

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

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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

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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; Pěkníková & Berchová-Bimová, 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 CO₂; range: 140–410 ppm CO₂ by 2,100), RCP4.5 (mean: 780 ppm CO₂; range: 595–1,005 ppm by 2,100) and RCP8.5 (mean: 1685 ppm CO₂; range: 1,415–1910 ppm CO₂ 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 ($< 2.5 \times 2.5$ 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	Palaearctic
<i>Acacia mearnsii</i>	Yes	-0.908	0.357	-0.632	32.455	5.128	-0.746	17.864
<i>Arundo donax</i>	Yes	-0.384	0.489	-0.069	18.651	0.315	0.081	6.727
<i>Caulerpa taxifolia</i>	Yes	0.522	0.596	0.545	6.843	0.654	0.282	2.930
<i>Cinchona pubescens</i>	Yes	-0.872	-0.578	-0.767	1.091	-0.760	-0.623	0.249
<i>Eichhornia crassipes</i>	Yes	0.092	0.584	0.174	10.352	0.573	0.184	5.162
<i>Euphorbia esula</i>	Yes	-0.360	-0.528	-0.191	-0.284	-0.273	-0.337	-0.265
<i>Fallopia japonica</i>	Yes	-0.001	-0.486	-0.013	1.934	-0.188	-0.198	0.435
<i>Hedychium gardnerianum</i>	Yes	-0.216	0.530	0.443	18.380	1.279	-0.231	12.555
<i>Imperata cylindrica</i>	Yes	0.135	0.865	0.432	36.351	1.506	0.463	12.700
<i>Ligustrum robustum</i>	Yes	6.374	2.966	4.869	19.443	8.686	5.769	7.414
<i>Lythrum salicaria</i>	Yes	-0.309	-0.415	-0.239	-0.403	-0.279	-0.351	-0.340
<i>Mikania micrantha</i>	Yes	-0.258	0.407	0.072	5.037	0.028	0.000	3.850
<i>Opuntia stricta</i>	Yes	26.225	11.427	25.999	20.948	59.045	30.414	32.905
<i>Prosopis glandulosa</i>	Yes	1.323	7.720	2.285	5.224	17.916	0.820	10.214
<i>Psidium cattleianum</i>	Yes	-0.608	0.975	-0.348	36.640	0.492	-0.273	21.393
<i>Pueraria montana var. lobata</i>	Yes	0.126	1.206	1.075	125.507	6.345	1.126	65.887
<i>Rubus ellipticus</i>	Yes	-0.705	0.460	-0.530	5.323	0.291	0.231	6.548
<i>Schinus terebinthifolius</i>	Yes	-0.360	1.364	-0.215	10.795	0.491	-0.110	6.406
<i>Spartina anglica</i>	Yes	-0.614	-0.650	-0.369	12.150	-0.371	-0.434	10.839
<i>Spathodea campanulata</i>	Yes	0.209	0.624	0.247	0.986	0.123	0.096	0.484
<i>Sphagneticola trilobata</i>	Yes	0.829	1.930	0.915	2.959	0.834	0.443	1.371
<i>Undaria pinnatifida</i>	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
<i>Ardisia elliptica</i>	No	1.526	1.202	0.391	1.217	0.560	0.346	0.503
<i>Cecropia peltata</i>	No	0.610	0.760	0.647	1.034	0.384	0.310	0.620
<i>Chromolaena odorata</i>	No	-0.020	1.625	0.102	4.835	0.333	0.240	3.456
<i>Clidemia hirta</i>	No	-0.181	0.904	-0.210	1.963	0.290	0.032	1.701
<i>Hiptage benghalensis</i>	No	2.121	1.410	1.593	3.327	1.726	1.664	1.668
<i>Lantana camara</i>	No	-0.264	1.297	-0.078	16.602	0.887	0.037	8.023
<i>Leucaena leucocephala</i>	No	0.312	1.135	0.406	4.267	0.596	0.410	3.339
<i>Melaleuca quinquenervia</i>	No	0.248	2.784	1.183	5.405	1.411	0.585	3.791
<i>Miconia calvescens</i>	No	-0.589	0.394	-0.617	2.003	-0.438	-0.351	2.232
<i>Mimosa pigra</i>	No	0.811	2.431	1.094	3.896	0.812	0.764	2.295
<i>Myrica faya</i>	No	-0.764	-0.480	-0.522	-0.314	-0.545	-0.562	-0.222
<i>Pinus pinaster</i>	No	-0.419	0.326	0.635	63.594	2.959	-0.099	55.659
<i>Tamarix ramosissima</i>	No	-0.432	0.651	0.207	2.846	2.492	1.221	3.200
<i>Ulex europaeus</i>	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 \times 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 $P_{i,k}$ 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_t 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 G_i^* 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 G_i^* 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 $\pm 5\%$; 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

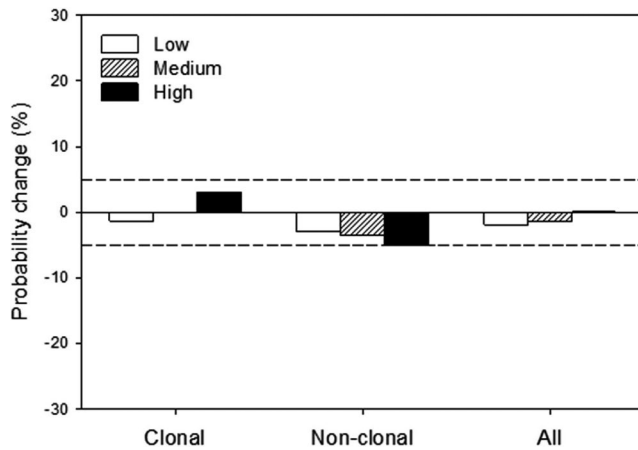


FIGURE 1 Change in the probability of clonal, non-clonal and all (clonal plus non-clonal) invasive alien plant species to invade global protected areas between the current situation and the three future concentration scenarios (low, medium and high). Dash lines represent values of +5% and -5%. RCPs 2.6, 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

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

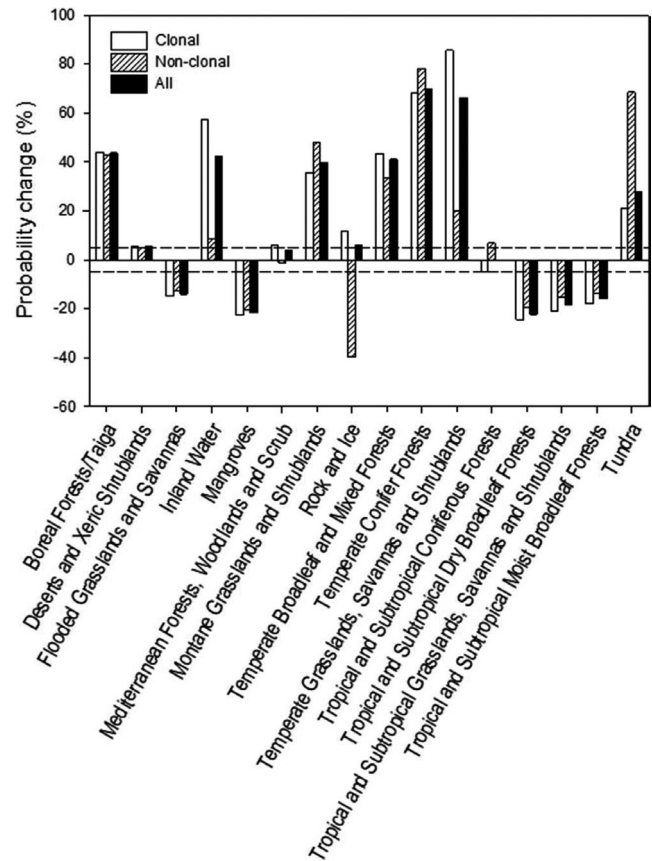


FIGURE 2 Change in the probability of all (clonal plus non-clonal), clonal and non-clonal invasive alien plant species to invade protected areas between the current situation and the high concentration scenario (RCP 8.5) according to the biome distribution of PAs. Dash lines represent values of +5% and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

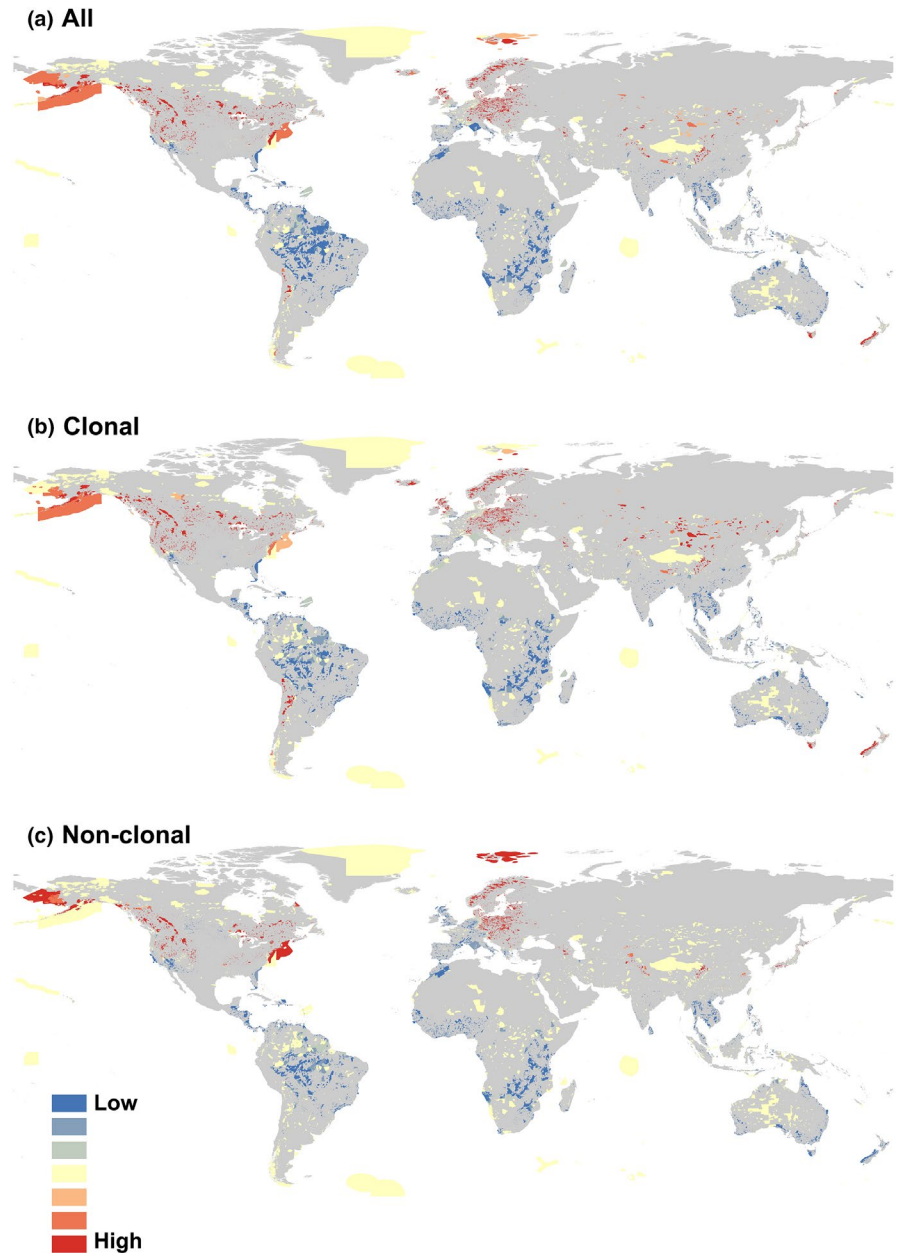
Zealand, northern Asia and Europe (Figure 3). Hot spots of non-clonal IAPS were located in South America, southeastern Asia and eastern Africa under the current and future climate scenarios (Figure S4). Compared to the current situation, PAs more strongly invaded by non-clonal IAPS under future scenarios 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.

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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


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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>).

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BIOSKETCH

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