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2 **Title: Predicting range shifts of *Davidia involucrata* Ball. under future climate change**

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13 **Abstract**

14 Understanding and predicting how species will respond to climate change is crucial
15 for biodiversity conservation. Here, we assessed future climate change impacts on the
16 distribution of a rare and endangered plant species, *Davidia involucrate* in China,
17 using the most recent global circulation models developed in the sixth Assessment
18 Report of the Intergovernmental Panel on Climate Change (IPCC6). We assessed the
19 potential range shifts in this species by using an ensemble of species distribution
20 models (SDMs). The ensemble SDMs exhibited high predictive ability and suggested
21 that the temperature annual range, annual mean temperature, and precipitation of the
22 driest month are the most influential predictors in shaping distribution patterns of this
23 species. The projections of the ensemble SDMs also suggested that *D. involucrate* is
24 very vulnerable to future climate change, with at least one-third of its suitable range
25 expected to be lost in all future climate change scenarios and will shift to the
26 northward of high-latitude regions. These findings suggest that it is of great
27 importance to ensure that adaptive conservation management strategies are in place to
28 mitigate the impacts of climate change on *D. involucrate*.

29 **Keywords:** *D. involucrate*, climate change, dove tree, ensemble species distribution
30 models (SDMs), range shifts, suitable habitats

31

32 **Introduction**

33 The recent global warming due to the increase of greenhouse gases caused by human activities is
34 driving global species redistributions (Pearson and Dawson, 2003; Hampe and Petit, 2005;
35 Jackson and Sax, 2010). In response to global warming, many species have attempted to keep
36 pace with climate change by adjusting their phenology and physiology to match new climatic
37 conditions (Walther et al., 2002), or shifting their distributions towards higher altitudes or
38 latitudes to track suitable habitats (Chen et al., 2011; Hampe and Petit, 2005; Jump and Penuelas,
39 2005; Walther et al., 2002). Unfortunately, those species that failed to shift their distribution lost
40 a substantial proportion of their suitable habitats, or have even become extinct globally
41 (Flagmeier et al., 2014; Sproull et al., 2015). Furthermore, this situation may worsen under future
42 climate change (Thomas et al., 2014; Warren et al., 2013). Thus, in order to mitigate the negative
43 effects of climate change on species, conservation strategies should include modelling species
44 distributions to identify to what extent they could be influenced by future climate change.

45 In the past two decades, species distribution models (SDMs) have been widely used to
46 assess the impacts of future climate change on species distributions and guide conservation
47 planning (Kujala et al., 2013; Maggini et al., 2014; Wiens et al., 2009). However, SDMs may
48 suffer from a lack of precision and portability due to the variation in covariate selections (Zhang
49 and Zhang, 2012), type of SDM used (Hartley et al., 2006; Pearson et al., 2006; Thuiller et al.,
50 2009; Wenger et al., 2013), and climate projections arising from different global circulation
51 models (GCMs) and CO₂ emission scenarios (Barry and Elith, 2006; Wenger et al., 2013), which
52 can yield misleading or inconsistent outcomes, posing challenges for decision-making (Elith et
53 al., 2006). Ensemble modelling approaches, which combined a series of SDMs, can produce
54 consensus projections that may outperform single SDMs, and reduce the predictive uncertainty

of single algorithm by combining their predictions (Thuiller et al., 2014). By using ensemble modelling approaches, more robust projections can be produced with reasonable interpretation (Araújo and Guisan, 2006). Consequently, these approaches have been widely used to estimate the distributions of species under future climate change scenarios for plants (Forester et al., 2013), amphibians (Zhang et al., 2020), insects (Marshall et al., 2018) and mammals (Ahmad et al., 2020; Yen et al., 2011).

Davidia involucrata Baill., commonly known as dove tree or handkerchief tree, is a rare and endangered species listed in the China Plant Red Data Book under first-grade state protection (Liu et al., 2019). It is also a Tertiary relict plant endemic to China (Fu and Jin, 1992), currently restricted to the mountains of southwestern and south-central China (Li, 1954; Liu et al., 2019; Takhtajan, 1980). Owing to the highly strict ecotope and recruitment limitation (i.e., low reproduction rate and dispersal ability), the population age structure of *D. involucrata* is declining (Wang et al., 2019). In addition, the increasing intensity of human activities has led to a sharp decrease of its remaining habitat. Despite its threatened status, few studies have explored the vulnerability of *D. involucrata* to climate change (Tang et al., 2017; Wang et al., 2019). By using ecological niche models, Tang et al. (2017) projected the potential suitable habitats of this species under past, current and future climatic conditions. In their work, the obsolete CMIP5 climate models were used to simulate future climate conditions (Tang et al., 2017). However, many studies have shown that the most recent CMIP6 climate models perform better in the simulation of future climate conditions compared to the CMIP5 climate models (Fan et al., 2020; Xin et al., 2020). Therefore, a rigorous analysis combined ensemble modelling approaches and the CMIP6 climate models investigating potential impacts of future climate change on the distribution of *D. involucrata* is of great urgency and significance.

Here, we conducted our study under the hypotheses that (a) future climate change will severely reduce suitable habitats of *D. involucrate*; and (b) will push this species to higher altitudes and/or latitudes. To explore these hypotheses, we compiled a large dataset on spatially explicit species presence records of the *D. involucrate* and environmental data covering China and subsequently use ensemble modelling approaches to projecting the potential suitable habitats of *D. involucrate* under current and future climatic conditions. According to our knowledge, our study is one of the first studies to investigate how *D. involucrate* will response to future climate change by using ensemble modelling approaches and the most recent CMIP6 global circulation models.

Material and methods

Species occurrence data

We obtained occurrence data for *D. involucrate* from multiple data sources, including Chinese Virtual Herbarium (CVH, <http://www.cvh.ac.cn>), National Specimen Information Infrastructure (NSII, www.nsii.org.cn), Global Biodiversity Information Facility (GBIF, <https://www.gbif.org>) and other publications (e.g., Wang et al., 2019). To reduce potential errors in species' geographic locations of occurrence data, we only include species occurrence data with geographic locations. To ensure that all occurrence records were in the species' native geographic locations, we exclude the species occurrence data collected in manual intervention areas, such as parks and experimental forests. From this process, we selected 337 occurrence records to model ecological niches for *D. involucrate* (Fig. 1).

Climate variables

19 bioclimatic variables (BIO1-BIO19; Table S1) for the time period 1979–2013 were obtained

from CHELSA (<http://chelsa-climate.org>; Karger et al., 2017), with a spatial resolution of 30 arc-seconds (~1 km). The future 19 bioclimatic variables with a 2.5 arc-minutes resolution for three time periods, 2050s (2041-2060), 2070s (2061-2080) and 2090s (2081-2100), under two representative concentration pathways (RCPs) scenarios, RCP2.6 and RCP8.5, from nine widely used global circulation models (GCMs): CNRM-CM6-1, CNRM-ESM2-1, CanESM5, IPSL-CM6A-LR, MIROC-ES2L and MIROC6, were extracted directly from the WorldClim Version 2.1 dataset (Fick and Hijmans, 2017). For each time period, each GCM and for each RCP scenarios, we projected all maps of current and future climate variables onto the same 10-km equal area grid as used for fitting the distribution models, using a bilinear interpolation.

The 19 climatic variables used in this study are usually strongly correlated (Marshall et al., 2018). To minimize multicollinearity among variables, we used Pearson's correlations and variance inflation factors (VIFs) to exclude highly correlated variables. Variables with a Pearson correlation >0.70 were considered highly correlated (Dormann et al., 2013), and a VIF >5 was used as a signal that a model had collinearity issues (Rogerson, 2010). Finally, six climatic variables were selected for modelling species distributions, including Annual mean temperature (BIO1), Isothermality (BIO3), Temperature annual range (BIO7), Precipitation of the driest month (BIO14), Precipitation seasonality (BIO15) and Precipitation of the warmest quarter (BIO18).

Species distribution modelling

An ensemble of species distribution models (Araújo and Guisan, 2006) was used to model potential suitable habitat for *D. involucrata* using the biomod2 package in the R platform (v. 4.0.4; <http://cran.r-project.org>). We chose the ensemble modelling approach because of its ability to create a consensus of the predictions of multiple algorithms and reduce the predictive

124 uncertainty of single algorithm (Thuiller et al., 2014). Ten algorithms were considered in the
125 ensemble model: artificial neural network (ANN), classification tree analysis (CTA), flexible
126 discriminant analysis (FDA), generalized additive model (GAM), generalized boosting model
127 (GBM), generalized linear model (GLM), multiple adaptive regression splines (MARS),
128 maximum entropy (MAXENT), random forest (RF) and surface range envelope (SRE). For
129 algorithms requiring species absence records, we generated 10,000 pseudo-absence points with
130 the equal number as the occupied grids for GAM, GBM, GLM and RF, and 10,000 background
131 points for MAXENT by randomly sampling without replacement. To avoid model over-fitting,
132 the selection of pseudo-absence or background points was limited to realm-biome combinations
133 occupied by the species' range map.

134 To evaluate the accuracy of each algorithm, we performed cross-validation on each
135 algorithm using bootstrap approach, where random subsets of 80% of each dataset for training
136 data and the remaining 20% for testing algorithm performance using the area under the receiver
137 operating characteristics curve (AUC) and true skill statistics (TSS). This procedure was repeated
138 10 times to create predictions independent of the training data. Algorithms with $AUC > 0.90$ and
139 $TSS > 0.80$ were considered to have good predictive performance (Allouche et al., 2006; Gallien
140 et al., 2012; Swets, 1988) and were thus kept in the final ensemble model. Based on the final
141 ensemble model, we estimated the response curve of each covariate and determined variable
142 contribution by calculating the change in correlation between the covariates and the response
143 with and with-out the selected variable (Thuiller et al., 2015). The final ensemble model was
144 then projected to current and future climatic conditions by using all occurrence and pseudo-
145 absence data. Finally, these habitat suitability maps were converted to binary presence absence
146 maps using a threshold that maximums model sensitivity plus specificity, which has been shown

generally to perform well (Thuiller et al., 2015).

Statistical analysis

Analyses were conducted on the ensemble model map projections of binary presence absence maps. To assess potential impacts of climate change on species ranges, following Zhang et al. (2015), we used two metrics to quantify species' vulnerability: the relative change in total area of suitable habitat (CSH) and the loss of current suitable habitat (LSH). The first metric assumes unlimited dispersal into the projected entire suitable habitats in the future time periods and can be calculated using the following equation:

$$CSH = (AREA_{future} - AREA_{current}) / AREA_{current} \times 100,$$

where $AREA_{future}$ and $AREA_{current}$ is the area of current and future suitable habitats. The second metric assumes no dispersal into the projected suitable habitats out of the current suitable habitats and can be calculated using the following equation:

$$CSH = \left(1 - \frac{Overlap(AREA_{future}, AREA_{current})}{AREA_{current}}\right) \times 100.$$

To detect the direction and distance of species range shifts under future conditions, we determined the centroids of current and future binary presence absence maps using the R package 'rgeos' with the 'gCentroid' function.

Results

Model performance and variable contribution

The AUC and TSS measures provided highly consistent estimates of the model performance of the 10 modelling algorithms (Table 1). As the mean AUC and TSS values of the 10 modelling algorithms except SRE are all above 0.9 and 0.8, respectively, we removed SRE from the final ensemble model. The AUC and TSS value of the final ensemble model is 0.975 and 0.898,

respectively, which is higher than of the individual modelling algorithms. Among the six selected predictor variables, the temperature annual range is the most influential variable, followed by annual mean temperature, precipitation of the driest month, isothermality, precipitation seasonality and precipitation of the warmest quarter (Table 2).

Species' range shifts under future climatic conditions

The projections of future habitat suitability for *D. involucrate* predicted severe range contraction under all scenarios (Fig. 2-3). Specifically, by assuming global dispersal, the proportion of current suitable habitats of this species projected to be lost ranged from 28.08% (under IPSL-CM6A-LR climate model and RCP 2.6 scenario) to 53.08% (under CanESM5 climate model and RCP 8.5 scenario) by the 2050s, and from 33.27% (under CNRM-ESM2-1 climate model and RCP 2.6 scenario) to 68.86% (under CNRM-CM6-1 climate model and RCP 8.5 scenario) by the 2070s (Fig. 2, Fig. 3a, b). The loss of potential suitable habitats under zero dispersal is more severe than those under global dispersal (Fig. 2, Fig. 3c, d), despite having a similar trend in predicted species range size.

Under future climatic conditions, centroids of potential suitable habitats of *D. involucrate* under most scenarios were projected to shift north-east (Fig. 4). The exception is that this species was projected to experience north-west shifts under CanESM5 and IPSL-CM6A-LR climatic models and RCP 8.5 scenario, respectively (Fig. 4c, d). The magnitude of species' range shifts varied greatly under different GCMs, different RCPs and different assumptions of species' dispersal ability (Fig. 4). The species would need move from 165.01 km (under the MIROC-ES2L climate model and RCP 8.5 scenario by the 2070s) to 419.10km (under the CanESM5 climate model and RCP 8.5 scenario by the 2070s) under global dispersal, and from 88.83 km (under the CNRM-ESM2-1 climate model and RCP 8.5 scenario by the 2070s) to 175.07km

(under the CNRM-CM6-1 climate model and RCP 8.5 scenario by the 2070s) under zero dispersal (Fig. 4).

Discussion

Understanding and predicting how species will response to future climate change is crucial for biodiversity conservation (Wiens et al., 2009) and has required novel approaches with high predictive performance and low predictive uncertainty (Elith et al., 2006; Thuiller W et al., 2014). In this study, by using ensemble SDMs and the CMIP6 GCMs, we projected the distribution of suitable habitats of *D. involucrate* under current and future climatic conditions. The results suggest that around 35% and 50% of its suitable habitats at present will be lost by 2050s and 2070s, respectively, and its range will shift towards higher latitudes but not higher altitudes. Our findings highlight the high vulnerability of *D. involucrate* to future climate change and thus have important implications for guiding future conservation planning.

Previous studies have reported that potential suitable habitats of *D. involucrate* were mainly distributed in mountainous areas with narrow annual temperature range and high precipitation (Liu et al., 2019; Su and Zhang, 1999), reflecting this species cold intolerance (Su and Zhang, 1999). Consistent with these previous studies, our results show that, among the selected six climatic variables, temperature annual range, annual mean temperature and precipitation of the driest month were the three most important predictors of the distribution of *D. involucrate*. Therefore, broad temperature annual range, extreme high and/or low temperature, together with low precipitation events, could lead to the loss of suitable habitats for this species.

It is often assumed that more complex and more up-to-date models will perform better and/or produce more robust projections than previous-generation models (USGCRP, 2017).

Consistent with previous studies (Elith et al., 2006; Thuiller W et al., 2014), our results showed that the ensemble SDMs have higher predictive ability than individual SDMs. Furthermore, numerous studies have concluded that the CMIP6 GCMs perform better than CMIP5 GCMs in simulating the future climatic conditions (Fan et al., 2020; Xin et al., 2020). In the present study, by using CMIP6 GCMs, our future projection suggested that *D. involucrate* will shift towards higher latitudes, and a large proportion of suitable habitats will be lost under future climate change. These findings support the hypothesis for northward shifts in response to climate change (Chen et al., 2011; Poloczanska et al., 2013), implying the usefulness of CMIP6 GCMs.

Despite the predictive power of the ensemble modelling of *D. involucrate*, an important limitation in the present study is that we assessed future habitat suitability under two extreme dispersal assumptions (i.e., no dispersal and unlimited dispersal), which ignores the realistic rates and modes of dispersal of this species (Saupe et al., 2012). These assumptions are likely inaccurate, which could lead to overestimation of suitable habitat under the unlimited dispersal assumption or underestimation under the zero-dispersal assumption (Engler and Guisan, 2009; Viana, 2017; Zanatta et al., 2020). For instance, Engler et al. (2009) assessed the potential impacts of climate change on habitat suitability of 287 mountain plants under four dispersal scenarios (unlimited dispersal, zero dispersal, realistic dispersal and realistic dispersal with long-distance dispersal events). Their result showed that the projected future distributions under realistic dispersal were significantly different from those of other dispersal scenarios. However, regardless of dispersal scenario, our results highlight the high vulnerability of *D. involucrate* to climate change, and provide the bounds to the magnitude of the change.

Overall, our research provides fundamental knowledge for understanding the potential impacts of climate change on the distribution of *D. involucrate*. This study also provides useful

information for comprehending vegetation changes at global scales under climate change, especially for the climate-related range shifts of Tertiary relict plants (Tang et al., 2017). However, to effectively improve the predictive power of SDM projections, we recommend incorporating diverse ecological processes, such as dispersal mechanisms, into the future projections.

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Conflict Interest

The authors declare no conflict of interest.

Author Contribution

Teng Long: Conceptualization (equal); Formal analysis (lead); Investigation (lead); Methodology (equal); Project administration (equal); Writing–original draft (lead); Writing–review & editing (equal). **Junfeng Tang**: Formal analysis (supporting); Methodology (equal); Supervision (equal); Writing–review & editing (equal). **Nicholas Pilfold**: Formal analysis (equal); Methodology (equal); Writing–review & editing (equal). **Xuzhe Zhao**: Conceptualization (equal); Funding acquisition (lead); Investigation (equal); Project administration (lead); Resources (lead); Supervision (lead); Writing–original draft (equal); Writing–review & editing (equal). **Tingfa Dong**: Conceptualization (equal); Project administration (equal); Supervision (equal); Writing–review & editing (equal).

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263 **Data Accessibility**

264 All data needed to evaluate the conclusions in the paper are present in the paper and/or the
265 Supplementary Materials. Additional data related to this paper may be requested from the
266 authors.

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440

441 Tables and Figures

442 **Table 1.** Performance of 10 modelling algorithms used to predict habitat suitability of *Davidia*
 443 *involucrate*. Results are shown as mean \pm SE. AUC: area under the receiver operating
 444 characteristic curve; TSS: true skill statistics.

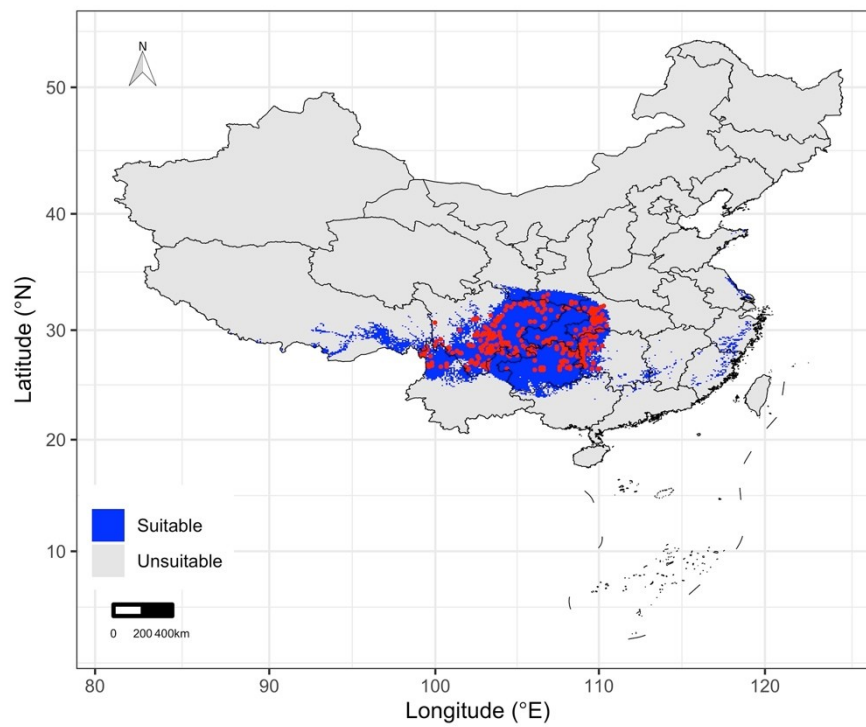
Modelling algorithms	AUC	TSS
Artificial neural network*	0.944 \pm 0.006	0.841 \pm 0.020
Classification tree analysis*	0.926 \pm 0.015	0.840 \pm 0.026
Flexible discriminant analysis*	0.945 \pm 0.005	0.822 \pm 0.017
Generalised additive model*	0.958 \pm 0.005	0.858 \pm 0.016
Generalised boosting model*	0.961 \pm 0.007	0.849 \pm 0.021
Generalised linear model*	0.952 \pm 0.003	0.847 \pm 0.013
Multiple adaptive regression splines*	0.954 \pm 0.006	0.846 \pm 0.012
MAXENT.Phillips*	0.964 \pm 0.005	0.851 \pm 0.020
Random forest*	0.966 \pm 0.005	0.870 \pm 0.016
Surface range envelope	0.849 \pm 0.011	0.697 \pm 0.023

445 *: models were selected to develop the ensemble model.

446 **Table 2.** Relative contributions of the nine selected predictor variables in the ensemble model of
 447 habitat suitability for *Davidia involucrate* Ball.

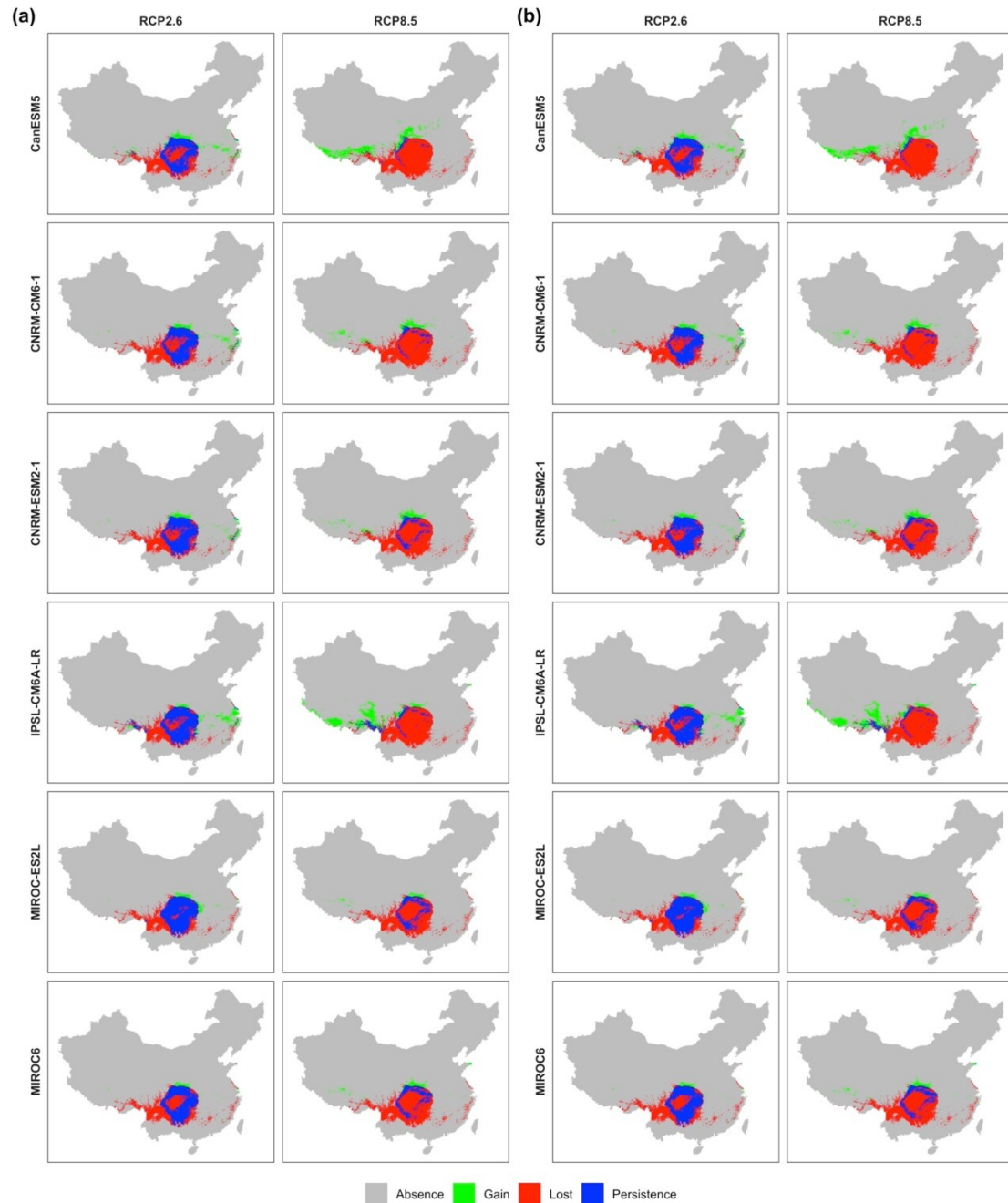
Predictor variables	Relative importance
Annual mean temperature (BIO1)	0.344 ± 0.009
Isothermality (BIO3)	0.091 ± 0.003
Temperature annual range (BIO7)	0.834 ± 0.017
Precipitation of the driest month (BIO14)	0.138 ± 0.002
Precipitation seasonality (BIO15)	0.013 ± 0.001
Precipitation of the warmest quarter (BIO18)	0.006 ± 0.001

448



450

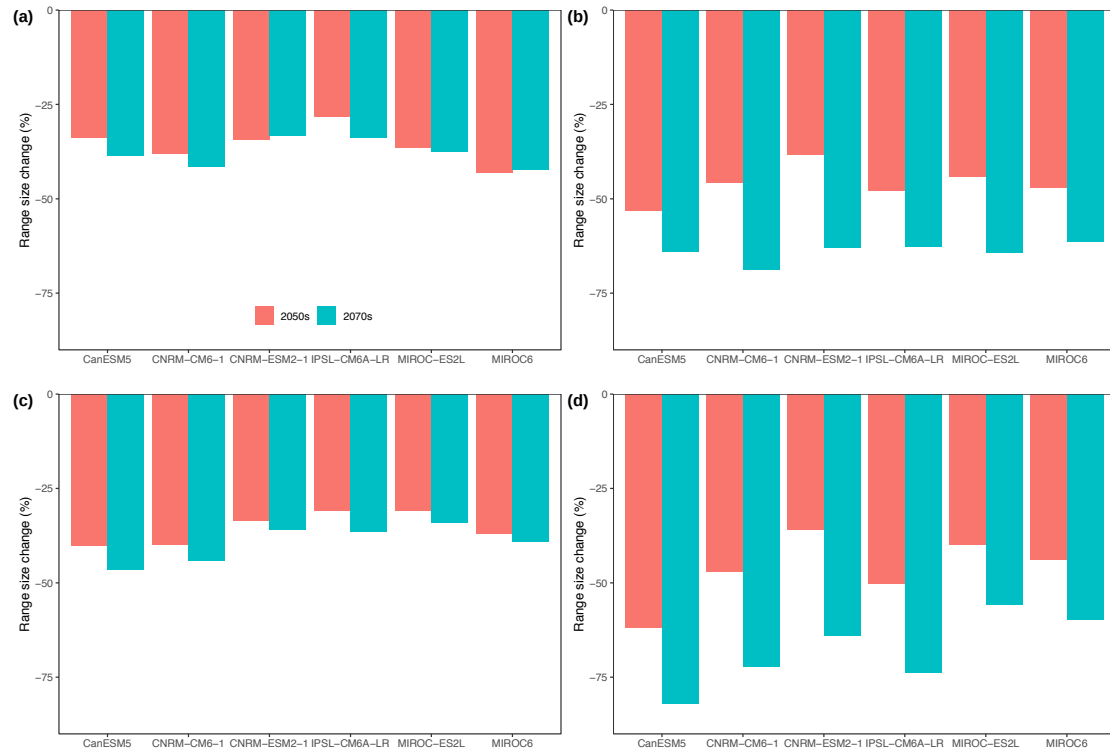
451 **Figure 1.** Potential suitable (blue) and unsuitable (grey) habitats suitability of *Davidia*
 452 *involucrata* Baill. under current climatic conditions in China. Red points represent
 453 occurrence records of *D. involucrata*.



454

455 **Figure 2.** Changes in suitable ranges of *Davidia involucrata* Baill. projected by
 456 ensemble SMDs under each GCMs and RCP scenario in: (a) 2050s and (b) 2070s.
 457 Four trajectories were assigned to each grid cell by comparing habitat suitability
 458 under current and future climatic conditions: ‘absence’, a grid that is unsuitable for
 459 this species under current climatic conditions remain unsuitable under future climatic

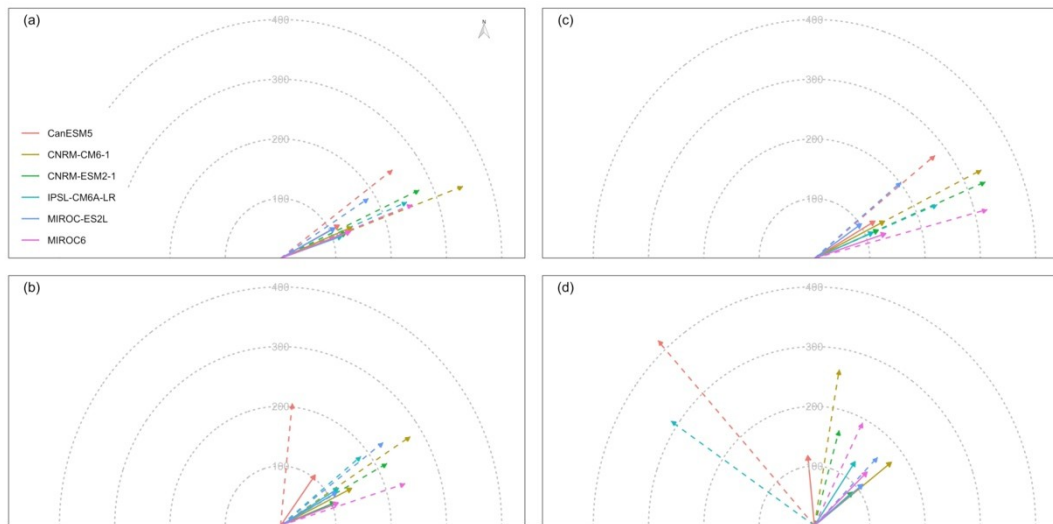
460 conditions; 'gain', a grid that is unsuitable for this species under current climatic
461 conditions become suitable under future climatic conditions; 'lost', a grid that is
462 suitable for this species under current climatic conditions become unsuitable under
463 future climatic conditions; 'persistence', a grid that is suitable for this species under
464 current climatic conditions remain suitable under future climatic conditions.



465

466 **Figure 3.** The projected range size changes of *Davidia involucrate* Ball. in 2050s and
 467 2070s. The range size changes (%) are relative to the predicted suitable areas of *D.*
 468 *invulcrate* under the current climate conditions. (a) – (d), Projections of range size
 469 changes of *Davidia involucrate* were obtained from the ensemble models under the
 470 unlimited dispersal ((a), (b)) and no dispersal ((c), (d)) scenarios using multiple future
 471 climate projections for two time periods from the selected nine GCMs, and under the
 472 representative concentration pathway RCP2.6 ((a), (c)) and RCP8.5 ((c), (d)). 48
 473 ensemble models were built for *D. involucrate*. The bars indicate the median value.

474 **Figure 4.** Centroid changes between current distributions of *Davidia involucrate* Ball.
 475 and projected distributions by ensemble species distribution model under future
 476 changing climate conditions: (a) under RCP 2.6 scenario in 2050s, (b) under RCP 8.5
 477 scenario in 2050s, (c) under RCP 2.6 scenario in 2070s, and (d) under RCP 8.5
 478 scenario in 2070s. The arrow in each map shows direction and distance between
 479 present and future distribution centroids. The start of arrow represents centroid of
 480 projected suitable area of *D. involucrate* under present climate conditions, while the
 481 end coincides with the position of the centroid under future climate scenarios. The
 482 real and dashed lines represent global dispersal and no dispersal, respectively.



485 **Table S1.** Definition and description of climate variables in our datasets.

Variables	Variable description and description	Units
BIO1	Mean annual temperature in each grid cell	°C
BIO2	Mean diurnal range (mean of maximal temperature - minimal temperature) in each grid cell	°C
BIO3	Isothermality (Bio2/Bio7) (* 100) in each grid cell	
BIO4	Temperature seasonality (standard deviation *100) in each grid cell	°C
BIO5	Maximal temperature of the warmest month in each grid cell	°C
BIO6	Minimal temperature of coldest month in each grid cell	°C
BIO7	Temperature annual range (Bio5-Bio6) in each grid cell	°C
BIO8	Mean temperature of the wettest quarter in each grid cell	°C
BIO9	Mean temperature of the driest quarter in each grid cell	°C
BIO10	Mean temperature of the warmest quarter in each grid cell	°C
BIO11	Mean temperature of the coldest quarter in each grid cell	°C
BIO12	Total annual precipitation in each grid cell	mm
BIO13	Precipitation of the wettest month in each grid cell	mm
BIO14	Precipitation of the driest month in each grid cell	mm
BIO15	Precipitation seasonality (coefficient of variation) in each grid cell	
BIO16	Precipitation of the wettest quarter in each grid cell	mm
BIO17	Precipitation of the driest quarter in each grid cell	mm
BIO18	Precipitation of the warmest quarter in each grid cell	mm
BIO19	Precipitation of the coldest quarter in each grid cell	mm