Current and future plant invasions in protected areas: does clonality matter?

Ji-Zhong Wan, Chun-Jing Wang, Niklaus Zimmermann, Mai-He Li, Robin Pouteau, Fei-Hai Yu

Received: 10 February 2021 | Revised: 22 August 2021 | Accepted: 2 September 2021

DOI: 10.1111/ddi.13425

RESEARCH ARTICLE

Diversity and Distributions WILEY

Current and future plant invasions in protected areas: Does clonality matter?

Ji-Zhong Wan[1,2,3,4] | Chun-Jing Wang[1,2] | Niklaus E. Zimmermann[5,6] | Mai-He Li[5] | Robin Pouteau[1] | Fei-Hai Yu[1]

[1]Institute of Wetland Ecology & Clone Ecology, Zhejiang Provincial Key Laboratory of Plant Evolutionary Ecology and Conservation, Taizhou University, Taizhou, China

[2]State Key Laboratory of Plateau Ecology and Agriculture, Qinghai University, Xining, China

[3]Department of Ecology, Pontifical University Catholic of Chile, Santiago, Chile

[4]Instituto de Ecología y Biodiversidad (IEB), Santiago, Chile

[5]Swiss Federal Research Institute WSL, Birmensdorf, Switzerland

[6]Department of Environmental Systems Science, Swiss Federal Institute of Technology ETH, Zurich, Switzerland

Correspondence
Fei-Hai Yu, Institute of Wetland Ecology & Clone Ecology, Taizhou University, Taizhou 318000, China.
Email: feihaiyu@126.com

Funding information
This study was supported by the Ten Thousand Talent Program of Zhejiang Province (2018R52016), the National Natural Science Foundation of China (31870610, 32071527) and the Joint Fund of Zhejiang Provincial Natural Science Foundation (LTZ20C030001). All the authors have approved the manuscript and agree with submission to your esteemed journal

Editor: John Lambrinos

Abstract

Aim: Protected areas (PAs) play an important role in biodiversity conservation, but remain increasingly threatened by invasive alien plant species (IAPS) in conjunction with global climate change. The latter is modifying the distribution of the former, and the magnitude and direction of distributional changes are predicted to vary depending on species dispersal mode. Here, we address the question of whether clonality is expected to affect the future invasion pattern in PAs.

Location: Worldwide.

Time period: 1950–2100.

Major taxa studied: 36 invasive alien plant species.

Methods: We used ensembles of three species distribution models (GLM, GAM and Maxent) based on >70,000 occurrence records to project the distribution of 36 of the world's most invasive clonal and non-clonal plants in >20,000 PAs. Projections were based on three greenhouse gas concentration scenarios (low, medium and high) for 2080.

Results: Climate change showed little impact on the global invasion pattern in PAs, and clonality showed little effect when all biomes were processed in concert. However, we discerned that the future invasion risk of clonal IAPS markedly increased in biomes located at high elevation and high latitude compared with non-clonal IAPS, while the risk decreased in lower-elevation tropical and subtropical biomes where asexual reproduction may be a less successful trait. We also showed that invasion hot spots overlapped with biodiversity hot spots and two realms (i.e. Nearctic and Palearctic), which calls for bridging the gap between invasion and conservation sciences and for more concerted management strategies.

Main conclusions: We suggest that effective management of IAPS in PAs should consider in which biomes PAs are located as well as the reproductive traits of IAPS that are present or may become so.

KEYWORDS

alien plant species, biomes, clonal plants, greenhouse gas emissions, macro-ecology, species distribution models, world's worst invasive species

1 | INTRODUCTION

Global climate change has the potential to alter the distribution of many organisms, including invasive alien species (Bellard et al., 2017; Bradley et al., 2010; Parepa et al., 2013; Shrestha & Shrestha, 2019). Because invasive alien species generally have broad physiological tolerances and/or specific traits that enhance their competitive performance or rapid adaptation to harsh environments, they may respond quickly to changing environmental conditions (Hoffmann & Sgro, 2011; Mathakutha et al., 2019; Warren et al., 2020; Whitney & Gabler, 2008). Therefore, it is a hot topic for ecologists and biological conservationists to explore the effects of climate change in biological invasions around the world.

Understanding how climate change affects the distribution of invasive alien species is of particular resonance in protected areas (PAs), which had been established to protect biodiversity, and threatened native species, habitats and ecosystems (Foxcroft et al., 2007, 2011, 2019). Climate change may further increase the capacity of alien species to invade PAs and subsequently damage the conservation efficiency of PAs (Foxcroft et al., 2007, 2011; Gallardo et al., 2017; Padmanaba et al., 2017; Pěknicová & Berchová-Bímová, 2016). At the global scale, however, it is still unknown the mechanism on how climate change is expected to affect invasions in PAs.

The impact of climate change is recognized to vary according to life forms, generation times, reproduction modes and dispersal abilities in plants (Corlett & Westcott, 2013; Nicotra et al., 2010). As a result, we can expect invasion risks in PAs to depend on whether invasive alien plant species (IAPS) are able to reproduce asexually or not (Gallardo et al., 2017; Gillson et al., 2013; Lamsal et al., 2018). Previous studies have shown that clonality can contribute greatly to plant invasions (e.g. Eckert et al., 2016; Fenollosa et al., 2016; Liu et al., 2006; Song et al., 2013). It has also been noted that many IAPS reproduce by clonal growth and that many of the most invasive plants in the world are clonal (Fenollosa et al., 2016; Liu et al., 2006; Yu et al., 2019). For instance, 2/3 of the most invasive plants in China and also about 2/3 of the world's worst invasive plants listed by the ISSG (Invasive Species Specialist Group) are clonal (Liu et al., 2006; Lowe et al., 2000). In addition to the ability to disperse by seeds, clonal plants can also spread their populations by clonal growth and may thus be less constrained by climate because they are not temperature-regulated regarding flowering and fruiting (Ye et al., 2014; Yu et al., 2019). Furthermore, clonal plants possess some distinguished characteristics that can assist them to quickly establish their populations in unexpectedly harsh environments (Negreiros et al., 2014). These differences may result in altered adaptability of clonal compared to non-clonal plants to environmental changes (Ye et al., 2014). Previous studies (e.g. Bellard et al., 2014; Burgess et al., 2017; Gillard et al., 2017; Osawa et al., 2019; Wan & Wang, 2018) used species distribution modellings (SDMs) to the distributions of these world's worst invasive plants. However, these studies only established correlative SDMs based on effects of environmental changes on IAPS distributions using presence and absence points. The early studies on SDMs do not allow to mechanistically model the direct effects of clonal versus non-clonal life strategies on IAPS distributions from local to global scales. Therefore, to develop adapted conservation strategies and reduce invasion risks, it is critical to know about the distributional responses of clonal versus non-clonal IAPS in PAs in the course of climate change.

The influence of climate change in the distribution of IAPS in PAs may also depend on biomes, that is the major vegetation complexes classified based on dominant vegetation types and associated climatic and other major environmental conditions (Bradley et al., 2010; Gallagher et al., 2010; Thuiller et al., 2005). Indeed, plant invasions differ greatly among different biomes because biotic and abiotic conditions vary considerably among them (Bradley et al., 2010; Gallagher et al., 2010). Furthermore, the abundance of clonal plants varies greatly among biomes (Kalusová et al., 2013; Rood et al., 2007). For instance, clonal plants are dominant species in grasslands, wetlands and tundra, but occur less frequently in conifer forests (Klimešová et al., 2017). Therefore, the influence of climate change in the prevalence of clonal and non-clonal IAPS in PAs can also differ among biomes. So far, however, no study has tested whether the susceptibility of PAs to clonal and non-clonal IAPS differs among biomes in the course of climate change.

We modelled the current and future distribution of 36 plant species found in the list of "100 of the world's worst invasive alien species" established by the Invasive Species Specialist Group (Lowe et al., 2000). We split this set of species into clonal and non-clonal categories and assessed their current probability to invade global PAs distributed in 16 biomes and seven realms as well as their future invasion risk under three climate change scenarios. The use of species distribution models does not allow to mechanistically model the direct effect of the different life strategies (i.e. clonal vs. non-clonal) on invasion risks. However, it allows modelling the different climate sensitivities that may have established due to their different life strategies. Specifically, we addressed the following questions. (a) Will climate change affect the prevalence of the worst IAPS in PAs at the global scale? (b) Will this change be evenly distributed across biomes? (c) Will this change be the same among clonal and non-clonal plants?

2 | METHODS

2.1 | Species data

The Invasive Species Specialist Group (ISSG) of the International Union for Conservation of Nature (IUCN) has compiled a list of "100 of world's worst invasive alien species" (Lowe et al., 2000; http://www.issg.org/database/species/search.asp?st=100ss). We used the 36 IAPS from this list (Table S1) as the most geographically and taxonomically representative set of the most noxious IAPS around the world, causing significant impacts on biodiversity and/or human activity. Clonal plants are those that reproduce asexually by means of vegetative offspring that remain attached to the parent, at least until they establish (Dong et al., 2014). We identified clonal IAPS based on whether the species has potential clonality in life-history strategies from the perspectives on the clonal and bud bank traits (Klimešová et al., 2017). First, we checked whether 36 species are clonal from the list of CLO-PLA3 database (www.clopla.butbn.cas.cz/). Then, we determined the clonal and bud bank traits for each species based on the TRY database (www.try-db.org/TryWeb/Home.php; Kattge et al., 2020) and the Botanical Information and Ecology Network (BIEN) database (Maitner et al., 2018). Finally, clonal plant species could be identified if the species was listed in CLO-PLA3 database and had the clonal and bud bank traits in life-history strategies. Among the 36 IAPS, 13 were identified as non-clonal and 23 as clonal according to ISSG and other references (Liu et al., 2006; Table 1 and Table S1). Contemporaneous occurrence data with geographic coordinates were obtained for each IAPS from several online databases including: (a) the Global Biodiversity Information Facility (GBIF; www.gbif.org), (b) LIFEMAPPER (www.lifemapper.com), (c) SPECIESLINK (www.splink.cria.org.br), (d) the Chinese Virtual Herbarium (CVH; www.cvh.org.cn), (e) the IUCN/SSC ISSG (Lowe et al., 2000) and (f) published literatures. All extracted occurrences were resampled at 2.5-arc-minute resolution (ca. 5 km at the equator), and duplicated records were removed to reduce the effect of sampling bias. Overall, we obtained 70,020 unique records, that is 1,945 records for each IAPS on average (ranging from 52 for the coralberry *Ardisia elliptica* to 26,506 for the purple loosestrife *Lythrum salicaria*) across the world, with the exception of the Sahara region, most regions of Russia, northern Canada and Greenland (Table S1 and Figure S1).

2.2 | Climate data

Nineteen climatic variables derived from the WorldClim database (representing 1950–2000 averages; Table S2; Hijmans et al., 2005; www.worldclim.org) were used for modelling purposes. We selected these variables at a 2.5-arc-minute resolution because a finer resolution would cast a false sense of precision despite potentially giving higher accuracy scores (Ramirez-Villegas & Jarvis, 2010). Among these variables, we removed those with Pearson's correlation coefficient $|r| > 0.7$ to avoid multi-collinearity effects in the parameter estimates of species distribution models (Elith et al., 2011). The four resulting variables were annual mean temperature, temperature seasonality, precipitation of the driest month and precipitation of the wettest quarter.

As a reference for modelling the potential invasion of IAPS under future climate change, we relied on scenarios from the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC, 2013). We used data from five global climate models for 2080 (2071–2099), namely, mohc_hadgem2 (es), csiro_mk3_6_0, cccma_canesm2, mpi_esm (lr) and ncar_ccsm4. From each model, we used three representative concentration pathways (RCPs), namely, RCP2.6 (mean: 270 ppm CO_2; range: 140–410 ppm CO_2 by 2,100), RCP4.5 (mean: 780 ppm CO_2; range: 595–1,005 ppm by 2,100) and RCP8.5 (mean: 1685 ppm CO_2; range: 1,415–1910 ppm CO_2 by 2,100). These represent the low, medium and high greenhouse gas concentration scenarios, respectively (IPCC, 2013).

2.3 | Protected areas, biomes and realms

A global map of PAs was obtained from the World Database on Protected Areas (WDPA; http://www.wdpa.org/). We excluded protected seascape or PAs lacking information on area coverage. We also excluded PAs too small to be represented in one grid cell (<2.5 × 2.5 arc minutes). Finally, we used more than 20,000 PAs whose size ranged from 1 to 194,166 cells.

The terrestrial area of the globe was further classified into 16 biomes, representing the major global plant communities determined by temperature and precipitation (Figure S2; Olson et al., 2001). The map of these biomes was obtained from http://maps.tnc.org/gis_data.html#ERA as described by the World Wildlife Fund (WWF) and The Nature Conservancy (TNC; Olson et al., 2001). Based on gridded maps of PAs and biomes, we assigned each PA to one of the 16 biome types using a majority function. This allowed us to analyse the effect of the biome type on the distribution of clonal and non-clonal IAPS in PAs under future climate change. We also assigned PAs to the types of realms based on a global ecoregion map from http://maps.tnc.org/gis_data.html#ERA as described by the World Wildlife Fund (WWF) and The Nature Conservancy (TNC; Olson et al., 2001) through a majority function (Figure S2).

2.4 | Modelling approach and evaluation

We projected the current and future global potential distributions of the 36 IAPS based on contemporary occurrence localities and current and future climatic data. We used three species distribution models, that is general linear models (GLM; McCullagh & Nelder, 1989), general additive models (GAM; Hastie & Tibshirani, 1986) and Maxent (Phillips et al., 2006). GLM is considered to result in simple, GAM in moderately complex and MaxEnt in highly complex response shapes (Mainali et al., 2015). We set the regularization multiplier (*beta*) to 1.5 to produce a smooth and general response shape that stands for a biologically realistic behaviour in Maxent. The maximum number of background points was set to 10,000, and we used a 10-fold cross-validation approach to remove bias with respect to recorded occurrence points.

We evaluated the predictive precision of the species distribution models using the area under the curve (AUC) of the receiver operation characteristic (ROC). The AUC values range from 0 (systematically wrong) to 1.0 (highest predictive ability), while a value of 0.5 indicates a random model fit. The three models built for each species with values above 0.7 were considered useful in our study. We averaged the results of SDM across GLM, GAM and MaxEnt for each IAPS, and AUC values of SDMs were higher than 0.7. However, AUC was insufficient for assessing the performance of Maxent modelling. Therefore, we used a binomial test based on the omission rate to evaluate the performance of Maxent modelling for the 36 IPS (Anderson et al., 2002, 2003). The omission rates of training and test occurrence records were calculated as the proportion of the sample points within grid cells that were predicted to yield the absences of the species for the occurrence localities of test data (Anderson

TABLE 1 Change in the probability of invasive alien plant species to invade protected areas between the current situation and the high concentration scenario (RCP 8.5) according to the realm distribution of protected areas

Species	Clonality	Afrotropic	Australasia	Indo-Malay	Nearctic	Neotropic	Oceania	Palearctic
Acacia mearnsii	Yes	−0.908	0.357	−0.632	32.455	5.128	−0.746	17.864
Arundo donax	Yes	−0.384	0.489	−0.069	18.651	0.315	0.081	6.727
Caulerpa taxifolia	Yes	0.522	0.596	0.545	6.843	0.654	0.282	2.930
Cinchona pubescens	Yes	−0.872	−0.578	−0.767	1.091	−0.760	−0.623	0.249
Eichhornia crassipes	Yes	0.092	0.584	0.174	10.352	0.573	0.184	5.162
Euphorbia esula	Yes	−0.360	−0.528	−0.191	−0.284	−0.273	−0.337	−0.265
Fallopia japonica	Yes	−0.001	−0.486	−0.013	1.934	−0.188	−0.198	0.435
Hedychium gardnerianum	Yes	−0.216	0.530	0.443	18.380	1.279	−0.231	12.555
Imperata cylindrica	Yes	0.135	0.865	0.432	36.351	1.506	0.463	12.700
Ligustrum robustum	Yes	6.374	2.966	4.869	19.443	8.686	5.769	7.414
Lythrum salicaria	Yes	−0.309	−0.415	−0.239	−0.403	−0.279	−0.351	−0.340
Mikania micrantha	Yes	−0.258	0.407	0.072	5.037	0.028	0.000	3.850
Opuntia stricta	Yes	26.225	11.427	25.999	20.948	59.045	30.414	32.905
Prosopis glandulosa	Yes	1.323	7.720	2.285	5.224	17.916	0.820	10.214
Psidium cattleianum	Yes	−0.608	0.975	−0.348	36.640	0.492	−0.273	21.393
Pueraria montana var. lobata	Yes	0.126	1.206	1.075	125.507	6.345	1.126	65.887
Rubus ellipticus	Yes	−0.705	0.460	−0.530	5.323	0.291	0.231	6.548
Schinus terebinthifolius	Yes	−0.360	1.364	−0.215	10.795	0.491	−0.110	6.406
Spartina anglica	Yes	−0.614	−0.650	−0.369	12.150	−0.371	−0.434	10.839
Spathodea campanulata	Yes	0.209	0.624	0.247	0.986	0.123	0.096	0.484
Sphagneticola trilobata	Yes	0.829	1.930	0.915	2.959	0.834	0.443	1.371
Undaria pinnatifida	Yes	−0.958	0.787	11.385	6,726.214	2.166	−0.547	144.864
Clonal		−0.147	0.099	−0.132	0.760	−0.045	−0.083	0.425
Ardisia elliptica	No	1.526	1.202	0.391	1.217	0.560	0.346	0.503
Cecropia peltata	No	0.610	0.760	0.647	1.034	0.384	0.310	0.620
Chromolaena odorata	No	−0.020	1.625	0.102	4.835	0.333	0.240	3.456
Clidemia hirta	No	−0.181	0.904	−0.210	1.963	0.290	0.032	1.701
Hiptage benghalensis	No	2.121	1.410	1.593	3.327	1.726	1.664	1.668
Lantana camara	No	−0.264	1.297	−0.078	16.602	0.887	0.037	8.023
Leucaena leucocephala	No	0.312	1.135	0.406	4.267	0.596	0.410	3.339
Melaleuca quinquenervia	No	0.248	2.784	1.183	5.405	1.411	0.585	3.791
Miconia calvescens	No	−0.589	0.394	−0.617	2.003	−0.438	−0.351	2.232
Mimosa pigra	No	0.811	2.431	1.094	3.896	0.812	0.764	2.295
Myrica faya	No	−0.764	−0.480	−0.522	−0.314	−0.545	−0.562	−0.222
Pinus pinaster	No	−0.419	0.326	0.635	63.594	2.959	−0.099	55.659
Tamarix ramosissima	No	−0.432	0.651	0.207	2.846	2.492	1.221	3.200
Ulex europaeus	No	−0.335	−0.543	−0.153	3.569	−0.283	−0.367	1.905
Non-clonal		−0.107	0.156	0.009	1.529	−0.053	0.022	0.972
Clonal plus non-clonal		−0.135	0.114	−0.102	0.755	−0.066	−0.040	0.459

et al., 2002, 2003). Then, one-sided *p*-values were used to test the null hypothesis, and the test points are predicted no better than those by a random prediction with the same fractional predicted area (Anderson et al., 2002). The binomial probabilities were based on 11 common threshold defaults by Maxent modelling (detailed information in Phillips et al., 2006). Although the training and test omission rates may not be sufficient, a low omission rate (i.e. 15%) is a necessary condition for a good model (Anderson et al., 2002, 2003). The average omission rates of training and test occurrence records were lower 15% for all 36 IAPS.

2.5 | Potential of IAPS to invade PAs

We analysed the probability of clonal IAPS, non-clonal IAPS and all IAPS (clonal plus non-clonal) to invade PAs at three geographic levels (globe, biome and PA). To do so, we calculated the current and future potential distribution for each species, climate model and climate scenario.

To estimate the future distribution of single IAPS under the three concentration scenarios, we superimposed the potential future distribution maps of single IAPS for each of the 4 GCMs ×3 RCPs with identical weight. We then averaged the potential distribution of co-occurring IAPS in the low, medium and high greenhouse gas concentration scenarios and analysed the potential of co-occurring IAPS to colonize PAs using the present distributions as a basis for comparison. Many previous studies have set a presence/absence threshold for each individual species to estimate species richness through ensemble modelling. However, these thresholds are problematic and can produce bias in predictions (Calabrese et al., 2014). Here, we used the modified method of Calabrese et al. (2014) to compute the invasion extent of co-occurring IAPS in each pixel:

$$E_j = \sum_{k=1}^{k} P_{i,k}$$

where E_j represents the current or future invasion extent of co-occurring IAPS in pixel j, k is the number of species in pixel j, and $P_{j,k}$ is the probability of potential distribution of species i in pixel j.

We calculated the probability of multiple IAPS to invade the PA as follows:

$$S_t = \sum_{j=1}^{n} X_j Y_j$$

where S_t is the current or future probability of co-occurring IAPS to invade PA t, X_j an indicator of the distribution possibility of co-occurring IAPS (E_j value) in grid j of PA t, Y_j the distribution area percentage of all IAPS in PA t and n the total number of grids. For the global-level assessment, n is the number of grids of PAs across the globe; for the biome- and realm-level assessment n is the number of grids of PAs belonging to the certain types of biome and realm; and for the PA-level assessment, n is the number of grids of the PA.

We calculated the change in the probability of multiple IAPS for each PA between the current scenario and the 2080s (in the low, medium and high concentration scenarios):

$$A_t = \frac{S_{\text{Future}} - S_{\text{Current}}}{S_{\text{Current}}}$$

where A_i is the change in the probability of multiple IAPS to invade PAs and S_{Future} and S_{Current} are the future and current probabilities of multiple IAPS to invade PAs. We calculated the probability change for clonal IAPS, non-clonal IAPS and all IAPS.

2.6 | Risk hot spots of IAPS invasions in PAs

We used the Optimizing Hot Spot Analysis (ESRI, 2014) to identify PA with the highest risk of IAPS invasions. The analysis objectives were to determine: (a) the probability of multiple IAPS (all, clonal and non-clonal IAPS) to invade PAs and (b) for each PA, the change in probability of multiple IAPS between current and future conditions. This analysis consisted of a spatial clustering analysis for identifying hot and cold spots with statistical significance by computing the Getis-Ord Gi* statistic (ESRI, 2014). The resultant z-scores and *p*-values indicated where features with either high or low values cluster spatially by looking at each feature within the context of neighbouring features based on the Getis-Ord Gi* statistic (ESRI, 2014). Here, we determined the feature clusters with high values or low values in PAs. To determine clusters of PA hot spots of invasions with statistical significance, we used the Optimizing Hot Spot Analysis based on spatial correlation between the changes in probabilities of multiple IAPS to invade the PAs under current and future climates.

3 | RESULTS

3.1 | Influences of climate change and clonality on plant invasions in PAs

The future probability of all IAPS (i.e. clonal plus non-clonal IAPS) to invade PAs changed very little from the current situation to the low (−1.94%), medium (−1.40%) and the high greenhouse gas concentration scenarios (0.05%) (Figure 1). The consequence of climate change in the probability of clonal IAPS alone and non-clonal IAPS alone to invade PAs was also small (probability change between present and future was less than ±5%; Figure 1), with little difference between clonal and non-clonal IAPS (Figure 1).

Climate change greatly increased the probability of all IAPS to invade PAs located in seven biomes (Boreal forests/Taiga; Inland Water; Montane Grasslands and Shrublands; Temperate Broadleaf and Mixed Forests; Temperate Conifer Forests; Temperate Grasslands, Savannas and Shrublands; and Tundra), but markedly decreased that in five biomes (Flooded Grasslands and Savannas; Mangroves; Tropical and Subtropical Dry Broadleaf Forests; Tropical and Subtropical Grasslands, Savannas and Shrublands; and Tropical and Subtropical Moist Broadleaf Forests; Figure 2 and Figure S3). Climate change had little impact on the probability of all IAPS to invade PAs in the other four biomes (Figure 2 and Figure S3).

Impacts of climate change in the invasion probability of clonal and non-clonal IAPS varied greatly among biomes (Figure 2). The probability change was much larger for clonal IAPS than for non-clonal IAPS in Inland Water (57.18 vs. 8.36%), and Temperate Grasslands, Savannas and Shrublands (85.51 vs. 19.79%; Figure 2). However, this

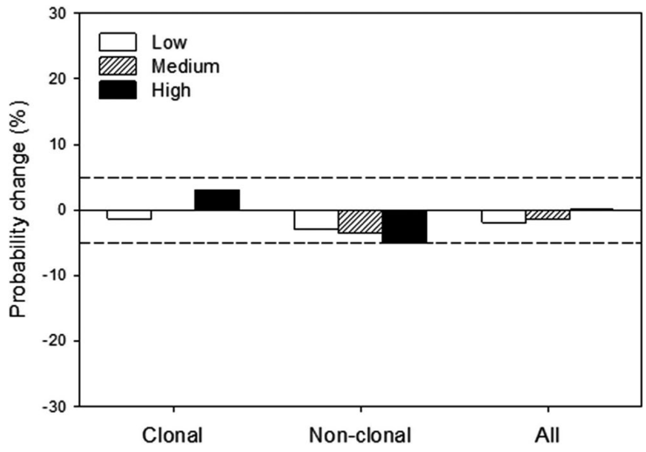

FIGURE 1 Change in the probability of clonal, non-clonal and all (clonal plus non-clonal) invasive alien plant species to invade global protected areas between the current situation and the three future concentration scenarios (low, medium and high). Dash lines represent values of +5% and −5%. RCPs 2.6, 4.5 and 8.5 were used for the low, medium and high climate scenarios. The probabilities were derived from assemble species distribution modelling for invasive alien plant species

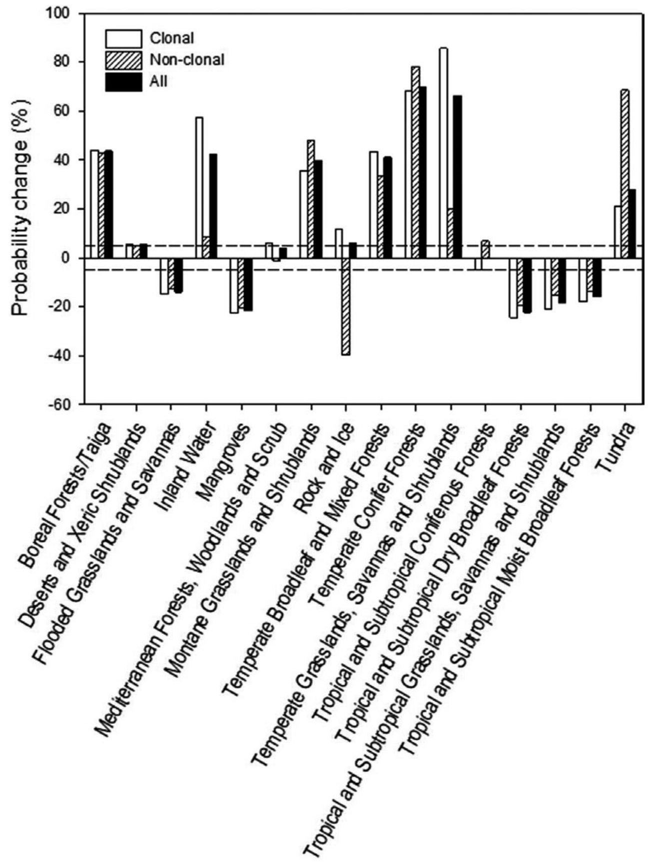

FIGURE 2 Change in the probability of all (clonal plus non-clonal), clonal and non-clonal invasive alien plant species to invade protected areas between the current situation and the high concentration scenario (RCP 8.5) according to the biome distribution of PAs. Dash lines represent values of +5% and −5%. The probabilities were derived from assemble species distribution modelling for invasive alien plant species

probability change was much smaller for clonal IAPS than for non-clonal IAPS in Tundra (21.14 vs. 68.42%; Figure 2). Over Rock and Ice, the change was slightly positive for clonal IAPS (11.56%), but negative for non-clonal IAPS (−39.81%; Figure 2). Clonality had little impact on the probability change in the other biomes (Figure 2).

The largest impacts of climate change in the invasion probability of both clonal and non-clonal IAPS occur in PAs of Nearctic and Palearctic (Table 1). However, such impacts could differ depending on different species and regions (Table 1). *Undaria pinnatifida* was the clonal IAPS, and *Pinus pinaster* and *Lantana camara* were the non-clonal IAPS with the largest impacts of climate change in the invasion probability in PAs of Nearctic and Palearctic (Table 1). Clonal IAPS had the significantly larger impacts of climate change in the invasion probability in PAs of Afrotropic, Indo-Malay and Oceania than non-clonal IAPS, and vice versa for non-clonal IAPS in other realms (Table 1).

3.2 | Hot spots of plant invasions

Based on the distribution of all IAPS, invasion hot spots were similar under the current and future climate scenarios (Figure S4). They included southwestern and southeastern Australia, New Zealand, Central Africa, Mexico, southeastern Asia and southern China (Figure S4). Compared to the current situation, PAs distributed in North America and Europe were more strongly invaded by all IAPS under future scenarios, while those located in South America, Australia and central Africa were less invaded (Figure 3). Hot spots of clonal IAPS were mainly distributed in North America, New Zealand and Europe under the current and future climates (Figure S4). Compared to the current situation, PAs more strongly invaded by clonal IAPS under future scenarios were mainly distributed in North America, New Zealand, northern Asia and Europe (Figure 3). Hot spots of non-clonal IAPS were located in South America, southeastern Asia and eastern Africa under the current and future climate scenarios (Figure S4). Compared to the current situation, PAs more strongly invaded by non-clonal IAPS under future scenarios were mainly distributed in Europe, North America and central China (Figure 3).

4 | DISCUSSION

4.1 | Effects of climate change in plant invasions in PAs

At the global scale, climate change had little impact on the probability of IAPS to invade PAs, suggesting that global climate change will unlikely promote the invasions of our set of IAPS into PAs across the globe. This finding is consistent with that of a recent study showing that the potential distributions of species, including plants, animals and microbes, were not significantly related to global climate change (e.g. Bellard et al., 2013, 2014). However, when we analysed

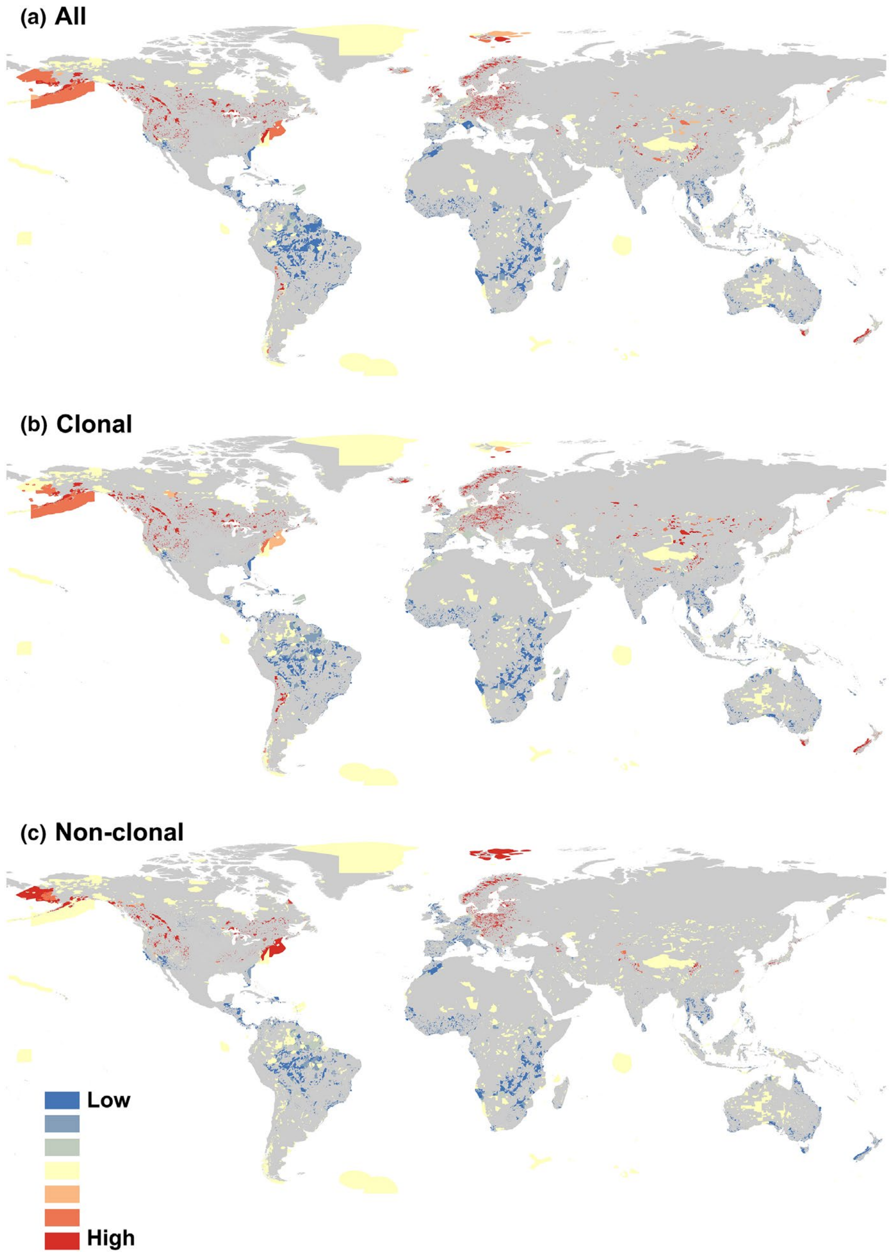

FIGURE 3 Hot spots of probability change of all (clonal plus non-clonal), clonal and non-clonal invasive alien plant species to invade protected areas in the current situation and the high gas concentration scenario (RCP 8.5). The probabilities and hot spots were derived from assemble species distribution modelling. The colour from blue to red represented the increasing probability of invasive alien plant species to invade protected areas

projected distributions at the biome scale, we found that climate change had positive, negative or neutral effects on plant invasions in PAs depending on the biomes in which PAs were located. These contrasted effects likely counteracted and resulted in no significant impact at the global scale. However, the impacts of climate change in the invasion probability of clonal and non-clonal IAPS may vary depending on species and realms. For example, climate change had the largest effects on the invasion probability of clonal and non-clonal IAPS in Nearctic and Palearctic. In these two realms, *Undaria pinnatifida* is the clonal IAPS, and *Pinus pinaster* and *Lantana camara* are the non-clonal IAPS with the largest impacts of climate change in the invasion probability.

Climate change was predicted to promote the distribution of IAPS in PAs in seven biomes located at high elevation or latitude. IAPS often have a wide niche breadth and can adapt to extreme climatic events (Allen & Bradley, 2016; Panda et al., 2018; Parepa et al., 2013). Hence, they have a high opportunity to invade the PAs of these biomes. Inland Water for its part can act as conduits for the efficient dispersal of propagules of aquatic plants (Bickel, 2017; Biswas et al., 2018; Coughlan et al., 2018; Gallardo et al., 2020). With rapid climate change, aquatic plants are easily released into the wild by aquarists easily (Gallardo et al., 2020; Hussner et al., 2017; Teixeira et al., 2017). Hence, PAs encompassing Inland Waters could be increasingly damaged by IAPS under climate change. Furthermore, the largest impacts of climate change in the invasion probability of clonal and non-clonal IAPS occur in Nearctic and Palearctic. Our result showed that these biomes and realms should be prioritized for invasion management.

On the other hand, climate change was predicted to decrease the range of IAPS in PAs in five biomes mainly located in tropical and subtropical climates. Global warming is expected to reduce plant diversity in tropical areas, and IAPS would be no exception (Bellard et al., 2014; Brodie et al., 2012). Hence, regarding the limited financial resources available for coordinated regional conservation actions, we believe fewer efforts can be spent in PAs located in these biomes.

4.2 | Impacts of clonality on plant invasions in PAs

While clonality had little impact on the invasion risk in PAs mediated by climate change at the global scale, clonality significantly influenced the invasion risk at the biome scale. In two biomes (Inland Water; Temperate Grasslands, Savannas and Shrublands), climate change is expected to favour the prevalence of clonal IAPS in PAs more than that of non-clonal IAPS. Both biomes are already overwhelmingly dominated by clonal plants, confirming that their environmental characteristics are very suitable for clonal plants.

Aquatic ecosystems are prone to biological invasions, and many inland aquatic ecosystems in the world are heavily invaded by aquatic clonal plants (Eckert et al., 2016; Hussner et al., 2017; Santamaría, 2002; Teixeira et al., 2017). For some aquatics such as the common water hyacinth *Eichhornia crassipes*, the main way to spread and invade is by clonal growth, and the spread of clonal propagules is also much easier in such ecosystems (Herben & Klimešová, 2020; Yu et al., 2019). Hence, in the future, we need to pay much attention to clonal IAPS in PAs which function to conserve Inland Water.

Clonal plant species play an important role in Temperate grasslands, Savannas and Shrublands, and PAs found in this biome usually harbour a rich biodiversity (Olson et al., 2001). Clonal plants are able to successfully invade new habitats because they do not necessarily need to establish a population by producing seeds and they just need a single individual to do well enough to produce ramets (Bittebiere et al., 2020; Byun et al., 2015). Furthermore, clonal plants are widely distributed in Temperate Grasslands, Savannas and Shrublands and are sensitive to increasing nitrogen deposition (Negreiros et al., 2014; Osborne et al., 2018). Enhanced nitrogen deposition may increase the number of ramets of IAPS, which could lead to dynamic changes in plant communities in PAs of the aforementioned biomes (Negreiros et al., 2014; Osborne et al., 2018). As clonal plant species have a strong invasion ability in this kind of biome under climate change, we need to improve our knowledge on the role of clonal traits during the invasions of clonal plants, as well as to develop effective measures that may block or weaken the spread of these IAPS. Hence, we should focus on clonal plants in the PAs of this biome.

Over Rock and Ice, future climate change would slightly increase the invasions of clonal IAPS in PAs, but dramatically decreased the invasions of non-clonal IAPS in PAs. There, environmental conditions are harsh (Olson et al., 2001). There may be few vascular plant species currently established in the Rock and Ice. However, the colonization of plants to areas currently classified as Rock and Ice will likely change the classification to something else, for example Tundra under climate change. Clonal plant species are especially able to resist harsh environmental conditions by clonal plant reproduction and plasticity due to their unique clonal life-history traits (Negreiros et al., 2014). Efforts should then be allocated mostly to clonal plants and not to non-clonal plants (Goldberg et al., 2020; van Kleunen et al., 2001; Kleyer & Minden, 2015). In Tundra, future climate change will probably increase the invasions of non-clonal IAPS in PAs much more than that of clonal IAPS. Hence, we need to pay attention to the invasion of non-clonal IAPS in PAs of this biome.

Climate change may change the types of biomes for PAs around the world. For example, it is potential that Temperate Grasslands, Savannas and Shrublands and Rock and Ice can be changed into other biomes, leading to biome transition zones or in periods of biome transition. Based on our results, clonal IAPS can adapt to harsh environmental conditions of these two biomes in current situation. Connected individuals (ramets) of clonal plants can translocate and share, for example, photosynthates, water and nutrients, and such physiological integration may affect performance of clonal plants both in heterogeneous and homogeneous environments (Wang et al., 2021). Hence, clonal plants have a strong ability to adapt to the changing environment conditions and heterogeneity across biome transition zones or in periods of biome transition (Santamaría, 2002; Wang et al., 2021).

4.3 | Current and future hot spots of plant invasions

We found that hot spots of the 36 worst IAPS under all three future climate scenarios matched with current hot spots. We stressed the importance of monitoring PAs in regions such as southwestern and southeastern Australia, New Zealand, Mexico, southeastern Asia and southern China, which are also known to be biodiversity hot spots of conservation priorities (www.conservation.org/how/pages/hotspots.aspx; Myers et al., 2000). The overlap between invasion hot spots and biodiversity hot spots stands for a serious problem as the expansion of IAPS, facilitated or unfacilitated by climate change, will decrease the space available for native species, which is likely to lead to ecosystem disorders and, ultimately, to species extinctions (Bellard et al., 2013, 2014). In some regions, IAPS are projected to spread from one into other PAs (Foxcroft et al., 2011, 2017, 2019). For example, the invasion hot spots showed a tendency of moving northward in Europe, and the density of invasion hot spots in northern Latin America is higher in the future than today based on our results.

Rapid globalization associated with high human mobility promotes the establishment of populations of IAPS in new habitats (Chapman et al., 2017; van Kleunen et al., 2020). For example, international trade is a critical force for the spread of IAPS due to frequent escapes and releases of introduced species into the wild (Chapman et al., 2017; Seebens et al., 2015). Furthermore, the economic use of IAPS plays a significant role in their naturalization success (van Kleunen et al., 2020). Perhaps the highest naturalization success for IAPS is its use as animal food or its use in horticulture or as ornamentals (van Kleunen et al., 2020). Invasion patterns are governed to a large extent by the global trade networks connecting source areas of IAPS and their dispersal through multiple networks (e.g. trade and transport; Chapman et al., 2017; Seebens et al., 2015). Our results do not explicitly address these invasion pathways, but they provide spatially explicit information about invasion hot spots around the world. Therefore, rapid globalization and high human mobility, coupled with distributional changes, could promote plant invasions in global PAs under climate change (Foxcroft et al., 2017; Seebens et al., 2015).

When observing invasions of clonal IAPS in a PA, we need to take immediate measures to prevent the spread of clonal IAPS, thus avoiding to "infect" other PAs around the invaded region. These measures include developing global indicators of biological invasions and designing long-term management plans at different geographical scales (Foxcroft et al., 2017). These measures should not be taken in a hurry, and it is important to commit to scientific assessments such as the species distribution and life history of clonal species (Herben et al., 2014; Thuiller et al., 2012). Resource utilization strategies of IAPS could promote their invasions (Funk & Vitousek, 2007; Parepa et al., 2013). IAPS must have access to available resources (e.g. nutrients, light, and water) to successfully invade a community and will have a high chance of invasion success if they do not encounter intense competition for these resources from resident species (Davis et al., 2000; Parepa et al., 2013). High growth rate and the ability to rapidly exploit available resources (e.g. nitrogen nutrients) are widely recognized as fundamental plant strategies and are a potential determinant of invasion success (Davis et al., 2000; Funk & Vitousek, 2007; Parepa et al., 2013). Therefore, nitrogen deposition can promote growth and provide eco-physiological advantages for IAPS (Bradley et al., 2010; Funk & Vitousek, 2007; Perry et al., 2010). Resources such as nutrients, light and water taken up by plants can be easily released into soils through hydraulic redistribution and can also be translocated by clonal integration within a plant clonal network (Liu et al., 2016; Ye et al., 2016). Clonal IAPS can benefit from high resource availability through clonal integration (Song et al., 2013; Wang et al., 2017; Yu et al., 2019). When detecting the distribution of IAPS, especially in invasion hot spots, areas of high resource availability (e.g. those with high nitrogen depositions) should receive special attention in strategies to prevent and control invasions of IAPS under climate change (Gough et al., 2012). However, early remediation actions have shown to be more effective and less costly than measures that are taken only after massive invasion success in North America, New Zealand and Europe, although details about the exact strategy related to the timing, frequency and intensity of actions tend to be species-specific (Foxcroft et al., 2011; Meier et al., 2014).

IAPS can invade PAs, benefiting from clonal reproduction and plasticity (Fenollosa et al., 2016). Many plants have the capacity for facultative clonal growth (Dong et al., 2014; Liu et al., 2006; Song et al., 2013), and clonal plants in general have the capacity for facultative sexual reproduction (Dong et al., 2014; Klimešová et al., 2017). Usually, PAs have rich species diversity, which may resist to plant invasion (Crutsinger et al., 2008; Dalrymple et al., 2015; Maron & Marler, 2007). Clonal IAPS can switch strategies between sexual and non-sexual reproductions for shaping species coexistence so that they can adapt to different levels of species diversity and climate change (Yamamichi et al., 2020; Zobel, 2008). Asexual plants change just as often and just as fast as do sexual plants when introduced to a new range (Dalrymple et al., 2015). Furthermore, clonal plasticity facilitates the adaptation of IAPS to rapid changing environments (Nicotra et al., 2010; Wang et al., 2018). Clonal plasticity could enhance the exploitation of resource heterogeneity by clonal IAPS, which have a significant contribution to maintenance or improvement of fitness under climate change (Nicotra et al., 2010; Santamaría, 2002; Wang et al., 2021). Clonal reproduction and plasticity may make the difference in invasion ability to PAs between clonal and non-clonal IAPS under climate change. Thus, clonality may be a key indicator of IAPS to invade PAs under climate change around the world.

For targeted observations of clonal IAPS, we suggest using Figure 3 to facilitate negotiations with stakeholders and decision-makers. In Figure 3, we could determine the priority protected areas belonging to North America, New Zealand and Europe for invasion risk depending on biomes and realms. We should make a deep understanding on invasion mechanism on clonal IAPS in Inland Water and Temperate Grasslands, Savannas and Shrublands because clonal IAPS favour climate change in these two biomes. The two realms, Nearctic and Palearctic, should be attention due to the largest impacts of climate change in the invasion probability of clonal (e.g. *Undaria pinnatifida*) and non-clonal IAPS (e.g. *Pinus pinaster* and *Lantana camara*). In these two realms, it is a high risk that PAs may be invaded by both clonal and non-clonal IAPS. We propose the following actions: (a) to improve basic data on IAPS and track their spread and (b) to map, evaluate and monitor the actual distributions of IAPS especially in hot spots (Hussner et al., 2017; Teixeira et al., 2017). In two biomes (Inland Water and Temperate Grasslands, Savannas and Shrublands), climate change is expected to favour the prevalence of clonal IAPS in PAs more than that of non-clonal IAPS. Furthermore, clonality should be developed as an indicator of plant invasion for PAs in Inland Water; Temperate Grasslands, Savannas and Shrublands of Nearctic and Palearctic under climate change.

Further helpful strategies are the use of effective methods such as species distribution models to predict the invasion risk of IAPS, the integration of experimental ecology and field investigations to set up efficient prevention and control actions for clonal IAPS (Bellard et al., 2013, 2014). While we focused explicitly on the importance of clonality in invasions of IAPS under climate change, future studies may want to consider the role of other functional traits (e.g. plant height, specific leaf area, nitrogen content, stem specific density and seed or diaspore mass) that are linked to, for example light, nutrient or water use efficiency, reproductive strategy, evolutionary history and biotic interactions in complex food chains. Such functional traits have already been related to plant invasions (Drenovsky et al., 2012). Variation of these traits may affect the distribution pattern and species interactions of clonal and non-clonal plants under environmental changes (Bittebiere et al., 2019; Herben & Klimešová, 2020) and thus the invasion success of clonal versus non-clonal IAPS (Wang et al., 2017). Hence, other functional traits of IAPS than clonality could be integrated into species distribution models to improve their performance at the global scale (Benito Garzón et al., 2019). In addition, dynamic hybrid models combined with species distribution models may facilitate the development of optimization strategies (Buchadas et al., 2017). These tools are essential for designing long-term management plans at the national to regional scales in order to create a concerted mitigation strategy for IAPS invasions into PAs under climate change.

4.4 | Limitations

Although our study provided the global maps of current and future plant invasions in protected areas for clonal and non-clonal plants, the limitations still exist in our study. First, the observations are with respect to known clonal and known non-clonal invasives, which may introduce some bias into our analysis. Thus, there may be more clonal or non-clonal invasive plants that can take advantage of future climate change due to constraint on a fixed number of species based on ISSG. Our study could provide the evidence on influences of climate change and clonality on plant invasions in PAs. However, specific mechanisms on effects of clonality on plant invasions did not be explored, which should be conducted in future studies. Second, the number of study species may potentially influence the results and interpretation in our study. Previous studies (e.g. Bellard et al., 2014; Burgess et al., 2017; Gillard et al., 2017; Kariyawasam et al., 2021; Osawa et al., 2019; Wan & Wang, 2018) used the list of "100 of world's worst invasive alien species" to address scientific questions on plant invasion. Many clonal plant species are potentially invasive (Gough et al., 2012; Liu et al., 2006; Wang et al., 2017). Third, we did not consider biome transition zones or in periods of biome transition. In the transition biomes and realms, instability and heterogeneity can promote plant invasions. Finally, there are many uncertainties on SDM results (e.g. model transferability) for projecting distributions of IAPS across different spatial scales (Araújo et al., 2019; Buisson et al., 2010; Chen et al., 2019; Guo et al., 2015; Liu et al., 2020; Zurell et al., 2020). The reliability of transferring SDMs to new ranges and future climates has been widely debated (Liu et al., 2020). Model transferability is intrinsically determined by the significant relationships between environmental predictors and species distributions, and the number of occurrence records for modelling distributions of IAPS (Liu et al., 2020; Petitpierre et al., 2012). Our study only considered the relationships between climatic predictors and distributions of IAPS at the global scale. Future studies should take the relationships between other environmental predictors (e.g. land use and land cover, and soil factors) and distributions of IAPS into SDMs. It is also important to collect a larger number of occurrence records as the input of SDMs for modelling distributions of IAPS (Araújo et al., 2019; Chen et al., 2019; Liu et al., 2020; Zurell et al., 2020).

5 | CONCLUSIONS

Global climate change may not promote the invasions of IAPS in PAs and plant clonality shows little impact at the global scale. However, climate change can markedly change plant invasion patterns in PAs at the scale of biomes and realms, and clonal and non-clonal plants also play contrasting roles in different biomes and realms. Therefore, to design effective strategies to prevent and control IAPS in PAs, biomes and plant reproductive traits should be carefully considered.

ACKNOWLEDGEMENTS

We thank Prof. Hai-Ning Qing for allowing us to use the CVH data.

CONFLICT OF INTEREST

The authors have no interest or relationship, financial or otherwise that might be perceived as influencing the author's objectivity with this work and thus have no conflicts of interest to declare.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13425.

DATA AVAILABILITY STATEMENT

All of the data in this paper are downloaded from publicly accessible websites cited in the main text. The original occurrence data are deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.6djh9w123).

ORCID

Ji-Zhong Wan https://orcid.org/0000-0001-6438-251X
Niklaus E. Zimmermann https://orcid.org/0000-0003-3099-9604
Robin Pouteau https://orcid.org/0000-0003-3090-6551
Fei-Hai Yu https://orcid.org/0000-0001-5007-1745

REFERENCES

Allen, J. M., & Bradley, B. A. (2016). Out of the weeds? Reduced plant invasion risk with climate change in the continental United States. *Biological Conservation*, *203*, 306–312. https://doi.org/10.1016/j.biocon.2016.09.015

Anderson, R. P., Gómez-Laverde, M., & Peterson, A. T. (2002). Geographical distributions of spiny pocket mice in South America: Insights from predictive models. *Global Ecology and Biogeography*, *11*, 131–141. https://doi.org/10.1046/j.1466-822X.2002.00275.x

Anderson, R. P., Lew, D., & Peterson, A. T. (2003). Evaluating predictive models of species' distributions: Criteria for selecting optimal models. *Ecological Modelling*, *162*, 211–232. https://doi.org/10.1016/S0304-3800(02)00349-6

Araújo, M. B., Anderson, R. P., Márcia Barbosa, A., Beale, C. M., Dormann, C. F., Early, R., Garcia, R. A., Guisan, A., Maiorano, L., Naimi, B., O'Hara, R. B., Zimmermann, N. E., & Rahbek, C. (2019). Standards for distribution models in biodiversity assessments. *Science Advances*, *5*, eaat4858. https://doi.org/10.1126/sciadv.aat4858

Bellard, C., Leclerc, C., Leroy, B., Bakkenes, M., Veloz, S., Thuiller, W., & Courchamp, F. (2014). Vulnerability of biodiversity hotspots to global change. *Global Ecology and Biogeography*, *23*, 1376–1386. https://doi.org/10.1111/geb.12228

Bellard, C., Rysman, J. F., Leroy, B., Claud, C., & Mace, G. M. (2017). A global picture of biological invasion threat on islands. *Nature Ecology & Evolution*, *1*, 1862–1869. https://doi.org/10.1038/s41559-017-0365-6

Bellard, C., Thuiller, W., Leroy, B., Genovesi, P., Bakkenes, M., & Courchamp, F. (2013). Will climate change promote future invasions? *Global Change Biology*, *19*, 3740–3748. https://doi.org/10.1111/gcb.12344

Benito Garzón, M., Robson, T. M., & Hampe, A. (2019). ΔTrait SDMs: Species distribution models that account for local adaptation and phenotypic plasticity. *New Phytologist*, *222*, 1757–1765.

Bickel, T. O. (2017). Processes and factors that affect regeneration and establishment of the invasive aquatic plant *Cabomba caroliniana*. *Hydrobiologia*, *788*, 157–168. https://doi.org/10.1007/s10750-016-2995-0

Biswas, S. R., Biswas, P. L., Limon, S. H., Yan, E. R., Xu, M. S., & Khan, M. S. I. (2018). Plant invasion in mangrove forests worldwide. *Forest Ecology and Management*, *429*, 480–492. https://doi.org/10.1016/j.foreco.2018.07.046

Bittebiere, A. K., Benot, M. L., & Mony, C. (2020). Clonality as a key but overlooked driver of biotic interactions in plants. *Perspectives in Plant Ecology, Evolution and Systematics*, *43*, 125510. https://doi.org/10.1016/j.ppees.2020.125510

Bittebiere, A. K., Saiz, H., & Mony, C. (2019). New insights from multidimensional trait space responses to competition in two clonal plant species. *Functional Ecology*, *33*, 297–307. https://doi.org/10.1111/1365-2435.13220

Bradley, B. A., Wilcove, D. S., & Oppenheimer, M. (2010). Climate change increases risk of plant invasion in the Eastern United States. *Biological Invasions*, *12*, 1855–1872. https://doi.org/10.1007/s10530-009-9597-y

Brodie, J., Post, E., & Laurance, W. F. (2012). Climate change and tropical biodiversity: A new focus. *Trends in Ecology & Evolution*, *27*, 145–150. https://doi.org/10.1016/j.tree.2011.09.008

Buchadas, A., Vaz, A. S., Honrado, J. P., Alagador, D., Bastos, R., Cabral, J. A., Santos, M., & Vicente, J. R. (2017). Dynamic models in research and management of biological invasions. *Journal of Environmental Management*, *196*, 594–606. https://doi.org/10.1016/j.jenvman.2017.03.060

Buisson, L., Thuiller, W., Casajus, N., Lek, S., & Grenouillet, G. (2010). Uncertainty in ensemble forecasting of species distribution. *Global Change Biology*, *16*, 1145–1157. https://doi.org/10.1111/j.1365-2486.2009.02000.x

Burgess, T. I., Scott, J. K., Mcdougall, K. L., Stukely, M. J., Crane, C., Dunstan, W. A., & Hardy, G. E. S. J. (2017). Current and projected global distribution of *Phytophthora cinnamomi*, one of the world's worst plant pathogens. *Global Change Biology*, *23*, 1661–1674.

Byun, C., de Blois, S., & Brisson, J. (2015). Interactions between abiotic constraint, propagule pressure, and biotic resistance regulate plant invasion. *Oecologia*, *178*, 285–296. https://doi.org/10.1007/s00442-014-3188-z

Calabrese, J. M., Certain, G., Kraan, C., & Dormann, C. F. (2014). Stacking species distribution models and adjusting bias by linking them to macroecological models. *Global Ecology and Biogeography*, *23*, 99–112. https://doi.org/10.1111/geb.12102

Chapman, D., Purse, B. V., Roy, H. E., & Bullock, J. M. (2017). Global trade networks determine the distribution of invasive non-native species. *Global Ecology and Biogeography*, *26*, 907–917. https://doi.org/10.1111/geb.12599

Chen, X., Dimitrov, N. B., & Meyers, L. A. (2019). Uncertainty analysis of species distribution models. *PLoS One*, *14*, e0214190.

Corlett, R. T., & Westcott, D. A. (2013). Will plant movements keep up with climate change? *Trends in Ecology & Evolution*, *28*, 482–488. https://doi.org/10.1016/j.tree.2013.04.003

Coughlan, N. E., Cuthbert, R. N., Kelly, T. C., & Jansen, M. A. (2018). Parched plants: Survival and viability of invasive aquatic macrophytes following exposure to various desiccation regimes. *Aquatic Botany*, *150*, 9–15. https://doi.org/10.1016/j.aquabot.2018.06.001

Crutsinger, G. M., Souza, L., & Sanders, N. J. (2008). Intraspecific diversity and dominant genotypes resist plant invasions. *Ecology Letters*, *11*, 16–23.

Dalrymple, R. L., Buswell, J. M., & Moles, A. T. (2015). Asexual plants change just as often and just as fast as do sexual plants when introduced to a new range. *Oikos*, *124*, 196–205. https://doi.org/10.1111/oik.01582

Davis, M. A., Grime, J. P., & Thompson, K. (2000). Fluctuating resources in plant communities: A general theory of invasibility. *Journal of Ecology*, *88*, 528–534. https://doi.org/10.1046/j.1365-2745.2000.00473.x

Dong, M., Yu, F. H., & Alpert, P. (2014). Ecological consequences of plant clonality. *Annals of Botany*, *114*, 367. https://doi.org/10.1093/aob/mcu137

Drenovsky, R. E., Grewell, B. J., D'Antonio, C. M., Funk, J. L., James, J. J., Molinari, N., Parker, I. M., & Richards, C. L. (2012). A functional trait perspective on plant invasion. *Annals of Botany*, *110*, 141–153. https://doi.org/10.1093/aob/mcs100

Eckert, C. G., Dorken, M. E., & Barrett, S. C. (2016). Ecological and evolutionary consequences of sexual and clonal reproduction in aquatic plants. *Aquatic Botany*, *135*, 46–61. https://doi.org/10.1016/j.aquabot.2016.03.006

Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E., & Yates, C. J. (2011). A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, *17*, 43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x

ESRI (2014). *ArcGIS desktop*. Retrieved from http://resources.arcgis.com/en/help/main/10.2

Fenollosa, E., Roach, D. A., & Munné-Bosch, S. (2016). Death and plasticity in clones influence invasion success. *Trends in Plant Science*, *21*, 551–553. https://doi.org/10.1016/j.tplants.2016.05.002

Foxcroft, L. C., Jarošík, V., Pyšek, P., Richardson, D. M., & Rouget, M. (2011). Protected-area boundaries as filters of plant invasions. *Conservation Biology*, *25*, 400–405.

Foxcroft, L. C., Pyšek, P., Richardson, D. M., Genovesi, P., & MacFadyen, S. (2017). Plant invasion science in protected areas: Progress and priorities. *Biological Invasions*, *19*, 1353–1378. https://doi.org/10.1007/s10530-016-1367-z

Foxcroft, L. C., Rouget, M., & Richardson, D. M. (2007). Risk assessment of riparian plant invasions into protected areas. *Conservation Biology*, *21*, 412–421. https://doi.org/10.1111/j.1523-1739.2007.00673.x

Foxcroft, L. C., Spear, D., van Wilgen, N. J., & McGeoch, M. A. (2019). Assessing the association between pathways of alien plant invaders and their impacts in protected areas. *NeoBiota*, *43*, 1. https://doi.org/10.3897/neobiota.43.29644

Funk, J. L., & Vitousek, P. M. (2007). Resource-use efficiency and plant invasion in low-resource systems. *Nature*, *446*, 1079–1081. https://doi.org/10.1038/nature05719

Gallagher, R. V., Beaumont, L. J., Hughes, L., & Leishman, M. R. (2010). Evidence for climatic niche and biome shifts between native and novel ranges in plant species introduced to Australia. *Journal of Ecology*, *98*, 790–799. https://doi.org/10.1111/j.1365-2745.2010.01677.x

Gallardo, B., Aldridge, D. C., González-Moreno, P., Pergl, J., Pizarro, M., Pyšek, P., Thuiller, W., Yesson, C., & Vilà, M. (2017). Protected areas offer refuge from invasive species spreading under climate change. *Global Change Biology*, *23*, 5331–5343. https://doi.org/10.1111/gcb.13798

Gallardo, B., Castro-Díez, P., Saldaña-López, A., & Alonso, Á. (2020). Integrating climate, water chemistry and propagule pressure indicators into aquatic species distribution models. *Ecological Indicators*, *112*, 106060. https://doi.org/10.1016/j.ecolind.2019.106060

Gillard, M., Thiébaut, G., Deleu, C., & Leroy, B. (2017). Present and future distribution of three aquatic plants taxa across the world: Decrease in native and increase in invasive ranges. *Biological Invasions*, *19*, 2159–2170. https://doi.org/10.1007/s10530-017-1428-y

Gillson, L., Dawson, T. P., Jack, S., & McGeoch, M. A. (2013). Accommodating climate change contingencies in conservation strategy. *Trends in Ecology & Evolution*, *28*, 135–142. https://doi.org/10.1016/j.tree.2012.10.008

Goldberg, D. E., Batzer, E., Elgersma, K., Martina, J., & Klimešová, J. (2020). Allocation to clonal growth: Critical questions and protocols to answer them. *Perspectives in Plant Ecology, Evolution and Systematics*, *43*, 125511. https://doi.org/10.1016/j.ppees.2020.125511

Gough, L., Gross, K. L., Cleland, E. E., Clark, C. M., Collins, S. L., Fargione, J. E., Pennings, S. C., & Suding, K. N. (2012). Incorporating clonal growth form clarifies the role of plant height in response to nitrogen addition. *Oecologia*, *169*, 1053–1062. https://doi.org/10.1007/s00442-012-2264-5

Guo, C., Lek, S., Ye, S., Li, W., Liu, J., & Li, Z. (2015). Uncertainty in ensemble modelling of large-scale species distribution: Effects from species characteristics and model techniques. *Ecological Modelling*, *306*, 67–75. https://doi.org/10.1016/j.ecolmodel.2014.08.002

Hastie, T., & Tibshirani, R. (1986). Generalized additive models. *Statistical Sciences*, *1*, 297–318. https://doi.org/10.1214/ss/1177013604

Herben, T., & Klimešová, J. (2020). Evolution of clonal growth forms in angiosperms. *New Phytologist*, *225*, 999–1010. https://doi.org/10.1111/nph.16188

Herben, T., Nováková, Z., & Klimešová, J. (2014). Clonal growth and plant species abundance. *Annals of Botany*, *114*, 377–388. https://doi.org/10.1093/aob/mct308

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25*, 1965–1978. https://doi.org/10.1002/joc.1276

Hoffmann, A. A., & Sgro, C. M. (2011). Climate change and evolutionary adaptation. *Nature*, *470*, 479–485. https://doi.org/10.1038/nature09670

Hussner, A., Stiers, I., Verhofstad, M., Bakker, E. S., Grutters, B., Haury, J., van Valkenburg, J., Brundu, G., Newman, J., Clayton, J. S., Anderson, L., & Hofstra, D. (2017). Management and control methods of invasive alien freshwater aquatic plants: A review. *Aquatic Botany*, *136*, 112–137. https://doi.org/10.1016/j.aquabot.2016.08.002

IPCC (2013). *Climate Change 2013: The physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change*. Cambridge University Press.

Kalusová, V., Chytrý, M., Kartesz, J. T., Nishino, M., & Pyšek, P. (2013). Where do they come from and where do they go? European natural habitats as donors of invasive alien plants globally. *Diversity and Distributions*, *19*, 199–214. https://doi.org/10.1111/ddi.12008

Kariyawasam, C. S., Kumar, L., & Ratnayake, S. S. (2021). Potential distribution of aquatic invasive alien plants, *Eichhornia crassipes* and *Salvinia molesta* under climate change in Sri Lanka. *Wetlands Ecology and Management*, *29*, 531–545. https://doi.org/10.1007/s11273-021-09799-4

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Tautenhahn, S., Werner, G. D. A., Aakala, T., Abedi, M., Acosta, A. T. R., Adamidis, G. C., Adamson, K., Aiba, M., Albert, C. H., Alcántara, J. M., Alcázar C, C., Aleixo, I., Ali, H., ... Wirth, C. (2020). TRY plant trait database–enhanced coverage and open access. *Global Change Biology*, *26*, 119–188. https://doi.org/10.1111/gcb.14904

Kleyer, M., & Minden, V. (2015). Why functional ecology should consider all plant organs: An allocation-based perspective. *Basic and Applied Ecology*, *16*, 1–9. https://doi.org/10.1016/j.baae.2014.11.002

Klimešová, J., Danihelka, J., Chrtek, J., de Bello, F., & Herben, T. (2017). CLO-PLA: A database of clonal and bud-bank traits of the Central European flora. *Ecology*, *98*, 1179. https://doi.org/10.1002/ecy.1745

Lamsal, P., Kumar, L., Aryal, A., & Atreya, K. (2018). Invasive alien plant species dynamics in the Himalayan region under climate change. *Ambio*, *47*, 697–710. https://doi.org/10.1007/s13280-018-1017-z

Liu, C., Wolter, C., Xian, W., & Jeschke, J. M. (2020). Species distribution models have limited spatial transferability for invasive species. *Ecology Letters*, *23*, 1682–1692. https://doi.org/10.1111/ele.13577

Liu, F., Liu, J., & Dong, M. (2016). Ecological consequences of clonal integration in plants. *Frontiers in Plant Science*, *7*, 770. https://doi.org/10.3389/fpls.2016.00770

Liu, J., Dong, M., Miao, S. L., Li, Z. Y., Song, M. H., & Wang, R. Q. (2006). Invasive alien plants in China: Role of clonality and geographical origin. *Biological Invasions*, *8*, 1461–1470. https://doi.org/10.1007/s10530-005-5838-x

Lowe, S., Browne, M., Boudjelas, S., & De Poorter, M. (2000). *100 of the World's Worst Invasive Alien Species: A Selection from the Global Invasive Species Database. Published by the Invasive Species Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN)* (12 pp). Retrieved from www.issg.org/booklet.pdf

Mainali, K. P., Warren, D. L., Dhileepan, K., McConnachie, A., Strathie, L., Hassan, G., Karki, D., Shrestha, B. B., & Parmesan, C. (2015). Projecting future expansion of invasive species: Comparing and improving methodologies for species distribution modeling. *Global Change Biology*, *21*, 4464–4480. https://doi.org/10.1111/gcb.13038

Maitner, B. S., Boyle, B., Casler, N., Condit, R., Donoghue, J., Durán, S. M., & Enquist, B. J. (2018). The bien r package: A tool to access the Botanical Information and Ecology Network (BIEN) database. *Methods in Ecology and Evolution*, *9*, 373–379.

Maron, J., & Marler, M. (2007). Native plant diversity resists invasion at both low and high resource levels. *Ecology*, *88*, 2651–2661. https://doi.org/10.1890/06-1993.1

Mathakutha, R., Steyn, C., le Roux, P. C., Blom, I. J., Chown, S. L., Daru, B. H., Ripley, B. S., Louw, A., & Greve, M. (2019). Invasive species differ in key functional traits from native and non-invasive alien plant species. *Journal of Vegetation Science*, *30*, 994–1006. https://doi.org/10.1111/jvs.12772

McCullagh, P., & Nelder, J. A. (1989). *Generalized linear models* (2nd ed.). Chapman & Hall.

Meier, E. S., Dullinger, S., Zimmermann, N. E., Baumgartner, D., Gattringer, A., & Hülber, K. (2014). Space matters when defining effective management for invasive plants. *Diversity and Distribution*, *20*, 1029–1043. https://doi.org/10.1111/ddi.12201

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*, 853. https://doi.org/10.1038/35002501

Negreiros, D., Le Stradic, S., Fernandes, G. W., & Rennó, H. C. (2014). CSR analysis of plant functional types in highly diverse tropical grasslands of harsh environments. *Plant Ecology*, *215*, 379–388. https://doi.org/10.1007/s11258-014-0302-6

Nicotra, A. B., Atkin, O. K., Bonser, S. P., Davidson, A. M., Finnegan, E. J., Mathesius, U., Poot, P., Purugganan, M. D., Richards, C. L., Valladares, F., & van Kleunen, M. (2010). Plant phenotypic plasticity in a changing climate. *Trends in Plant Science*, *15*, 684–692. https://doi.org/10.1016/j.tplants.2010.09.008

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P., & Kassem, K. R. (2001). Terrestrial ecoregions of the world: A new map of life on Earth: A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience*, *51*, 933–938. https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

Osawa, T., Akasaka, M., & Kachi, N. (2019). Facilitation of management plan development via spatial classification of areas invaded by alien invasive plant. *Biological Invasions*, *21*, 2067–2080. https://doi.org/10.1007/s10530-019-01958-2

Osborne, C. P., Charles-Dominique, T., Stevens, N., Bond, W. J., Midgley, G., & Lehmann, C. E. (2018). Human impacts in African savannas are mediated by plant functional traits. *New Phytologist*, *220*, 10–24. https://doi.org/10.1111/nph.15236

Padmanaba, M., Tomlinson, K. W., Hughes, A. C., & Corlett, R. T. (2017). Alien plant invasions of protected areas in Java, Indonesia. *Scientific Reports*, *7*, 1–11. https://doi.org/10.1038/s41598-017-09768-z

Panda, R. M., Behera, M. D., & Roy, P. S. (2018). Assessing distributions of two invasive species of contrasting habits in future climate. *Journal of Environmental Management*, *213*, 478–488. https://doi.org/10.1016/j.jenvman.2017.12.053

Parepa, M., Fischer, M., & Bossdorf, O. (2013). Environmental variability promotes plant invasion. *Nature Communications*, *4*, 1–4. https://doi.org/10.1038/ncomms2632

Pěknicová, J., & Berchová-Bímová, K. (2016). Application of species distribution models for protected areas threatened by invasive plants. *Journal for Nature Conservation*, *34*, 1–7. https://doi.org/10.1016/j.jnc.2016.08.004

Perry, L. G., Blumenthal, D. M., Monaco, T. A., Paschke, M. W., & Redente, E. F. (2010). Immobilizing nitrogen to control plant invasion. *Oecologia*, *163*, 13–24. https://doi.org/10.1007/s00442-010-1580-x

Petitpierre, B., Kueffer, C., Broennimann, O., Randin, C., Daehler, C., & Guisan, A. (2012). Climatic niche shifts are rare among terrestrial plant invaders. *Science*, *335*, 1344–1348. https://doi.org/10.1126/science.1215933

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, *190*, 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Ramirez-Villegas, J., & Jarvis, A. (2010). Downscaling global circulation model outputs: The delta method decision and policy analysis. *Policy Analysis*, *1*, 1–18.

Rood, S. B., Berg, K. J., & Pearce, D. W. (2007). Localized temperature adaptation of cottonwoods from elevational ecoregions in the Rocky Mountains. *Trees*, *21*, 171–180. https://doi.org/10.1007/s00468-006-0109-8

Santamaría, L. (2002). Why are most aquatic plants widely distributed? Dispersal, clonal growth and small-scale heterogeneity in a stressful environment. *Acta Oecologica*, *23*, 137–154. https://doi.org/10.1016/S1146-609X(02)01146-3

Seebens, H., Essl, F., Dawson, W., Fuentes, N., Moser, D., Pergl, J., Pyšek, P., van Kleunen, M., Weber, E., Winter, M., & Blasius, B. (2015). Global trade will accelerate plant invasions in emerging economies under climate change. *Global Change Biology*, *21*, 4128–4140. https://doi.org/10.1111/gcb.13021

Shrestha, U. B., & Shrestha, B. B. (2019). Climate change amplifies plant invasion hotspots in Nepal. *Diversity and Distributions*, *25*, 1599–1612. https://doi.org/10.1111/ddi.12963

Song, Y. B., Yu, F. H., Keser, L. H., Dawson, W., Fischer, M., Dong, M., & van Kleunen, M. (2013). United we stand, divided we fall: A meta-analysis of experiments on clonal integration and its relationship to invasiveness. *Oecologia*, *171*, 317–327. https://doi.org/10.1007/s00442-012-2430-9

Teixeira, M. C., Bini, L. M., & Thomaz, S. M. (2017). Biotic resistance buffers the effects of nutrient enrichment on the success of a highly invasive aquatic plant. *Freshwater Biology*, *62*, 65–71. https://doi.org/10.1111/fwb.12849

Thuiller, W., Gassó, N., Pino, J., & Vila, M. (2012). Ecological niche and species traits: Key drivers of regional plant invader assemblages. *Biological Invasions*, *14*, 1963–1980. https://doi.org/10.1007/s10530-012-0206-0

Thuiller, W., Richardson, D. M., Pyšek, P., Midgley, G. F., Hughes, G. O., & Rouget, M. (2005). Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Global Change Biology*, *11*, 2234–2250. https://doi.org/10.1111/j.1365-2486.2005.001018.x

van Kleunen, M., Fischer, M., & Schmid, B. (2001). Effects of intraspecific competition on size variation and reproductive allocation in a clonal plant. *Oikos*, *94*, 515–524. https://doi.org/10.1034/j.1600-0706.2001.940313.x

van Kleunen, M., Xu, X., Yang, Q., Maurel, N., Zhang, Z., Dawson, W., Essl, F., Kreft, H., Pergl, J., Pyšek, P., Weigelt, P., Moser, D., Lenzner, B., & Fristoe, T. S. (2020). Economic use of plants is key to their naturalization success. *Nature Communications*, *11*, 1–12. https://doi.org/10.1038/s41467-020-16982-3

Wan, J. Z., & Wang, C. J. (2018). Expansion risk of invasive plants in regions of high plant diversity: A global assessment using 36 species. *Ecological Informatics*, *46*, 8–18. https://doi.org/10.1016/j.ecoinf.2018.04.004

Wang, J., Xu, T., Wang, Y., Li, G., Abdullah, I., Zhong, Z., Liu, J., Zhu, W., Wang, L., Wang, D., & Yu, F.-H. (2021). A meta-analysis of effects of physiological integration in clonal plants under homogeneous vs. heterogeneous environments. *Functional Ecology*, *35*, 578–589. https://doi.org/10.1111/1365-2435.13732

Wang, M. Z., Bu, X. Q., Li, L., Dong, B. C., Li, H. L., & Yu, F. H. (2018). Constraints on the evolution of phenotypic plasticity in the clonal plant Hydrocotyle vulgaris. *Journal of Evolutionary Biology*, *31*, 1006–1017.

Wang, Y.-J., Müller-Schärer, H., Kleunen, M., Cai, A.-M., Zhang, P., Yan, R., Dong, B.-C., & Yu, F.-H. (2017). Invasive alien plants benefit more from clonal integration in heterogeneous environments than natives. *New Phytologist*, *216*, 1072–1078. https://doi.org/10.1111/nph.14820

Warren, R. J., Candeias, M., Lafferty, A., & Chick, L. D. (2020). Regional-scale environmental resistance to non-native ant invasion. *Biological Invasions*, *22*, 813–825. https://doi.org/10.1007/s10530-019-02133-3

Whitney, K. D., & Gabler, C. A. (2008). Rapid evolution in introduced species, 'invasive traits' and recipient communities: Challenges for predicting invasive potential. *Diversity and Distributions*, *14*, 569–580. https://doi.org/10.1111/j.1472-4642.2008.00473.x

Yamamichi, M., Kyogoku, D., Iritani, R., Kobayashi, K., Takahashi, Y., Tsurui-Sato, K., Yamawo, A., Dobata, S., Tsuji, K., & Kondoh, M. (2020). Intraspecific adaptation load: A mechanism for species coexistence. *Trends in Ecology & Evolution*, *35*, 897–907. https://doi.org/10.1016/j.tree.2020.05.011

Ye, D., Hu, Y., Song, M., Pan, X. U., Xie, X., Liu, G., Ye, X., & Dong, M. (2014). Clonality-climate relationships along latitudinal gradient across China: Adaptation of clonality to environments. *PLoS One*, *9*, e94009. https://doi.org/10.1371/journal.pone.0094009

Ye, X. H., Zhang, Y. L., Liu, Z. L., Gao, S. Q., Song, Y. B., Liu, F. H., & Dong, M. (2016). Plant clonal integration mediates the horizontal redistribution of soil resources, benefiting neighboring plants. *Frontiers in Plant Science*, *7*, 77. https://doi.org/10.3389/fpls.2016.00077

Yu, H., Shen, N., Yu, D., & Liu, C. (2019). Clonal integration increases growth performance and expansion of *Eichhornia crassipes* in littoral zones: A simulation study. *Environmental and Experimental Botany*, *159*, 13–22. https://doi.org/10.1016/j.envexpbot.2018.12.008

Zobel, K. (2008). On the forces that govern clonality versus sexuality in plant communities. *Evolutionary Ecology*, *22*, 487–492. https://doi.org/10.1007/s10682-007-9236-y

Zurell, D., Franklin, J., König, C., Bouchet, P. J., Dormann, C. F., Elith, J., Fandos, G., Feng, X., Guillera-Arroita, G., Guisan, A., Lahoz-Monfort, J. J., Leitão, P. J., Park, D. S., Peterson, A. T., Rapacciuolo, G., Schmatz, D. R., Schröder, B., Serra-Diaz, J. M., Thuiller, W., … Merow, C. (2020). A standard protocol for reporting species distribution models. *Ecography*, *43*, 1261–1277. https://doi.org/10.1111/ecog.04960

BIOSKETCH

Ji-Zhong Wan is a professor at Qinghai University, China. He is mainly interested in ecological niche theory and conservation management under global change.

Author contributions: Ji-Zhong Wan contributed to methodology, data curation, data analysis, original draft preparation and writing; Chun-Jing Wang curated the data and analysed the data; Niklaus E. Zimmermann and Robin Pouteau contributed to methodology, original draft preparation and reviewing; Mai-He Li reviewed the article; Fei-Hai Yu contribute to original draft preparation, writing, reviewing, editing and supervision. All authors took part in the conceptualization of the work and have read and approved the final version of the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Wan, J.-Z., Wang, C.-J., Zimmermann, N. E., Li, M.-H., Pouteau, R., & Yu, F.-H. (2021). Current and future plant invasions in protected areas: Does clonality matter? *Diversity and Distributions*, 27, 2465–2478. https://doi.org/10.1111/ddi.13425