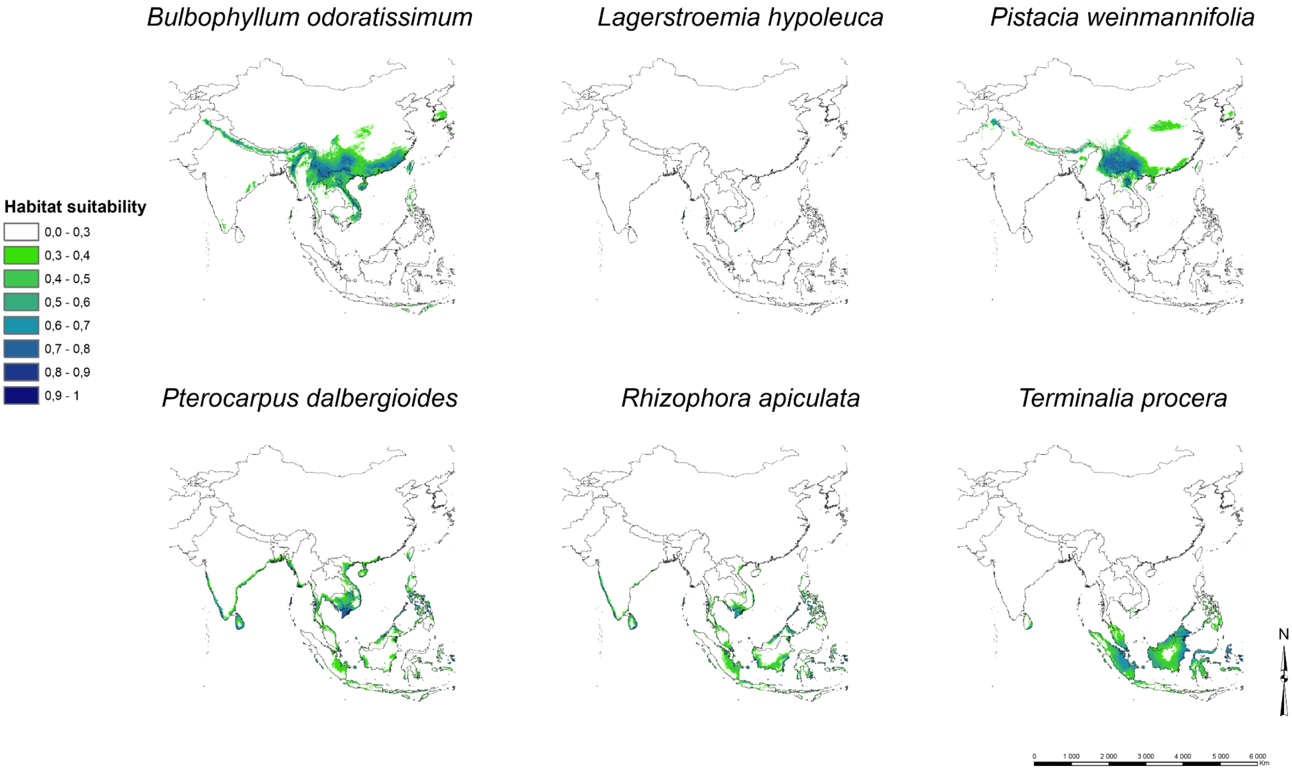

**Fig. 2.** Present potential range of *Bulbophyllum odoratissimum* and its phorophytes.

| Species | Scenario | Range expansion | No range change | Range contraction | Change |
|---|---|---|---|---|---|
| *Bulbophyllum odoratissimum* | SSP1-2.6 | 165,273.7 | 1,214,818 | 522,581.4 | − 20.57% |
| | SSP3-7.0 | 151,404 | 552,836.4 | 1,184,563 | − 59.47% |
| | SSP5-8.5 | 190,192.6 | 425,765.6 | 1,311,634 | − 64.55% |
| *Lagerstroemia hypoleuca* | SSP1-2.6 | 21,605.99 | 13,497.9 | 1585.825 | + 132.73% |
| | SSP3-7.0 | 42,015.9 | 12,960.02 | 2123.713 | + 264.47% |
| | SSP5-8.5 | 355,021.9 | 12,219.3 | 2864.427 | + 2334.68% |
| *Pistacia weinmannifolia* | SSP1-2.6 | 138,233.2 | 609,838.6 | 263,807.6 | − 14.37% |
| | SSP3-7.0 | 155,434.7 | 438,125.1 | 435,521.1 | − 32.06% |
| | SSP5-8.5 | 239,300.4 | 393,789.6 | 479,856.6 | − 27.53% |
| *Pterocarpus dalbergioides* | SSP1-2.6 | 1,063,299 | 738,506.1 | 48,571.97 | + 128.92% |
| | SSP3-7.0 | 3,097,008 | 786,504.4 | 573.6808 | + 393.41% |
| | SSP5-8.5 | 3,612,794 | 786,939.9 | 138.2004 | + 459.00% |
| *Rhizophora apiculata* | SSP1-2.6 | 1,356,065 | 586,025.3 | 231.6597 | + 231.27% |
| | SSP3-7.0 | 1,271,746 | 250,096 | 336,161 | + 159.59% |
| | SSP5-8.5 | 2,912,193 | 586,147.6 | 109.3672 | + 496.72% |
| *Terminalia procera* | SSP1-2.6 | 249,741 | 873,735.7 | 19,459.41 | + 25.78% |
| | SSP3-7.0 | 564,908.5 | 886,666.9 | 6528.229 | + 62.51% |
| | SSP5-8.5 | 665,367.3 | 890,636.9 | 2558.199 | + 74.21% |

**Table 3.** Changes in the coverage (km$^2$) of the suitable niches of *Bulbophyllum odoratissimum* and its phorophytes.

Global warming will also damage stability of *P. weinmannifolia* populations which will face 14–32% habitat loss (Fig. S2). Range contraction in the southern ragion is predicted. This reduction will be accompanied by the expansion of the suitable niches in the central part of the geographical range of the species. The potential range of *L. hypoleuca* will significantly expand in response to climate change (Fig. S1). According to the estimations presented in the SSP5-8.5 scenario, this value can be even 23 times greater than currently observed. A significant

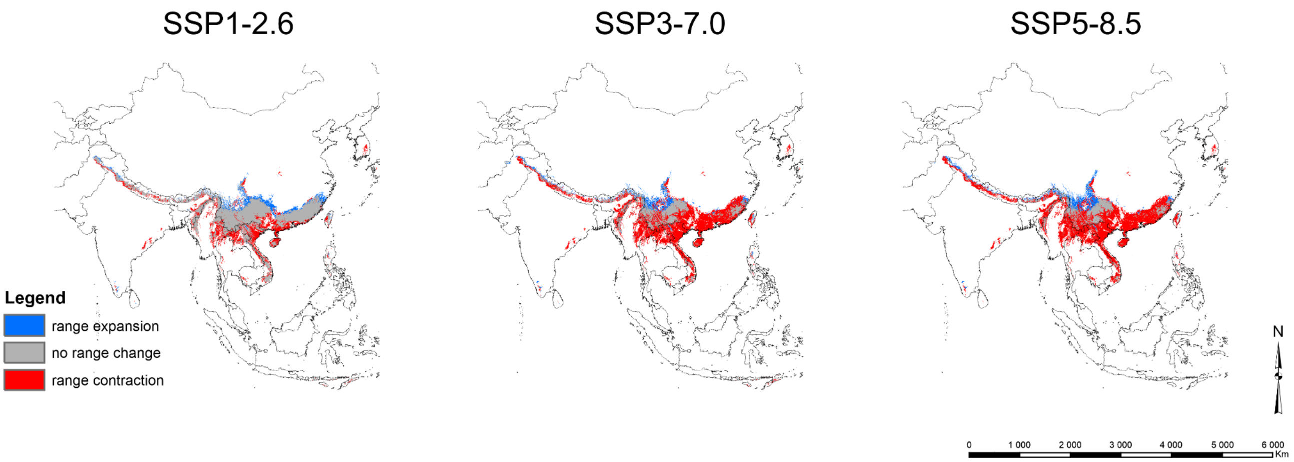

**Fig. 3**. Future distribution of the suitable niches of *Bulbophyllum odoratissimum* in various climate change scenarios.

| Phorophyte | Scenario | Overlap with orchid |
|---|---|---|
| *Lagerstroemia hypoleuca* | Present | 0.000% |
| | SSP1-2.6 | 0.000% |
| | SSP3-7.0 | 0.000% |
| | SSP5-8.5 | 0.166% |
| *Pistacia weinmannifolia* | Present | 39.312% |
| | SSP1-2.6 | 37.474% |
| | SSP3-7.0 | 49.903% |
| | SSP5-8.5 | 56.369% |
| *Pterocarpus dalbergioides* | Present | 2.533% |
| | SSP1-2.6 | 2.421% |
| | SSP3-7.0 | 2.983% |
| | SSP5-8.5 | 2.952% |
| *Rhizophora apiculata* | Present | 0.044% |
| | SSP1-2.6 | 0.034% |
| | SSP3-7.0 | 0.076% |
| | SSP5-8.5 | 0.146% |
| *Terminalia procera* | Present | 0.000% |
| | SSP1-2.6 | 0.000% |
| | SSP3-7.0 | 0.000% |
| | SSP5-8.5 | 0.000% |

**Table 4**. Overlap of the potential geographical range of *B. odoratissimum* and its phorophytes.

though not as extraordinary increase in the coverage of suitable niches was also predicted for *P. dalbergioides* (Fig. S3), *R. apiculata* (Fig. S4), and *T. procera* (Fig. S5).

## Future overlap of orchid and its hosts

The results of the analysis of the overlap of the potential geographical range of *B. odoratissimum* and its phorophytes are presented in Table 4. Among all trees studied, only *P. weinmannifolia* can be considered an important phorophyte for the orchid. This is the only species which is present in a significant part of the *B. odoratissimum* geographical range. All other trees appear to serve as occasional hosts (Figs. S6-S9).

Climate change will significantly increase the overlap of geographical ranges of *P. weinmannifolia* and the orchid. In the SSP5-8.5 scenario, the trees will be available for more than 56% of the orchid populations (Fig. 4). *Pterocarpus dalbergioides* is currently present in only 2.5% of the geographical range of *B. odoratissimum*, while global warming will not significantly change its availability as an orchid phorophyte (Fig. S7). Currently, *Rhizophora apiculata* is available for just 0.04% of the orchid populations, but it will become more common within the *B. odoratissimum* geographical range, especially in the SSP5-8.5 scenario (Fig. S8). *Lagerstroemia hypoleuca* which currently only occasionally serves as an orchid host will be more available for *B. odoratissimum*

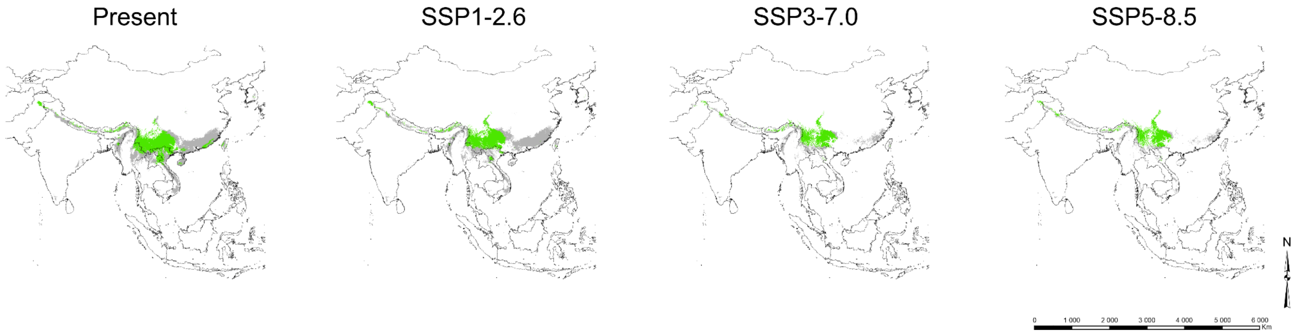

**Fig. 4**. Overlap of potential ranges of *Bulbophyllum odoratissimum* and *Pistacia weinmannifolia* in the present time and in various climate change scenarios. Areas suitable for the occurrence of both species marked in green, areas suitable only for orchid occurrence marked in grey.

only in the SSP5-8.5 scenario (Fig. S6). *Terminalia procera* will not become an important host for the orchid (Fig. S9).

## Discussion

### Impact of global warming and species conservation implications

While more than 50 orchid species are used in traditional medicine[64], numerous more orchid species should be tested for their therapeutic potential[65]. Unfortunately, the future survival of these potentially useful plants is uncertain. The simulations of climate change's impact on Asian medicinal orchids are limited to terrestrial species such as *Crepidium acuminatum*[66], *Dactylorhiza hatagirea*[67,68] and *Satyrium nepalense*[66]. These published analyses indicate that the first two species will face habitat loss, while *S. nepalense* can increase its potential geographical range. However, it is important to note that all these studies were based exclusively on climate data. Unlike the three aforementioned species, *B. odoratissimum* usually grows as an epiphyte and it is relative fragile with regard to changes in the environment[23]. Previous studies conducted on pantropical orchid species that can grow as epiphyte, lithophyte or terrestrial and that, in some regions, is used as therapeutic plant, *Polystachya concreta* (Jacq.) Garay & H.R.Sweet, revealed that the global warming has various effects on this species in different geographical regions[69]. This study is the first report on the impact of global warming on epiphytic medicinal orchid that includes also an analysis of the future overlap of the plant and its phorophytes.

As simulated in this research, global warming will cause a decline in the total coverage of the suitable niches for *B. odoratissimum* and its main phorophyte. The most significant habitat loss in the case of the studied orchid and *P. weinmannifolia* will be observed along the southern part of their geographical ranges, while some new niches will simultaneously become available for these plants in the northern part. This poleward range shift is commonly predicted to occur as a result of climate change in numerous organisms[70–72].

The potential geographical range of four other trees reported as occasional phorophytes of *B. odoratissimum* will increase. The suitable niches of a mangrove, *Rhizophora apiculata*, will relocate inland. This modelling result is consistent with previous studies conducted on the tall-stilt mangrove in India[73]. A similar pattern of inland range shift is predicted to occur in the case of *Terminalia procera*. The created models revealed the enormous expansion of the suitable niches for *Pterocarpus dalbergioides* and *Lagerstroemia hypoleuca* which are endemic to the Andaman Islands. However, these plants are unlikely to migrate into areas characterized by proper bioclimatic conditions. While *Pterocarpus dalbergioides* has already been introduced into Bangladesh, Jawa, Madagascar and Myanmar, no natural dispersion outside the Andaman Islands has been reported thus far. The future potential range of both endemics will be limited by their low dispersal abilities[74].

This study provides an important insight into location of climate refugia which considering limitations of ex situ conservation[75,76] are crucial for orchid long-term survival. The conservation efforts should be focused on the areas which were identified as suitable for the occurrence of *B. odoratissimum* and its phorophytes in the future. These climate refugia are located mostly along southern Himalayas and the eastern part of the Tibetan Plateau.

### Model limitations

Two ecological factors should be considered when predicting the impact of global warming on the long-term survival of orchids – availability of pollinator(s) and presence of organisms crucial for orchid development[77,78]. The life cycle of all Orchidaceae depends on symbiosis with mycorrhizal fungi and endophytic bacteria during germination[79–81]. To date, both fungal and bacterial partners of *B. odoratissimum* have been poorly explored[28], and it is not possible to evaluate the availability of these organisms for orchids studied under global warming conditions using ENM techniques.

The reproduction of Orchidaceae representatives mostly relies on very few specific animal pollen vectors[82,83]. The pollen vector of *B. odoratissimum* remains unknown, but generally, the genus representatives are assumed to be pollinated by flies[84,85]. While worldwide analyses of the general pattern of the response of Diptera to global warming have not been conducted, some studies have indicated that the phenology of insects changes in response to rising temperatures[86], resulting in disturbances in the pollination[87]. More observations of *B. odoratissimum* pollination are needed to evaluate the possible disturbance to the sexual reproduction of this species caused by global warming.

In this study, the overlap of the orchid and its phorophytes was analyzed; however, while *B. odoratissimum* occurs on tree trunks in semievergreen and mixed forests, it can also grow as lithophyte, especially in the valleys[88]. For this reason, outside forests, where the phorophyte of this species is absent, the studied orchid can potentially survive on rocks if the bioclimatic conditions are suitable for its occurrence. The records of *B. odoratissimum* in the GBIF include both epiphytic and lithophytic populations and it is not possible to assess which populations are growing on the rocks, and which are found on the trees. Thus, at this point, evaluating whether epiphytic populations significantly differ in their climatic preferences from lithophytic populations to improve the precision of the evaluation of the future distribution of phorophyte-related populations is not possible. Indeed, the topic of the differences in climatic preferences in the case of facultative epiphytes/lithophytes remains poorly explored. Apparently, some species, such as *Lepanthes rupestris* Stimson, can grow both on trees and on rocks in the same relatively small area, which suggests that the macroclimatic preferences of both types of habits do not differ significantly[89].

Considering technical issues, after spatial thinning only 3 (out of 8 georeferenced records) and 9 (out of 28 georeferenced records) distribution points were used for *L. hypoleuca* and *P. dalbergioides*, respectively. While the small sample size can negatively influence the outcome of modelling, MaxEnt is robust to sample size[90], and the high model performance scores, together with the consistency of the modelled current potential ranges of both species with their known distributions (see Fig. 2), suggest that analyses of *L. hypoleuca* and *P. dalbergioides* are reliable.

## Conclusions

The conservation of medicinal plants which are valuable sources of therapeutic compounds and potential reservoir of new drugs should be prioritized worldwide[30]. Due to the challenges in ex situ preservation and reintroduction of orchids, the conservation efforts should be primarily focused on the natural habitats of these plants. This study provides data on the distribution of climatic refugia of *B. odoratissimum* under global warming. Moreover, this is the first evaluation of the future changes of the potential geographical ranges of the studied orchid phorophytes. According to the conducted analyses, only one of the previously reported tree species which are inhabited by *B. odoratissimum*—*P. weinmannifolia*—can serve as a phorophyte for this orchid in the future. Areas designated in the presented analyses as suitable for occurrence of both, orchid and its phorophytes, should be considered as priority conservation areas for studied medicinal plant. These climatic refugia are buffered from contemporary climate change over time enabling persistence of physical and ecological resources despite changes in the climate in the surrounding landscape. Determining the best location of climate change refugia and assuring the proper management of these areas is a key analytic process for establihing effective conservation stategies[91]. Morelli et al.[92] provided the information about practical usefullness of identification of climate refugia in nature management agendas.

This study revealed also the need for additional research on several aspects of *B. odoratissimum* ecology – (1) recognition of fungal symbionts of this orchis, (2) identification of pollen vectors, (3) evaluation of similarity of climatic preferences of lithophytic and epiphytic populations within the geographical range of the species. These poorly explored topics will allow to improve the conservation activities by providing additional data which can be used to further specify the location of the most suitable climatic refugia which will assure the survival of complicated ecological networks allowing orchid to effectively reproduce and germinate under climate change.

## Data availability

The datasets analyzed during the current study are available as supplementary information.

Received: 12 June 2024; Accepted: 16 September 2024

## References

1. POWO. (ed Kew Royal Botanic Gardens) (2023).
2. Dressler, R. *The Orchids: Natural History and Classification* (Harvard University Press, 1981).
3. Vitt, P. *et al.* Global conservation prioritization for the Orchidaceae. *Sci. Rep.* **13**, 6718. https://doi.org/10.1038/s41598-023-30177-y (2023).
4. Hinsley, A. *et al.* A review of the trade in orchids and its implications for conservation. *Bot. J. Linn. Soc.* **186**, 435–455. https://doi.org/10.1093/botlinnean/box083 (2018).
5. Duggal, S. C. Orchids in human affairs (a review). *Q. J. Crude Drug Res.* **11**, 1727–1734 (1971).
6. Subedi, A. *et al.* Collection and trade of wild-harvested orchids in Nepal. *J. Ethnobiol. Ethnomed.* **9**, 64. https://doi.org/10.1186/1746-4269-9-64 (2013).
7. Kreziou, A., de Boer, H. & Gravendeel, B. Harvesting of salep orchids in north-western Greece continues to threaten natural populations. *Oryx* **50**, 393–396. https://doi.org/10.1017/S0030605315000265 (2016).
8. Lawler, L. J. & Slaytor, M. Uses of Australian orchids by Aborigines and early settlers. *Med. J. Aust.* **2**, 1259–1261. https://doi.org/10.5694/j.1326-5377.1970.tb63459.x (1970).
9. Kong, J., Goh, N., Chia, L. & Chia, T. Recent advances in traditional plant drugs and orchids. *Acta Pharmacol. Sin.* **24**, 7–21 (2003).
10. Bulpitt, C. J. The uses and misuses of orchids in medicine. *QJM* **98**, 625–631. https://doi.org/10.1093/qjmed/hci094 (2005).
11. Singh, A. & Duggal, S. Medicinal orchids-an overview. *Ethnobot. Leafl.* **1**, 3 (2009).
12. Pignal, M., Laudereau, C. & Laudereau, P. Notes on bulbophyllum sect. Pelma (Orchidaceae) in New Caledonia. *Candollea* **76**, 65–70. https://doi.org/10.15553/c202Xv761a5 (2021).
13. Vermeulen, J., Schuiteman, A. & De Vogel, E. Nomenclatural changes in Bulbophyllum (Orchidaceae; Epidendroideae). *Phytotaxa* **166**, 101–113. https://doi.org/10.11646/phytotaxa.166.2.1 (2014).
14. Lin, D., Zhou, K., Hidayat, A. & Jin, X. Bulbophyllum papuaense (Orchidaceae), a new species from Indonesia. *Phytokeys* https://doi.org/10.3897/phytokeys.138.38714 (2020).
15. Gutierrez, R. Orchids: A review of uses in traditional medicine, its phytochemistry and pharmacology. *J. Med. Plants Res.* **4**, 592–638 (2010).

16. Heinrich, M. *et al.* Best practice in research—Overcoming common challenges in phytopharmacological research. *J. Ethnopharmacol.* **246**, 112230. https://doi.org/10.1016/j.jep.2019.112230 (2020).
17. Zhang, W. G. *et al.* Total synthesis of two new dihydrostilbenes from *Bulbophyllum odoratissimum*. *J. Asian Nat. Prod. Res.* **9**, 23–28. https://doi.org/10.1080/10286020500289543 (2007).
18. Chen, Y. *et al.* Cytotoxic phenolics from *Bulbophyllum odoratissimum*. *Food Chem.* **107**, 169–173. https://doi.org/10.1016/j.foodchem.2007.07.077 (2008).
19. Xu, J. *et al.* Two new biphenanthrenes with cytotoxic activity from *Bulbophyllum odoratissimum*. *Fitoterapia* **80**, 381–384. https://doi.org/10.1016/j.fitote.2009.05.007 (2009).
20. Prasad, G., Seal, T., Mao, A. A., Vijayan, D. & Lokho, A. Assessment of clonal fidelity and phytomedicinal potential in micropropagated plants of *Bulbophyllum odoratissimum*—An endangered medicinal orchid of Indo Burma megabiodiversity hotspot. *S. Afr. J. Bot.* **141**, 487–497. https://doi.org/10.1016/j.sajb.2021.05.015 (2021).
21. Trenberth, K. E. Changes in precipitation with climate change. *Clim. Res.* **47**, 123–138. https://doi.org/10.3354/cr0095 (2011).
22. Sentinella, A. T., Warton, D. I., Sherwin, W. B., Offord, C. A. & Moles, A. T. Tropical plants do not have narrower temperature tolerances, but are more at risk from warming because they are close to their upper thermal limits. *Global Ecol. Biogeogr.* **29**, 1387–1398. https://doi.org/10.1111/geb.13117 (2020).
23. Zotz, G. & Bader, M. Y. in *Progress in Botany* (eds Lüttge, U., Beyschlag, W., Büdel, B., & Francis, D.) 147–170 (Springer, 2009).
24. Loope, L., Duever, M., Herndon, A., Snyder, J. & Jansen, D. Hurricane impact on uplands and freshwater swamp forest. *BioScience* **44**, 238–246. https://doi.org/10.2307/1312228 (1994).
25. Novais, S. *et al.* Anthropogenic and hurricane disturbances had similar negative effects on epiphytic Tillandsia species in a tropical dry forest. *For. Ecol. Manag.* **458**, 117797. https://doi.org/10.1016/j.foreco.2019.117797 (2020).
26. Zarate-Garcia, A. *et al.* Bark water storage capacity influences epiphytic orchid preference for host trees. *Am. J. Bot.* **107**, 726–734. https://doi.org/10.1002/ajb2.1470 (2020).
27. McCormick, M. K. & Jacquemyn, H. What constrains the distribution of orchid populations?. *New Phytol.* **202**, 392–400. https://doi.org/10.1111/nph.12639 (2014).
28. Pecoraro, L. *et al.* Fungal diversity driven by bark features affects phorophyte preference in epiphytic orchids from southern China. *Sci. Rep.* **11**, 11287. https://doi.org/10.1038/s41598-021-90877-1 (2021).
29. Alappatt, J. P. Additions to the orchid flora of Andaman and Nicobar Islands, India. *Rheeda* **26**, 83–88 (2016).
30. Chen, S.-L. *et al.* Conservation and sustainable use of medicinal plants: Problems, progress, and prospects. *Chin. Med.* **11**, 37. https://doi.org/10.1186/s13020-016-0108-7 (2016).
31. Bellard, C., Marino, C. & Courchamp, F. Ranking threats to biodiversity and why it doesn't matter. *Nat. Commun.* **13**, 2616. https://doi.org/10.1038/s41467-022-30339-y (2022).
32. Shivanna, K. R. Climate change and its impact on biodiversity and human welfare. *Proc. Indian Natl. Sci. Acad.* **88**, 160–171. https://doi.org/10.1007/s43538-022-00073-6 (2022).
33. Beaumont, L. J., Esperón-Rodríguez, M., Nipperess, D. A., Wauchope-Drumm, M. & Baumgartner, J. B. Incorporating future climate uncertainty into the identification of climate change refugia for threatened species. *Biol. Conserv.* **237**, 230–237. https://doi.org/10.1016/j.biocon.2019.07.013 (2019).
34. Kolanowska, M., Michalska, E. & Konowalik, K. The impact of global warming on the niches and pollinator availability of sexually deceptive orchid with a single pollen vector. *Sci. Total Environ.* **795**, 148850. https://doi.org/10.1016/j.scitotenv.2021.148850 (2021).
35. GBIF.org. (2024).
36. GBIF.org. GBIF Occurrence Download—*Pterocarpus dalbergioides*https://doi.org/10.15468/dl.2422n2 (2024).
37. GBIF.org. GBIF Occurrence Download—*Terminalia procera*. https://doi.org/10.15468/dl.d52jkb (2024).
38. GBIF.org. GBIF Occurrence Download—*Rhizophora apiculata*. https://doi.org/10.15468/dl.3wrjh8 (2024).
39. GBIF.org. GBIF Occurrence Download—*Pistacia weinmannifolia*. https://doi.org/10.15468/dl.mt3khq (2024).
40. GBIF.org. GBIF Occurrence Download—*Bulbophyllum odoratissimum*. https://doi.org/10.15468/dl.kpj6e5 (2024).
41. Luoto, M. & Heikkinen, R. K. Disregarding topographical heterogeneity biases species turnover assessments based on bioclimatic models. *Global Change Biol.* **14**, 483–494. https://doi.org/10.1111/j.1365-2486.2007.01527.x (2008).
42. Elith, J. *et al.* A statistical explanation of MaxEnt for ecologists. *Divers. Distrib.* **17**, 43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x (2011).
43. Phillips, S., Anderson, R. & Schapire, R. Maximum entropy modeling of species geographic distributions. *Ecol. Model.* **190**, 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026 (2006).
44. Phillips, S. & Dudik, M. Modeling of species distributions with Maxent: New extensions and a comprehensive evaluation. *Ecography* **31**, 161–175. https://doi.org/10.1111/j.0906-7590.2008.5203.x (2008).
45. Fick, S. & Hijmans, R. WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* **37**, 4302–4315. https://doi.org/10.1002/joc.5086 (2017).
46. Anderson, R. & Raza, A. The effect of the extent of the study region on GIS models of species geographic distributions and estimates of niche evolution: Preliminary tests with montane rodents (genus Nephelomys) in Venezuela. *J. Biogeogr.* **37**, 1378–1393. https://doi.org/10.1111/j.1365-2699.2010.02290.x (2010).
47. Barve, N. *et al.* The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecol. Model.* **222**, 1810–1819. https://doi.org/10.1016/j.ecolmodel.2011.02.011 (2011).
48. Brown, J. SDMtoolbox: A python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *Methods Ecol. Evol.* **5**, 694–700. https://doi.org/10.1111/2041-210X.12200 (2014).
49. Brown, J. L., Bennett, J. R. & French, C. M. SDMtoolbox 2.0: The next generation Python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *PeerJ* **5**, e4095. https://doi.org/10.7717/peerj.4095 (2017).
50. McGee, R., Williams, S., Poulton, R. & Moffitt, T. A longitudinal study of cannabis use and mental health from adolescence to early adulthood. *Addiction* **95**, 491–503. https://doi.org/10.1046/j.1360-0443.2000.9544912.x (2000).
51. Meinshausen, M. *et al.* The shared socio-economic pathway (SSP) greenhouse gas concentrations and their extensions to 2500. *Geosci. Model Dev.* **13**, 3571–3605. https://doi.org/10.5194/gmd-13-3571-2020 (2020).
52. Li, J. *et al.* Coupled SSPs-RCPs scenarios to project the future dynamic variations of water-soil-carbon-biodiversity services in Central Asia. *Ecol. Indic.* https://doi.org/10.1016/j.ecolind.2021.107936 (2021).
53. Consortium, E. C.-E. (Earth System Grid Federation, 2019).
54. Parding, K. M. *et al.* GCMeval—An interactive tool for evaluation and selection of climate model ensembles. *Clim. Serv.* **18**, 100167. https://doi.org/10.1016/j.cliser.2020.100167 (2020).
55. Riahi, K. *et al.* The Shared Socioeconomic Pathways and their energy, land use, and greenhouse gas emissions implications: An overview. *Global Environ. Change-Hum. Policy Dimens.* **42**, 153–168. https://doi.org/10.1016/j.gloenvcha.2016.05.009 (2017).
56. O'Neill, B. C. *et al.* The roads ahead: Narratives for shared socioeconomic pathways describing world futures in the 21st century. *Global Environ. Change* **42**, 169–180. https://doi.org/10.1016/j.gloenvcha.2015.01.004 (2017).
57. Owens, H. *et al.* Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. *Ecol. Model.* **263**, 10–18. https://doi.org/10.1016/j.ecolmodel.2013.04.011 (2013).
58. Mason, S. & Graham, N. Areas beneath the relative operating characteristics (ROC) and relative operating levels (ROL) curves: Statistical significance and interpretation. *Q. J. R. Meteorol. Soc.* **128**, 2145–2166. https://doi.org/10.1256/003590002320603584 (2002).

59. Čengić, M. *et al.* On the importance of predictor choice, modelling technique, and number of pseudo-absences for bioclimatic envelope model performance. *Ecol. Evol.* **10**, 12307–12317. https://doi.org/10.1002/ece3.6859 (2020).
60. Shabani, F., Kumar, L. & Ahmadi, M. A comparison of absolute performance of different correlative and mechanistic species distribution models in an independent area. *Ecol. Evol.* **6**, 5973–5986. https://doi.org/10.1002/ece3.2332 (2016).
61. Evans, M. E., Smith, S. A., Flynn, R. S. & Donoghue, M. J. Climate, niche evolution, and diversification of the "bird-cage" evening primroses (Oenothera, sections Anogra and Kleinia). *Am. Nat.* **173**, 225–240. https://doi.org/10.1086/595757 (2009).
62. Freeman, E. A. & Moisen, G. G. A comparison of the performance of threshold criteria for binary classification in terms of predicted prevalence and kappa. *Ecol. Model.* **217**, 48–58 (2008).
63. Kozhoridze, G., Orlovsky, N., Orlovsky, L., Blumberg, D. G. & Golan-Goldhirsh, A. Geographic distribution and migration pathways of Pistacia—Present, past and future. *Ecography* **38**, 1141–1154. https://doi.org/10.1111/ecog.01496 (2015).
64. Pérez Gutiérrez, R. M. Orchids: A review of uses in traditional medicine, its phytochemistry and pharmacology. *J. Med. Plants Res.* **4**, 592–638 (2010).
65. Rajeshbhai, V. A. & Ingalhalli, R. An overview of medicinal importance of orchids. *Acta Sci. Med. Sci.* **6**, 28–36 (2022).
66. Boral, D. & Moktan, S. Modelling current and future potential distribution of medicinal orchids in Darjeeling eastern Himalaya. *Plant Ecol.* **225**, 213–226. https://doi.org/10.1007/s11258-023-01392-4 (2024).
67. Wani, I. *et al.* Ecological analysis and environmental niche modelling of *Dactylorhiza hatagirea* (D. Don) Soo: A conservation approach for critically endangered medicinal orchid. *Saudi J. Biol. Sci.* **28**, 2109–2122. https://doi.org/10.1016/j.sjbs.2021.01.054 (2021).
68. Shrestha, B. *et al.* Suitability of habitats in Nepal for *Dactylorhiza hatagirea* now and under predicted future changes in climate. *Plants* https://doi.org/10.3390/plants10030467 (2021).
69. Kolanowska, M., Rewicz, A. & Baranow, P. Ecological niche modeling of the pantropical orchid *Polystachya concreta* (Orchidaceae) and its response to climate change. *Sci. Rep.* **10**, 14801. https://doi.org/10.1038/s41598-020-71732-1 (2020).
70. Thomas, M., Kremer, C., Klausmeier, C. & Litchman, E. a global pattern of thermal adaptation in marine phytoplankton. *Science* **338**, 1085–1088. https://doi.org/10.1126/science.1224836 (2012).
71. Mammola, S. & Isaia, M. Rapid poleward distributional shifts in the European cave-dwelling Meta spiders under the influence of competition dynamics. *J. Biogeogr.* **44**, 2789–2797. https://doi.org/10.1111/jbi.13087 (2017).
72. Bennett, M., Marquet, P., Sillero-Zubiri, C. & Marino, J. Shifts in habitat suitability and the conservation status of the Endangered Andean cat *Leopardus jacobita* under climate change scenarios. *Oryx* **53**, 356–367. https://doi.org/10.1017/S0030605317000503 (2019).
73. Samal, P., Srivastava, J., Charles, B. & Singarasubramanian, S. R. Species distribution models to predict the potential niche shift and priority conservation areas for mangroves (*Rhizophora apiculata*, *R. mucronata*) in response to climate and sea level fluctuations along coastal India. *Ecol. Indic.* **154**, 110631. https://doi.org/10.1016/j.ecolind.2023.110631 (2023).
74. Chandra Prasad, P. R., Sudhakar Reddy, C., Raza, S. H. & Dutt, C. B. S. Population structure, age gradations, and regeneration status of *Pterocarpus dalbergioides* Roxb., an Endemic Species of Andaman Islands, India. *Pac. J. Sci. Technol.* **9**, 658–664 (2008).
75. Whigham, D. F., O'Neill, J. P., Rasmussen, H. N., Caldwell, B. A. & McCormick, M. K. Seed longevity in terrestrial orchids—Potential for persistent in situ seed banks. *Biol. Conserv.* **129**, 24–30. https://doi.org/10.1016/j.biocon.2005.10.029 (2006).
76. International, B. G. C. & Garden, U. S. B. 2017 Global Ex situ Collections Assessment for Orchids. (Botanic Gardens Conservation International & United States Botanic Garden, 2017).
77. Kolanowska, M., Michalska, E. & Konowalik, K. The impact of global warming on the niches and pollinator availability of sexually deceptive orchid with a single pollen vector. *Sci. Total Environ.* https://doi.org/10.1016/j.scitotenv.2021.148850 (2021).
78. Kolanowska, M. Loss of fungal symbionts and changes in pollinator availability caused by climate change will affect the distribution and survival chances of myco-heterotrophic orchid species. *Sci. Rep.* **13**, 6848. https://doi.org/10.1038/s41598-023-33856-y (2023).
79. Sathiyadash, K., Muthukumar, T., Uma, E. & Pandey, R. R. Mycorrhizal association and morphology in orchids. *J. Plant Interact.* **7**, 238–247. https://doi.org/10.1080/17429145.2012.699105 (2012).
80. Saikia, J., Mazumdar, R. & Thakur, D. Phylogenetic affiliation of endophytic actinobacteria associated with selected orchid species and their role in growth promotion and suppression of phytopathogens. *Front. Plant Sci.* **13**, 1058867. https://doi.org/10.3389/fpls.2022.1058867 (2022).
81. Kaur, J. & Sharma, J. Orchid root associated bacteria: Linchpins or accessories?. *Front. Plant Sci.* **12**, 661966. https://doi.org/10.3389/fpls.2021.661966 (2021).
82. Micheneau, C., Johnson, S. & Fay, M. Orchid pollination: From Darwin to the present day. *Bot. J. Linn. Soc.* **162**, S10–S28 (2010).
83. Ackerman, J. D. *et al.* Beyond the various contrivances by which orchids are pollinated: Global patterns in orchid pollination biology. *Bot. J. Linn. Soc.* https://doi.org/10.1093/botlinnean/boac082 (2023).
84. Pakum, W., Kongbangkerd, A., Srimuang, K.-O., Gale, S. W. & Watthana, S. Reproductive biology of a rare, fly-pollinated orchid, *Bulbophyllum nipondhii Seidenf.*, in Thailand. *Flora* **260**, 151467. https://doi.org/10.1016/j.flora.2019.151467 (2019).
85. van der Pijl, L. & Dodson, C. *An Atlas of Orchid Pollination. America, Africa, Asia and Australia* 308 (A.A. Balkema Publishers, 1966).
86. Forrest, J. R. K. Complex responses of insect phenology to climate change. *Current Opin. Insect Sci.* **17**, 49–54. https://doi.org/10.1016/j.cois.2016.07.002 (2016).
87. Michelle, J. S., Jason, P. H. & Amy, C. G. Timing is everything: An overview of phenological changes to plants and their pollinators. *Nat. Areas J.* **34**, 227–234. https://doi.org/10.3375/043.034.0213 (2014).
88. Xinqi, C. & Vermeulen, J. J. In *Flora of China* Vol. 25 (eds X. Chen *et al.*) Ch. Orchidaceae, 404–440 (2009).
89. Gómez, N. R., Tremblay, R. L. & Meléndez-Ackerman, E. Distribution of life cycle stages in a lithophytic and epiphytic orchid. *Folia Geobot.* **41**, 107–120 (2006).
90. Wisz, M. *et al.* Effects of sample size on the performance of species distribution models. *Divers. Distrib.* **14**, 763–773. https://doi.org/10.1111/j.1472-4642.2008.00482.x (2008).
91. Morelli, T. L. & Millar, C. (USDA Forest Service Climate Change Resource Cente, USA, 2018).
92. Morelli, T. L. *et al.* Climate-change refugia: Biodiversity in the slow lane. *Front. Ecol. Environ.* **18**, 228–234. https://doi.org/10.1002/fee.2189 (2020).

## Acknowledgements

I would like to thank anonymous Reviewers for their insightful comments and suggestions.

## Author contributions

Complete study was made by Marta Kolanowska.

## Funding

The author declares that no funds, grants, or other support were received during the preparation of this manuscript.

## Declarations

### Competing interests

The author declares that she has no financial or non-financial conflicts of interest.

### Additional information

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1038/s41598-024-73248-4.

**Correspondence** and requests for materials should be addressed to M.K.

**Reprints and permissions information** is available at www.nature.com/reprints.

**Publisher's note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

**Open Access** This article is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License, which permits any non-commercial use, sharing, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if you modified the licensed material. You do not have permission under this licence to share adapted material derived from this article or parts of it. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by-nc-nd/4.0/.

© The Author(s) 2024