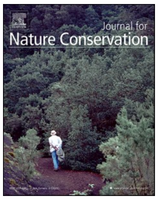
Journal for Nature Conservation 73 (2023) 126368

Contents lists available at ScienceDirect

Journal for Nature Conservation

journal homepage: www.elsevier.com/locate/jnc



The impact of climate change on the future distribution of priority crop wild relatives in Indonesia and implications for conservation planning

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ARTICLE INFO

Keywords:
Climate change
Climate refugia
crop wild relatives (CWR)
Distribution range shift
Holdouts
Protected areas

ABSTRACT

The analysis of climate change impact is essential to include in conservation planning of crop wild relatives (CWR) to provide the guideline for adequate long-term protection under unpredictable future environmental conditions. These resources play an important role in sustaining the future of food security, but the evidence shows that they are threatened by climate change. The current analyses show that five taxa were predicted to have contraction of more than 30 % of their current ranges: *Artocarpus sepicanus* (based on RCP 4.5 in both no dispersal and unlimited dispersal scenario and RCP 8.5 in no dispersal scenario by 2050), *Ficus oleifolia* (RCP 4.5 5 in both no dispersal and unlimited dispersal scenario by 2080), *Cocos nucifera* and *Dioscorea alata* (RCP 8.5 in both no dispersal and unlimited dispersal scenario by 2050), and *Ficus chartacea* (RCP 8.5 in both no dispersal and unlimited dispersal scenario by 2050 and 2080). It shows that the climate change impact is species-specific. Representative Concentration Pathways (RCP) of greenhouse gas (GHG) emission and dispersal scenarios influence the prediction models, and the actual future distribution range of species falls in between those scenarios. Climate refugia, holdout populations, and non-analogue community assemblages were identified based on the Protected Areas (PAs) network. PAs capacity is considered an important element in implementing a conservation strategy for the priority CWR. In areas where PAs are isolated and have less possibility to build corridors to connect each other, such as in Java, unlimited dispersal scenarios are unlikely to be achieved and assisted dispersal is suggested. The holdout populations should be the priority target for the *ex situ* collection. Therefore, by considering the climate refugia, PAs capacity and holdout populations, the goal of keeping high genetic variations for the long-term conservation of CWR in Indonesia can be achieved.

1. Introduction

Incorporating the impact of climate change on conservation planning is increasingly a routine activity in adjusting the conservation goals in the future (Prober et al., 2019). By anticipating species' future distribution range shifts from climate change, their extinction risk can be minimized (Morecroft et al., 2019; Thomas et al., 2004; Wiens et al., 2010). In this context, climate refugia and holdout populations should be identified and prioritized for conservation. Climate refugia are the extant or newly colonized natural areas where species will exist under climate change (Keppel et al., 2015). Holdout populations persist for a limited period and are likely to disappear in the near future due to adverse climatic conditions (Hannah et al., 2014). Thus, by including those two elements (i.e. climate refugia and holdout population) in conservation planning, adequate long-term protection as the goal of biodiversity conservation will be achieved.

Crop wild relatives (CWR), like all wild taxa, are threatened by climate change (Aguirre-Gutiérrez et al., 2017; Jarvis et al., 2008; Maxted et al., 1997; Phillips et al., 2017; Vincent et al., 2019). Some wild relatives of cultivated peanuts, potatoes, maize, and broad bean are predicted to go extinct by 2070 (Jarvis et al., 2008; Vincent et al., 2019). Moreover, Jablonski et al. (2002) reported that elevating the concentration of CO_2 disturbed wild plant species' reproduction system, disrupting their regenerating process. Higher concentrations of CO_2 increased the seed number of crops but not the wild species. The increasing level of CO_2 also reduced the Nitrogen content in seeds, particularly in non-legume plants, which is important for germination capacity. On the other hand, CWRs are keys for broadening the genetic

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https://doi.org/10.1016/j.jnc.2023.126368
Received 2 June 2022; Received in revised form 16 February 2023; Accepted 23 February 2023

diversity of related crops to be more adaptive in changing climates. Initiatives to establish a global *in situ* network of CWR sites (FAO, 2013, 2014; Maxted & Kell, 2009) and increase *ex situ* collections (Castañeda-Álvarez et al., 2016; Jarvis et al., 2010) are important to reduce the extinction risk of CWR by climate change.

Based on niche conservatism theory, each species has its niche, and the population will be maintained under this realized niche (Wiens et al., 2010; Wiens & Graham, 2005). The future existence will depend on how large their niche still exists or expands. In terms of climatic niche, it means how large the analogue climate condition will be available in the future. However, based on niche construction theory (Odling-Smee et al., 1996; Odling-Smee et al., 2013), the niche can also be shifted (Ackerly, 2003; Pearman et al., 2008) and evolved (Smith & Beaulieu, 2009; Wake et al., 2009). The recent finding showed that the climatic niche of plants mostly shifted when the plants were introduced cross-continent (Atwater et al., 2018).

The world is experiencing anthropogenic climate change (IPCC, 2014). One of the global biodiversity hotspots and mega-diverse countries (Mittermeier et al., 2011), Indonesia is vulnerable to the negative impact of climate change (The Ministry of Environment and Forestry of The Republic of Indonesia, 2018). Herawati & Santoso (2011) predicted that climate change would disrupt annual temperatures and rainfall patterns. The northern part of Indonesia is predicted to have more rainfall than the Southern part. They also stated that other extreme weather conditions, such as El-Niño and wildfires, are likely to become more frequent and severe in Indonesia.

Protected areas (PAs) are important to support the dynamic of species range shifts under climate change (Haight & Hammill, 2020; Thomas et al., 2012). However, there are pessimistic predictions that the current existing PAs in Indonesia might fail to support these shifts (Proctor et al., 2011; Scriven et al., 2015). Proctor et al. (2011) and Scriven et al. (2015) stated that land use fragmentation had promoted the isolation and lack of interconnectivity among PAs. The species with less capacity for long-distance dispersal will have a higher risk of extinction.

Conservation of CWR diversity for crop improvement and climate change adaptation is a growing priority in Indonesia. The country has to sustain food production since the future human population is predicted to increase. The utilisation of CWR in the development of climate-smart crop varieties requires active conservation action and ease of access to the national breeders' collections (Maxted et al., 2020). The problems are how much the existing PAs can be refugia and how to identify the location for more collecting programs. The aims of this research are: to determine the distribution range shift of priority CWR in Indonesia caused by climate change, to identify the capacity of the existing PAs as climate refugia, and to suggest ways to adapt CWR conservation planning and management in response to the predicted impacts of climate change in Indonesia. We hypothesise that the distribution range of taxa will have similar responses to different RCP models, years of prediction, and dispersal scenarios. Moreover, the existing PAs have enough capacity to be refugia.

2. Methods

2.1. Priority CWR of food crops in Indonesia and occurrence data collection

The process of prioritizing CWR in Indonesia can be seen in Rahman et al.(2019). From the checklist of 1,968 CWR taxa related to 224 crops, 234 were prioritized based on the importance of crops and potential use in breeding (Rahman et al., 2019). Occurrence points for each priority taxon were collected and compiled from Global Biodiversity Information Facility (GBIF), herbarium specimens deposited in Herbarium Bogoriense and Naturalis Leiden, and various publications. Occurrence records from GBIF were cleaned before being used in the analysis. Only records from their native range distribution were selected based on POWO (2019). Duplicate records were removed. Some records from herbarium specimens collected from the same locality by the same collector at the same collection time but deposited in different herbaria have different georeferenced points. In that case, only one record was included in the dataset. Records that did not have geographic coordinates were georeferencing. The georeferenced is based on information from the cyclopaedia of Malesian collectors (https://www.nationaalherbarium.nl/FMCollectors/). In total, 8,226 unique occurrence points were recorded (Table S1). Maps of observed richness and the number of observation records (biased maps) were created using DIVA-GIS ver.7.5.0 with a 50x50 km grid cell size (Fig. S1).

Table 1
Selected climate models.

Climate Model	Model code	Developer
Beijing Climate Centre Climate System Models	bcc_csm1_1	Beijing Climate Centre (BCC), China Meteorological Administration (CMA), China.
Goddard Institute for Space Studies GISS-E2-R model	giss_e2_r	NASA Goddard Institute for Space Studies, USA.
Institute Pierre-Simon Laplace (IPSL_CM5a_LR)	ipsl_cm5a_lr	Institute Pierre-Simon Laplace, France.
The Model for Interdisciplinary Research on Climate (MIROC 5 model)	miroc5	Atmosphere and Ocean Research Institute; Centre for Climate System Research-National Institute for Environmental Studies; and Japan Agency for Marine-Earth Science and Technology, Japan
Met Office Hadley Centre Hadley Global Environment Model 2-Earth System	mohc_hadgem2_es	Met Office, UK.

2.2. Species distribution modelling

Maxent version 3.4.1 k (Phillips et al., 2018) was used to develop the priority taxa's current and future species distribution models (SDMs). Cross-validation was used as a resampling method with different replications depending on the number of occurrence points for each taxon (four replicates = 10–30 presence points, five replicates = 30–50 presence points, ten replicates $\geq$ 50 presence points). Maximum training sensitivity plus specificity was chosen as the threshold rule as it gives good results when transforming the probabilities value into presence/absence data (Liu et al., 2005).

The produced models for the current climatic condition were validated through three criteria developed by Ramírez-Villegas et al. (2010). In order for a model to be accurate and stable, it should meet the three following criteria: the average AUC test should be higher than 0.7 (ATAUC greater than 0.7); the standard deviation of ATAUC should be$<$0.15 (STAUC $<$ 0.15); and the proportion of potential distribution area with STAUC greater than 0.15 should be$<$10 %. Only species with valid models were used to develop the distribution models under future climatic conditions. Validation results for current distribution range models can be found in Table S1 in supplementary materials.

2.3. Environmental variables selection

Initially, 103 variables (67 climatic, 31 edaphic, and five geophysics variables) with 30 arc-second resolution were provided as environmental background (Table S2). Those variables were extracted for every occurrence point for each priority taxon. A stepwise collinearity test selected uncorrelated variables with variation inflation factors (VIF) $<$ 5 as the threshold value. Only variables with VIF $<$ 5 were selected. One additional variable, the biogeographic unit, was added for all taxa as a dispersal limitation predictor to prevent over-prediction to other islands where they have never been recorded (Raes et al., 2013). The list of used

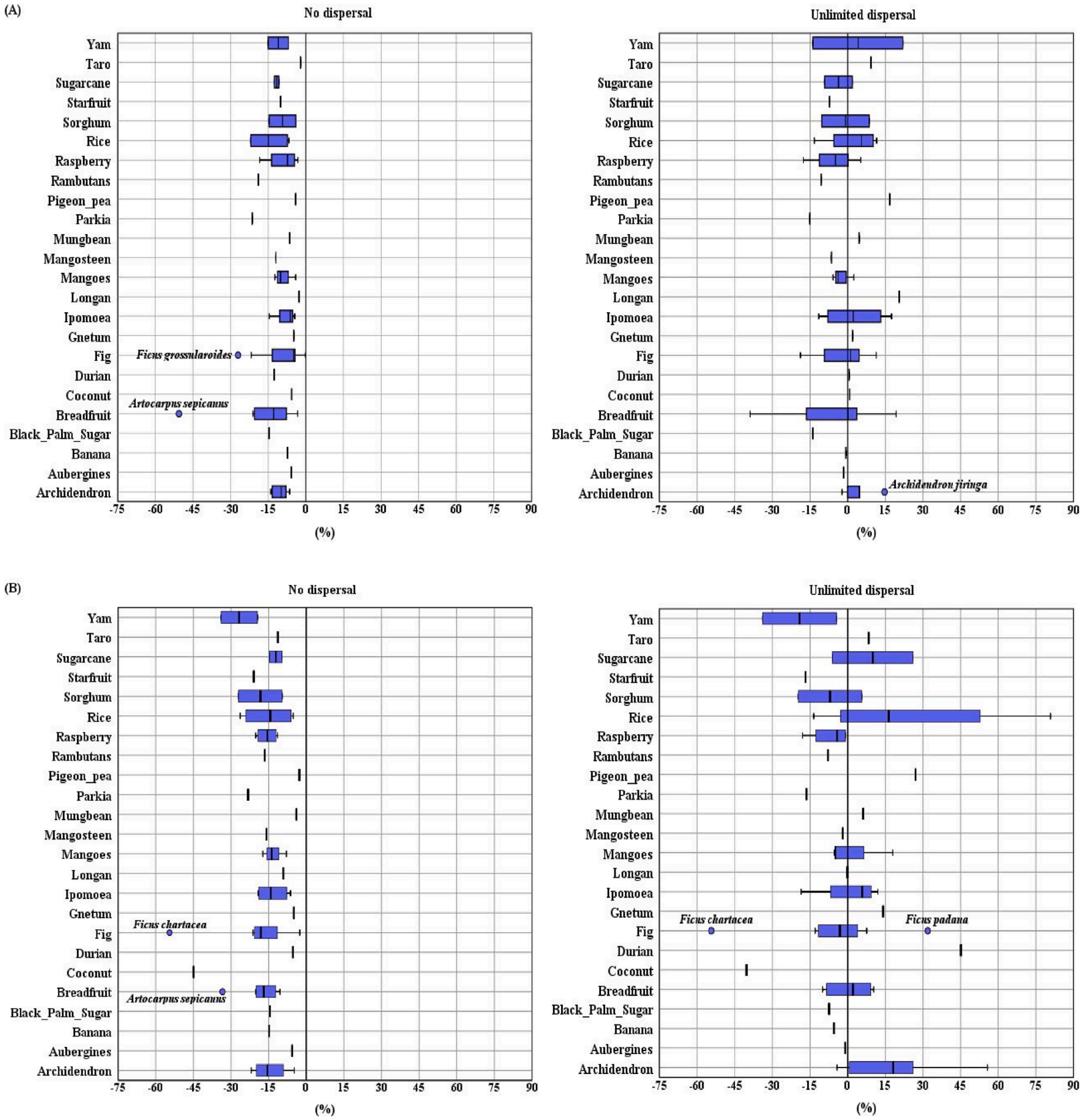

Fig. 1. Distribution range changes (%) of priority CWR for year 2050 based on (A) RCP 4.5 and (B) RCP 8.5.

variables for each priority taxa can be found in Table S3.

2.4. Future species distribution models

Future climate conditions were downscaled from the Global Circulation Model (GCM) and compiled from CCAFS (available at https://www.ccafs-climate.org/) (Navarro-Racines et al., 2020). Five climates models were used, as seen in Table 1. Based on IPCC report ARS 5 (Settele et al., 2014), each climate model gives a different response value of the impact of climate change on the global terrestrial systems. Those five selected climate models represent the highest, the upper middle, the middle, the lower middle, and the lowest climate models for the projection simulation of the future extent of Northern Permafrost as one of the key ecosystems for global climate change mitigation. Two Representative Concentration Pathways (RCP) of greenhouse gases (GHG) emission scenarios (RCP 4.5 and RCP 8.5) were selected for two different periods (the year 2050 and 2080), as those two RCP scenarios provided moderately optimistic and very pessimistic scenarios for the future GHG emission for the near and long term climate projections (Moss et al., 2010). The five climate models' global future climatic variables were clipped to the Indonesia territory as the study area. The ensemble of each variable from five climate models was created by their median value in Arcmap and used for further analysis.

The ensemble value of climatic variables for each scenario was used as the climatic predictors to develop future distribution models. The edaphic, geophysics, and biogeographic unit variables were the same for all scenarios. Validation of the future distribution models was based on three criteria used by Ramírez-Villegas et al. (2010), as mentioned before. Only species with valid models for all scenarios were used for climate change impact analysis. Validation results for the future distribution range models in all scenarios can be seen in Table S4-S7 in supplementary materials.

2.5. Climate change impact analysis

Two dispersal scenarios were used to analyse the impact of climate change on the priority taxa, i.e. unlimited dispersal and no dispersal. Unlimited dispersal means the species can colonise new areas without

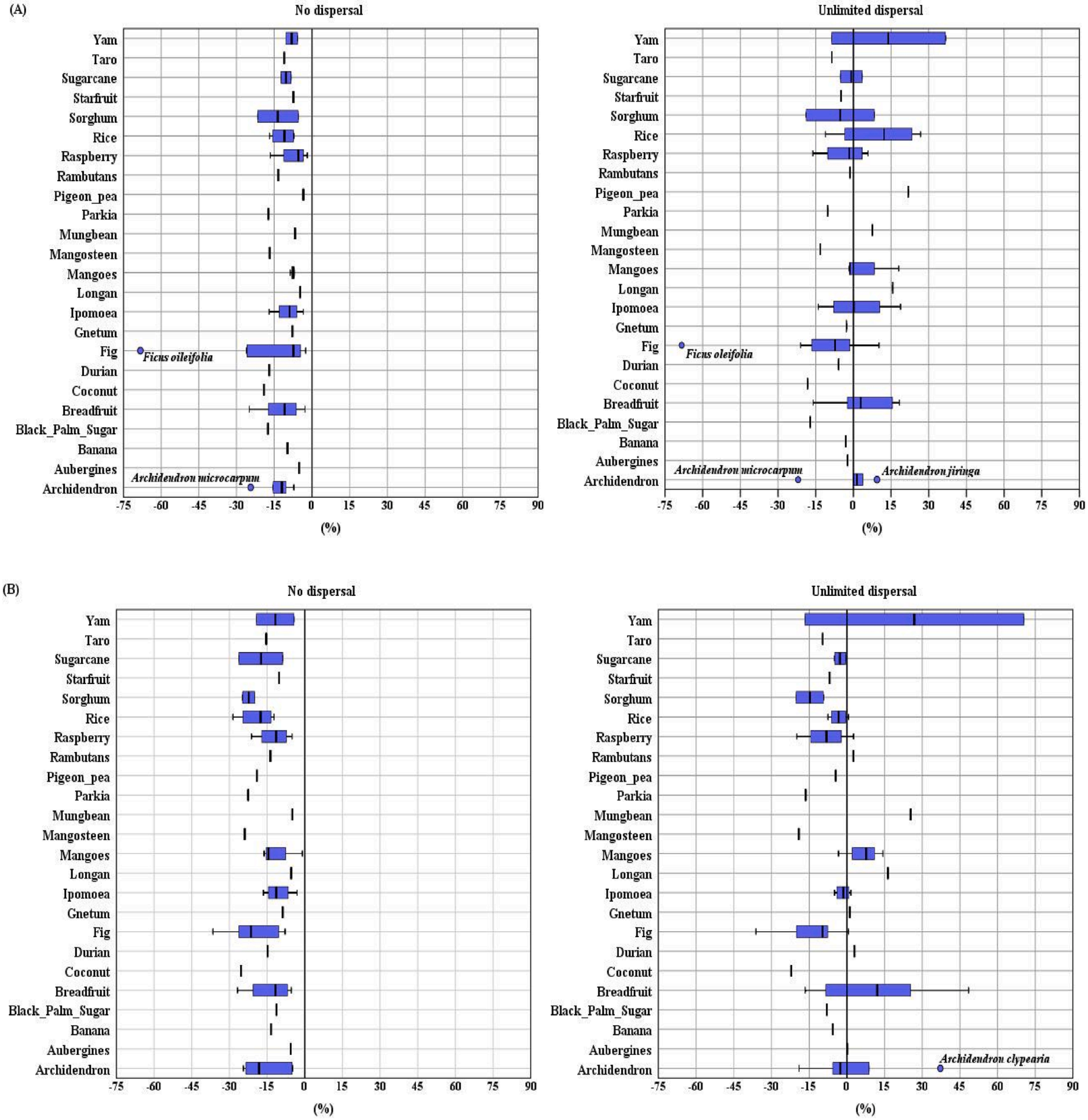

Fig. 2. Distribution range changes (%) of priority CWR for year 2080 based on (A) RCP 4.5 and (B) RCP 8.5.

future restrictions. Whilst no dispersal scenario means the species cannot migrate to new areas in the future and are restricted to the current distribution range. Eight future distribution models were created for each priority taxon by considering RCP scenarios, time projections, and dispersal scenarios.

Distribution range shifts for each taxon were predicted by comparing the future distribution to the current distribution. The species that have benefitted from climate change by increasing their distribution range (the winners) and species that have negative impacts from climate change (the losers) were determined by calculating the gain and loss areas of taxa based on the grid cells occupancy. A net change (net gain or loss) was calculated by comparing gain to lose areas for different RCP and time projections for each crop gene pool. Species richness was identified and mapped for the current and future distribution range by overlapping the models to determine the species' hotspots. Species turnover was also calculated and mapped to determine the future community assemblages. Based on changes at grid cells, the species turnover for the unlimited dispersal scenario is calculated as $(100 \times (\Sigma\text{loss}+\Sigma\text{gain})/(\text{current species richness}+\Sigma\text{gain}))$, while for the no dispersal scenario is $100 \times \Sigma\text{loss}/\text{current species richness}$ (Thuiller et al., 2005). The maps of species distribution changes (Fig. S2), gains (Fig. S3) and losses (Fig S4) were produced.

2.6. Protected areas (PAs) network capacity analysis for future conservation

The capacity of the existing PAs to conserve the future distribution of priority CWR taxa was measured by their potential to become climatic refugia (Haight & Hammill, 2020). In this context, species distribution models for all scenarios were overlayered with the national network of PAs. Grid cells as the product of species distribution models were used for refugia and holdouts analysis. PAs occupied by the target taxa in the current and future (2050 or 2080) in both dispersal scenarios (no dispersal and unlimited) were considered climatic refugia. Grid cells that lose occupancy in the future (between current-2050 or current-2080) were considered holdouts. PAs were considered to contain significant holdouts when loss of occupancy was greater than its gain. The average number of PAs as climate refugia and those with significant holdout

Table 2
Average gains and losses area of future distribution of priority crop genepool in Indonesia based on RCP 4.5 scenario for 2050 and 2080.

Crop Genepool	N	Current area (km^2)	RCP 4.5									
			2050				2080				Net change	Net change
			Gain (km^2)	% Gain	Loss (km^2)	% Loss	Gain (km^2)	% Gain	Loss (km^2)	% Loss	Current-2050	Current-2080
Archidendron	5	738,546	113,661	14.65	78,758	10.32	93,442	12.38	106,393	13.87	Gain	Loss
		(±124,027)	(±83,812)	(±8.74)	(±34,655)	(±3.32)	(±67,584)	(±7.57)	(±61,003)	(±6.59)		
Aubergine	1	500,316	20,106	4.02	28,522	5.70	14,510	2.90	25,552	5.11	Loss	Loss
Banana	1	609,984	40,166	6.58	44,838	7.35	41,428	6.79	59,056	9.68	Loss	Loss
BlackPalmSugar	1	805,872	6,726	0.83	118,252	14.67	3,456	0.43	141,474	17.56	Loss	Loss
Breadfruit	8	881,473	97,784	11.46	115,437	17.04	111,323	16.48	96,558	12.12	Loss	Gain
		(±398,767)	(±77,309)	(±6.27)	(±90,632)	(±15.05)	(±62,991)	(±10.81)	(±79,259)	(±7.61)		
Coconut	1	625,082	40,220	6.43	34,982	5.60	5,530	0.88	119,268	19.08	Gain	Loss
Durian	1	747,320	98,516	13.18	94,406	12.63	83,972	11.24	127,562	17.07	Gain	Loss
Fig	7	645,071	53,688	7.39	63,476	9.63	34,012	5.43	118,976	19.88	Loss	Loss
		(±324,040)	(±37,071)	(±3.41)	(±81,910)	(±10.34)	(±29,566)	(±5.69)	(±130,769)	(±23.61)		
Gnetum	1	963,088	65,094	6.76	46,776	4.86	48,680	5.05	75,090	7.80	Gain	Loss
Ipomoea	4	707,404	70,762	10.46	62,164	7.81	72,159	10.87	76,864	9.55	Gain	Gain
		(±225,396)	(±60,547)	(±9.71)	(±57,572)	(±4.57)	(±72,290)	(±11.94)	(±67,078)	(±5.6)		
Longan	1	1,130,878	263,354	23.29	31,302	2.77	230,386	20.37	53,080	4.69	Gain	Gain
Mangoes	3	831,454	50,069	6.49	69,845	8.85	86,843	12.76	64,047	7.71	Loss	Gain
		(±267,731)	(±7,524)	(±2.24)	(±35,038)	(±4.32)	(±43,560)	(±11.11)	(±20,989)	(±0.84)		
Mangosteen	1	874,000	47,792	5.47	103,958	11.89	32,386	3.71	147,558	16.88	Loss	Loss
Mungbean	1	433,194	47,528	10.97	28,004	6.46	62,190	14.36	29,348	6.77	Gain	Gain
Parkia	1	1,079,894	68,564	6.35	230,932	21.38	76,948	7.13	187,924	17.40	Loss	Loss
Pigeon_pea	1	235,964	49,300	20.89	9,668	4.10	59,450	25.19	8,150	3.45	Gain	Gain
Rambutan	1	1,483,344	123,186	8.30	280,954	18.94	180,098	12.14	199,110	13.42	Loss	Loss
Raspberry	4	243,708	7,404.5	3.56	29,525	9.12	10,064	4.01	24,083	7.34	Loss	Loss
		(±189,124)	(±6,967)	(±3.54)	(±34,356)	(±6.64)	(±12,887)	(±3.94)	(±31,078)	(±6.43)		
Rice	4	511,611	83,123	16.99	78,544	14.68	113,378	21.53	61,046	11.55	Gain	Gain
		(±129,602)	(±53,546)	(±11.24)	(±51,784)	(±8.4)	(±89,746)	(±15.05)	(±33,465)	(±4.87)		
Sorghum	2	784,722	70,336	8.43	67,759	9.32	71,104	8.35	98,451	13.58	Loss	Loss
		(±142,626)	(±58,138)	(±5.88)	(±45,652)	(±7.51)	(±73,038)	(±7.79)	(±70,129)	(±11.41)		
Starfruit	1	765,714	20,546	2.68	76,528	9.99	19,194	2.51	56,862	7.43	Loss	Loss
Sugarcane	2	689,188	53,851	8.01	80,506	11.64	63,721	9.51	70,524	10.32	Loss	Loss
		(±41,173)	(±41,325)	(±6.47)	(±13,845)	(±1.31)	(±57,625)	(±8.93)	(±15,061)	(±2.8)		
Taro	1	782,306	90,286	11.54	17,408	2.23	20,122	2.57	86,772	11.09	Gain	Loss
Yam	2	509,709	67,027	15.05	58,622	10.95	98,385	22.09	42,886	8.1	Gain	Gain
		(±98,634)	(±85,479)	(±19.68)	(±39,663)	(±5.66)	(±125,026)	(±28.8)	(±24,305)	(±3.2)		

populations were tabulated based on the crop gene pool.

Representa tool in Capfitogen (Parra-Quijano, 2016) was used to prioritize the PAs for further collecting programs to enhance the *ex situ* collections based on their ecogeographic representation. Therefore, species-specific Ecogeographic Land Characterization (ELC) maps were produced for each of the 55 taxa. The same environmental variables for developing species distribution modelling were used to create the ELC maps. At the same time, the information on *ex situ* accessions was compiled from a global database, such as Genesys (https://www.genesys-pgr.org/) and the Bioversity Collecting Mission Database (1978–1996) (https://bioversity.github.io/geosite/), and national botanic garden in Indonesia (Bogor, Cibodas, Purwodadi, and Bali botanic garden). The output table of the Representa tool that contains gap-type classes was used to select the priority ELC zone. Class 1 to 6 of the 13 classes of gap type were considered as the higher priority (Parra-Quijano, 2016). Class 1–4 means no *ex situ* collection for the related taxa, whether the taxa have a low or high frequency of occurrences and ELC zone. While classes 5 and 6 mean that there are *ex situ* collections for the related taxa, the frequency of occurrence of the taxa is low, whether the ELC zone frequency is low or high. Then, PAs which contain those ELC zones were identified. Those PAs were matched with those containing significant holdouts population. The PAs contain the highest diversity of priority ELC zone and have the highest average of holdouts population across all scenarios, which was selected as the priority.

3. Results

The occurrence records for taxa in the study ranged from 1 to 259. Twenty-five taxa only have one occurrence record, while 16 have more than 100. *Artocarpus elasticus* has the highest occurrence records (Table S1). Among Indonesia's 234 taxa of priority CWR, only 58 have valid distribution models for the current climate (Table S3). The other 176 taxa either had < 10 occurrence points (83 taxa) or did not pass the validation threshold values (93 taxa). Out of the 58 taxa for which future distribution models were created, 55 have valid models in all scenarios, and these were then used for climate change impact analysis (Table S4-S7). Those 55 taxa are related to 24 crop gene pools.

The impact of climate change on the species distribution range varies among the taxa and between the RCP scenarios, dispersal scenarios, and the year of projections. On average, the worst scenario is RCP 8.5 without dispersal ability for the year 2050. However, not all priority taxa will experience a negative impact on future climate change. Positive impacts were found in taxa which have the ability to disperse and colonize new areas without any restriction (unlimited dispersal).

By 2050, the distribution changes range from −54.5 % (RCP 8.5 with no dispersal) to 80.84 % (in RCP 8.5 with unlimited dispersal) (Fig. 1A and B). One wild fig relative (*Ficus chartacea* (Wall. *ex* Kurz) Wall. *ex* King) is predicted to get the worst negative impact by decreasing the distribution range for more than half of the current range (RCP 8.5 and no dispersal). *Artocarpus sepicanus* Diels (a wild relative of breadfruit) is also predicted to significantly decrease its distribution range by 2050 (RCP 4.5 and no dispersal). On the other hand, one wild relative of rice (*Oryza meyeriana* (Zoll. & Mor.) Baillon) is predicted to enlarge its distribution range by more than 80 % of its current range. (RCP 8.5 and unlimited dispersal).

By the year 2080, the distribution changes will be projected at

Table 3
Average gains and losses area of future distribution of priority crop genepool in Indonesia based on RCP 8.5 scenario for 2050 and 2080.

Crop Genepool	N	Current area (km^2)	RCP 8.5									
			2050				2080				Net change	Net change
			Gain (km^2)	% Gain	Loss (km^2)	% Loss	Gain (km^2)	% Gain	Loss (km^2)	% Loss	Current-2050	Current-2080
Archidendron	5	738,546 (±124,027)	233,560 (±100,183)	33.48 (±18.77)	111,764 (±68,573)	14.22 (±7.19)	133,210 (±84,654)	18.99 (±13.95)	121,682 (±88,388)	15.2 (±9.67)	Gain	Gain
Aubergine	1	500,316	23,184	4.63	28,226	5.64	28,300	5.66	27,824	5.56	Loss	Gain
Banana	1	609,984	56,758	9.30	90,332	14.81	47,812	7.84	82,236	13.48	Loss	Loss
BlackPalmSugar	1	805,872	57,096	7.08	116,714	14.48	26,654	3.31	90,396	11.22	Loss	Loss
Breadfruit	8	881,473 (±398,767)	130,338 (±69,938)	18.54 (±11.44)	134,989 (±61,821)	17.77 (±7.42)	140,046 (±81,396)	25.07 (±23.65)	112,794 (±90,592)	13.78 (±7.97)	Gain	Gain
Coconut	1	625,082	28,614	4.58	280,942	44.94	20,186	3.23	158,420	25.34	Loss	Loss
Durian	1	747,320	376,736	50.41	39,510	5.29	133,240	17.83	110,550	14.79	Gain	Gain
Fig	7	645,071 (±324,040)	72,814 (±55,851)	14.06 (±11.25)	162,102 (±192,860)	19.92 (±16.73)	35,749 (34,926)	5.52 (±5.18)	143,638 (±124,116)	19.87 (±10.72)	Loss	Loss
Gnetum	1	963,088	183,702	19.07	47,674	4.95	96,366	10.01	84,656	8.79	Gain	Gain
Ipomoea	4	707,404 (±225,396)	110,900 (±74,155)	14.68 (±10.15)	87,490 (±31,042)	13.41 (±6.55)	66,663 (±33,059)	9.04 (±2.96)	77,184 (±41,973)	10.55 (±5.61)	Gain	Loss
Longan	1	1,130,878	101,808	9.00	103,440	9.15	245,832	21.74	60,684	5.37	Loss	Gain
Mangoes	3	831,454 (±267,731)	113,637 (±24,819)	15.63 (±9.17)	115,132 (±62,778)	13.06 (±4.74)	127,947 (±93,15)	16.77 (±6.44)	82,628 (±72,578)	10.5 (±8.35)	Gain	Gain
Mangosteen	1	874,000	120,898	13.83	138,094	15.80	43,024	4.92	209,264	23.94	Loss	Loss
Mungbean	1	433,194	44,018	10.16	17,188	3.97	131,458	30.35	21,550	4.97	Gain	Gain
Parkia	1	1,079,894	74,096	6.86	250,908	23.23	67,008	6.21	243,860	22.58	Loss	Loss
Pigeon_pea	1	235,964	70,570	29.91	6,682	2.83	34,638	14.68	45,048	19.09	Gain	Loss
Rambutan	1	1,483,344	128,156	8.64	244,796	16.50	242,296	16.33	203,370	13.71	Loss	Gain
Raspberry	4	243,708 (±189,124)	18,464 (±17,409)	8.81 (±6.6)	38,862 (±33,471)	15.62 (±4.3)	9,527 (±10,162)	3.93 (±3.45)	37,509 (±39,767)	12.26 (±6.81)	Loss	Loss
Rice	4	511,611 (±129,602)	175,305 (±98,072)	40.09 (±32.76)	80,541 (±59,679)	15.06 (±10.6)	80,418 (±46,338)	15.73 (±9.15)	97,636 (±42,776)	19.05 (±7.27)	Gain	Loss
Sorghum	2	784,722 (±142,626)	92,645 (±60,122)	11.3 (±5.61)	135,011 (±70,551)	18.32 (±12.32)	62,935 (±45,296)	7.62 (±4.39)	172,871 (±5,274)	22.34 (±3.39)	Loss	Loss
Starfruit	1	765,714	31,148	4.07	159,918	20.88	25,656	3.35	78,120	10.20	Loss	Loss
Sugarcane	2	689,188 (±41,173)	148,507 (±122,922)	22.12 (±19.16)	84,524 (±28,969)	12.16 (±3.48)	100,212 (±57,083)	14.81 (±9.17)	118,060 (±77,208)	17.5 (±12.25)	Gain	Loss
Taro	1	782,306	153,492	19.62	88,124	11.26	44,504	5.69	119,864	15.32	Gain	Loss
Yam	2	509,709 (±98,634)	33,382 (±46,024)	7.56 (±10.49)	141,328 (±78,642)	26.73 (±10.26)	171,929 (±221,982)	38.67 (±51.03)	65,183 (±65,211)	11.77 (±10.52)	Loss	Gain

around −68.32 % (in RCP 4.5 with no dispersal scenario) to 70.74 % (in RCP 8.5 with unlimited dispersal scenario) (Fig. 2A and B). *Ficus oleifolia* King, a wild relative of figs, will be experiencing the highest reduction to close to 70 % of its current distribution based on the RCP 4.5 scenario without dispersal. While one of the yams wild relatives (*Dioscorea pyrifolia* Kunth.) will have more favourable areas, up to 70 % of the current distribution based on the RCP 8.5 scenario with unlimited dispersal.

Eleven of 24 crop gene pools are predicted to have a net loss in both time projections based on RCP 4.5 Scenario (Table 2). While only nine are predicted to have a net loss in both time projections based on RCP 8.5 scenario (Table 3). On the other hand, six crop gene pools are predicted to have a net gain in both time projections on RCP 4.5 and RCP 8.5. Mungbean is the only crop gene pool predicted to have a net gain in both RCP scenarios and time projections. Changes in gains and losses of distribution area for each priority taxon can be seen in Table S8 in supplementary materials.

Fig. S1(A), 3 and 4 show that the Island of Java is the richest area of the priority CWR for current and future climates in all scenarios. However, a biased map (Fig. S1(B)) should also be considered. The western part of Java is the richest area on this Island. The second richest Island is Sulawesi. This Island the richest areas were identified in the southern peninsula of the Island. In Sumatra, the west coast region is richer than the east coast. While in Kalimantan, the eastern part region has more priority CWR than the western part. In all cases, the eastern part of Indonesia, particularly the Papua region, shows the lowest area on the diversity of priority CWR taxa. Moreover, based on the species changes map (Fig. S2), the hotspot of gains area (Fig. S3) and the hotspots of losses area (Fig. S4), the future richness area in Sumatra tends to shift from the western to the eastern coast. While in Kalimantan and Sulawesi, it tends to expand to the centre of the islands.

Figs. 5 and 6 show species turnover of priority CWR future distribution based on the no dispersal and unlimited dispersal scenarios, respectively. Areas with the highest species turnover are identified in the Central-Southern part of Papua, the Central-Northern part, and the Southern part of Kalimantan. The lowest species turnover is mainly in Java, Lesser Sunda Islands, Moluccas, and Sulawesi. Many areas will be experiencing higher species turnover based on RCP 8.5 scenario rather than the RCP 4.5. Moreover, based on RCP 8.5, species turnover in 2050 will be higher than in 2080, but it is likely in contrast based on RCP 4.5.

The average number of PAs with a persistent population is expected to decline in most crop gene pools in all scenarios (Table 4). Based on no dispersal scenario, the area occupied by all the 55 priority taxa within the existing PA is expected to decrease. Based on unlimited dispersal, the average number of future refugia within the existing PAs varies among the taxa and between RCP scenarios. The number of PAs as refugia of six crop gene pools (e.g. Banana, Fig, Ipomoea, Mangosteen, Sorghum, Starfruit) will be declining in both 2050 and 2080 based on RCP 4.5 but only two (e.g. Fig and Sorghum) based on RCP 8.5. The number of PAs as refugia for Archidendron and Mungbean gene pools will increase in 2050 and 2080 based on RCP 8.5. A complete list of PAs as climate refugia for each CWR taxa can be seen in Table S9.

On average, the number of PAs with a significant holdout population based on the RCP 8.5 scenario is higher than RCP 4.5 (Table 5). The number of holdouts based on the no dispersal scenario is always higher than the unlimited dispersal for all taxa. The number of PAs containing significant holdouts will increase from 2050 to 2080 based on the RCP

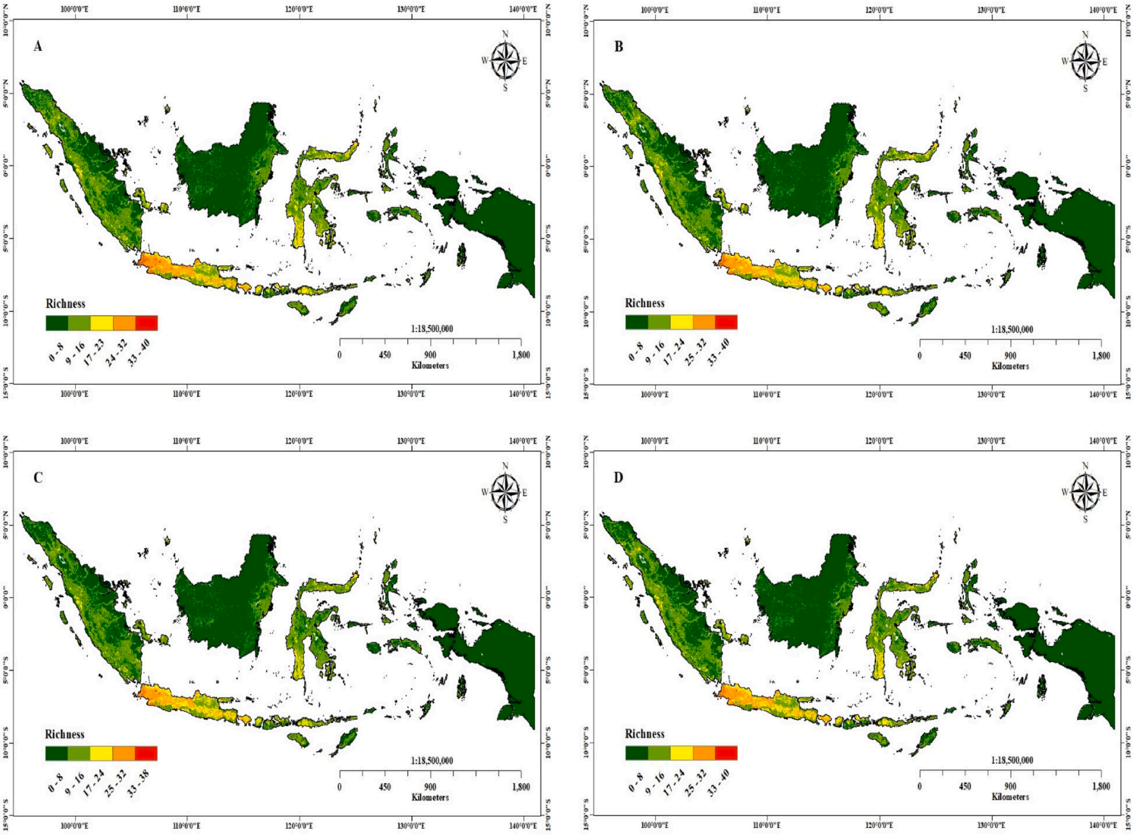

Fig. 3. Future species richness of 55 priority CWR taxa based on no dispersal scenario. A. RCP 4.5 in year 2050, B. RCP 4.5 in year 2080, C. RCP 8.5 in year 2050, D. RCP 8.5 in year 2080.

4.5 scenario. In contrast, the number of PAs containing significant holdouts in 2080 is lower than in 2050 based on RCP 8.5.

Only 35 of 55 priority CWR taxa currently have accessions in the *ex situ* collection. The accessions of all those taxa required more comprehensive to represent their potential genetic variation based on their ecogeographic distribution range. The number of priority PAs for further collecting programs was identified for each taxon (Table S10 in supplementary materials). For those taxa without current *ex situ* collection, most of the PAs containing the holdouts' population were also in the priority ELC zone. For *Ficus chartacea* and *F. oleifolia,* two of the Figs' wild relatives predicted to have the most significant contraction, the most priority PA for further collecting program is the Kerinci Seblat NP, where three and four priority ELC zones occurred. While *Artocarpus sepicanus*, a wild relative of breadfruit, one of the priority PAs is Waigeo Barat Timur NR in West Papua, where it holds three priority ELC zone. The detail of current and future distribution, priority PAs, and ELC zone of *Artocarpus sepicanus* can be seen in Fig. S5 (in supplementary materials).

4. Discussion

The result of the current analysis is necessarily based only on 55 of 234 priority CWR taxa in Indonesia. It is because of the need for more basic occurrence data for most species. However, valid distribution models can be produced for these taxa and generate useful information. Most of the 55 national priority taxa are widely spread distributed species. While many national endemics are not included in the models since their record numbers are limited. Thus, additional field surveys are required for most priority CWR in Indonesia to improve the baseline assessment.

The climate change impacts on the extinction risk of CWR remains uncertain based on the available information in the literature. Jarvis et al. (2008) predicted that 16–22 % of 207 CWR belong to three crop genera that would go extinct by 2055. While a study by Vincent et al. (2019) found that only two of 724 CWR are predicted to go extinct by 2070. In this current analysis, none of the 55 priority CWR in Indonesia are predicted to go extinct by either 2050 or 2080. CWR taxa that are most likely to be at extinction risks, the rare or lesser-known taxa, were excluded from the analysis because of insufficient baseline data. In a study by Vincent et al. (2019), 44 % of global priority CWR have fewer than ten occurrence records. This compares to 35 % of the total priority CWR in this study. Pimm et al. (2014) highlighted that there needs to be more data on the rarer CWR, and because they are likely to have narrow ranges, their probability of extinction may be higher than more common CWR. They stated that the current extinction rates are a thousand times faster than the background benchmark (0.1 extinction per million years species) based on the available fossil records and molecular dating phylogenies. Urban (2015) conclude that the biodiversity extinction risks of climate change are relatively smaller than the total impact the species obtain. Scheffers et al. (2016) showed that the recent climate change had changed species' genetic, physiology, morphology, phenology, and distribution characteristics. Species also have an adaptation mechanism through expressing the variation of adaptive phenotypes in different environments (adaptive phenotypic plasticity) or selection of genetic variation in the population (Fox et al., 2019).

The current results show that the distribution range of all the 55 priority taxa will decline without dispersal ability. Wild relatives of Breadfruit, Coconut, Fig, and Yam are predicted to reduce their distribution ranges significantly. The ability of plant species to disperse depends on their dispersal mechanism (Levin et al., 2003) and the connectivity of their habitats (McConkey et al., 2012). It means unlimited dispersal scenarios, where many habitats become fragmented and

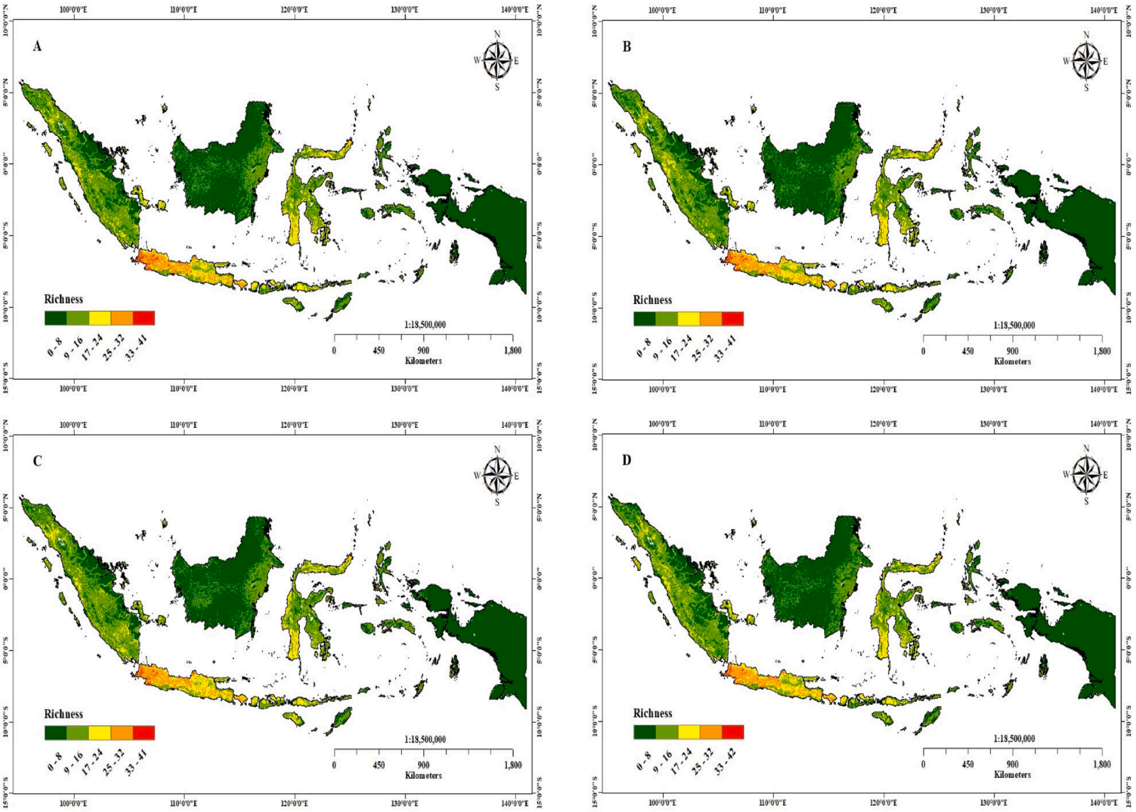

Fig. 4. Future species richness of 55 priority CWR taxa based on unlimited dispersal scenario. A. RCP 4.5 in year 2050, B. RCP 4.5 in year 2080, C. RCP 8.5 in year 2050, D. RCP 8.5 in year 2080.

isolated, are almost impossible. However, those species in which the seeds are dispersal by wind (wild relatives of Rice, Sugarcane, or Sorghum) have potencies to disperse over long distances beyond their habitat barriers without stepping stone population (Pearson & Dawson, 2005). Therefore, the future distribution range of the studied taxa will be in a different place on the continuum between no dispersal and unlimited dispersal, depending on their dispersal mechanism (Urban, 2015). The unlimited dispersal scenario is important as guidance to identify suitable habitats in the future, and no dispersal scenario allows us to anticipate the worst scenario.

In general, Urban (2015) predicted that the extinction rate of species increased in the pessimistic scenario of GHG emissions. However, the results from this study show that the studied taxa responded differently to the RCP scenario. The priority taxa that are predicted to have contraction of more than 30 % of their current ranges (the losers) are *Artocarpus sepicanus* (based on RCP 4.5 in both no dispersal and unlimited dispersal scenario and RCP 8.5 in no dispersal scenario by 2050), *Ficus oleifolia* (RCP 4.5 5 in both no dispersal and unlimited dispersal scenario by 2080), *Cocos nucifera* and *Dioscorea alata* (RCP 8.5 in both no dispersal and unlimited dispersal scenario by 2050), and *Ficus chartacea* (RCP 8.5 in both no dispersal and unlimited dispersal scenario by 2050 and 2080). While those are expected to benefit (the winners) in terms of expansion of their distribution range of more than 30 % are *Dioscorea pyrifolia* (based on both RCP 4.5 and 8.5 in unlimited dispersal by 2050 and 2080), *Archidendron clypearia* (RCP 8.5 in unlimited dispersal by 2050 and 2080), *Durio zibethinus, Ficus padana*, *Oryza meyeriana* (RCP 8.5 in unlimited dispersal scenario by 2050), and *Artocarpus sepicanus* (RCP 8.5 in unlimited dispersal by 2080). No clear pattern of traits is associated with differentiating the winners from the losers. Poorter and Navas (2003) observed that the fast-growing herbaceous C3 species, such as wild relatives of Aubergine, Rice and Mungbean, are more responsive to elevated CO_2 in terms of biomass enhancement for plant growth than woody plants (such as wild relatives of Breadfruit, Durian, Mangoes, and Mangosteen) or C4 species (such as wild relatives of Sorghum and Sugarcane). It means that the fast-growing herbaceous C3 plants have better performance to cope with an increasing level of CO_2.

Regarding dispersal capacity, plants should move at the corresponding velocity of climate change to maintain the future population (Corlett & Westcott, 2013). Still, there is evidence that the distribution shifting capacity of some species lags behind the local impact of climate change (Ash et al., 2017). Plants with abiotic pollination and long-distance dispersal, such as wild relatives of Rice, Sorghum, and Sugarcane, are likely to have higher dispersal capacity than those pollinated and dispersed by obligate animals, such as wild relatives of Figs (Wiegmann & Waller, 2006). Besides the long-distance dispersal ability, Corlett and Westcott (2013) stated that the availability of climate refugia could lower the extinction risk of climate change.

Identifying climate refugia is important in conservation planning (Beaumont et al., 2019; Keppel et al., 2015, 2012). This analysis could identify priority sites for active *in situ* conservation (Keppel et al., 2015). As climate change impact is species-specific, selecting priority sites based on multiple species is recommended (Beaumont et al., 2019; Keppel et al., 2015). The classical SLOSS (single large or several small) debates are still considered when prioritizing it. Does the single large area have better refugia capacity than the several small areas? Identifying multiple refugia based on the existing protected areas is more reliable since they are already established and managed (Haight & Hammill, 2020). For the 55 priority CWR in Indonesia, protected areas are the key to maintaining their future population. In Java, where most of the natural forest has been destroyed, some PAs in the western part of Java has been identified as the potential refugia with the highest diversity (Ujung Kulon National Park (NP), Halimun Salak NP, and Gede Pangrango NP). In Sulawesi, the second richest island for the priority taxa, Bantimurung Bulursaraung NP is identified as the potential for

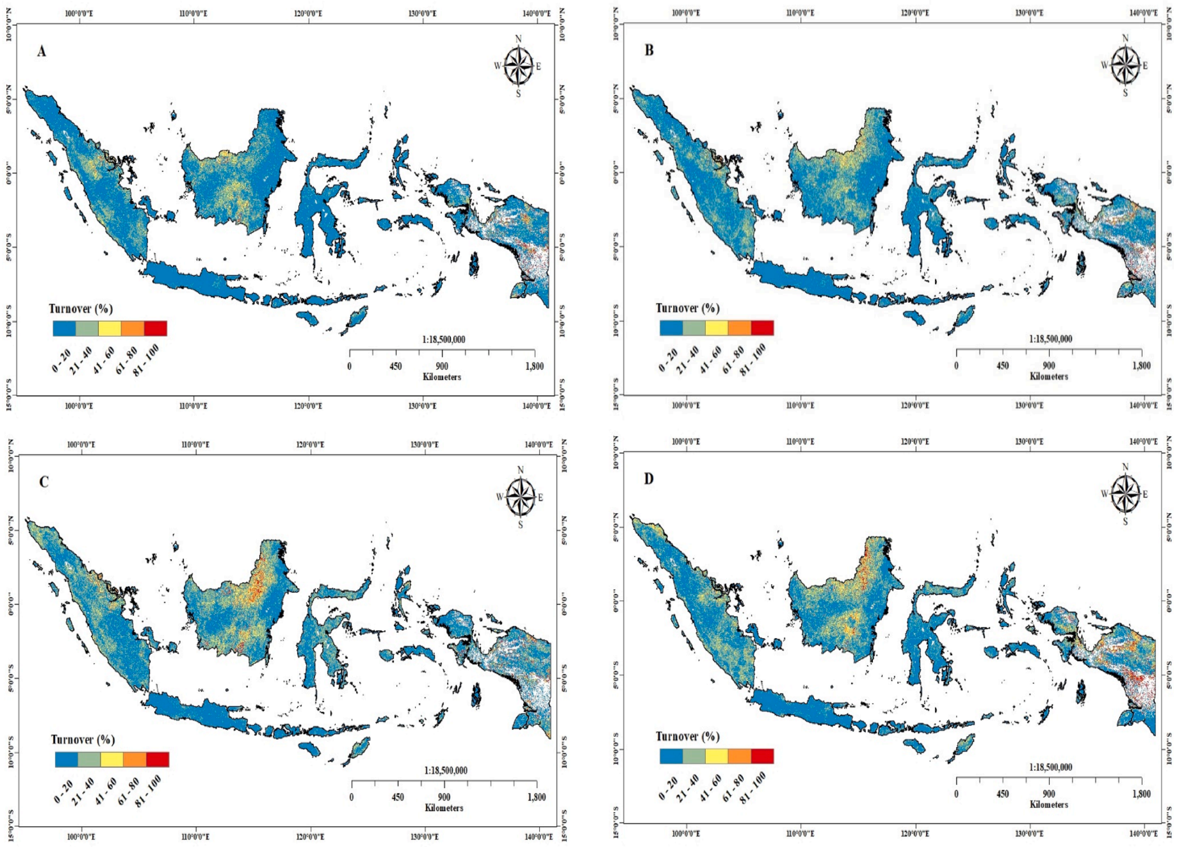

Fig. 5. Species turnover (%) based on no dispersal scenario of 55 priority CWR taxa A. RCP 4.5 in year 2050, B. RCP 4.5 in year 2080, C. RCP 8.5 in year 2050, D. RCP 8.5 in year 2080.

future refugia.

In terms of CWR conservation, the goal is to keep the broadest genetic variation in both *in situ* and *ex situ* conservation. Besides the refugia populations, holdout populations are important in CWR conservation planning. Holdout populations should be targeted for the *ex situ* collections and be used as a source for assisted dispersal (translocation), as they tend to deteriorate or, ultimately, go extinct and may have relevant adaptive diversity that needs to be conserved. The result shows that for multiple taxa, two PAs: Kerinci Seblat NP in Sumatra and Bogani Nani Wartabone NP in North Sulawesi, were identified to contain the highest number of holdout populations for the studied taxa. At least twelve taxa have a holdout population in those two PAs. ELC map can be used to identify priority PAs for more *ex situ* collecting programs by comparing the representativeness of the existing collection and diversity in the field. For example, Kerinci Seblat NP is the highest priority PA for *Ficus chartacea* and *F. oleifolia*. Waigeo Barat Timur NR in West Papua is the highest priority for *Artocarpus sepicanus*. Those PAs were selected since they contain the highest diversity of priority ecogeographic zones and have a significant holdouts population.

The future climate refugia with non-analogue community assemblages can be identified from the species turnover map (Thuiller et al., 2005). Refugia sites with the highest species turnover for the currently studied taxa were identified in Kalimantan (Indonesian Borneo) and Papua (Indonesian New Guinea). In Kalimantan, Kayan Mentarang NP and Bukit Sapat Hawung Nature Reserve, Tanjung Puting NP and Sebangau NP are predicted to be the future refugia with non-analogue assemblages. In Papua, a large area in the lowland plain of Boven-Digul and Mappi district does not have any protected areas that could be identified as climatic refugia except small parts of the Southern part of Lorentz NP. Those areas are also threatened by the expansion of new large-scale plantations and timber logging concessions (CIFOR, 2019). For example, forest loss in two districts in central Papua reached more than 111,373 ha since 2000. Therefore, it is important to establish new protected areas in these areas and establish less formal conservation agreements with local communities or landowners to manage their marginal areas (i.e. field margins or roadsides) to promote CWR population sustainability (Maxted et al., 2020).

Conservation planning should consider how to facilitate species dispersal to their predicted future refugia when the species cannot disperse to suitable areas. Increasing habitat connectivity and assisted dispersal are suggested as potential conservation tools (Morelli et al., 2017). Assisted dispersal is the key to allowing the persistence of the species in the future when natural dispersal is unlikely (Vitt et al., 2010). However, there are continuing debates about the ecological and socio-economic consequences of assisted dispersal as an effective conservation tool against climate change, particularly for species that are predicted to become newcomers in non-analogous assemblages (Cannon & Petit, 2019; McCormack, 2018; McLachlan et al., 2007; Ricciardi & Simberloff, 2009; Vitt et al., 2009). Despite the uncertainty of the risk, assisted dispersal is recommended in human-dominated landscapes for critically important taxa (Maxted et al., 2020). In Indonesia, most of the PAs in Java are isolated by urban and agricultural areas. In the southern part of Kalimantan, the PAs (i.e. Tanjung Puting NP and Sebangau NP) are isolated by industrial plantations and logging concessions and frequently affected by wildfires (CIFOR, 2019). Habitat connectivity can be increased between PAs in Southern Kalimantan by developing corridors between the PAs within the plantations. With assisted dispersal, the CWR diversity in those areas will be maintained. The decision to run this practice should be taken with caution to reduce the risk of the adverse effect of the introduction to the existing community, such as invasiveness or genetic contamination and the fact that moving a single species will break obligate association with other taxa (Hoegh-Guldberg

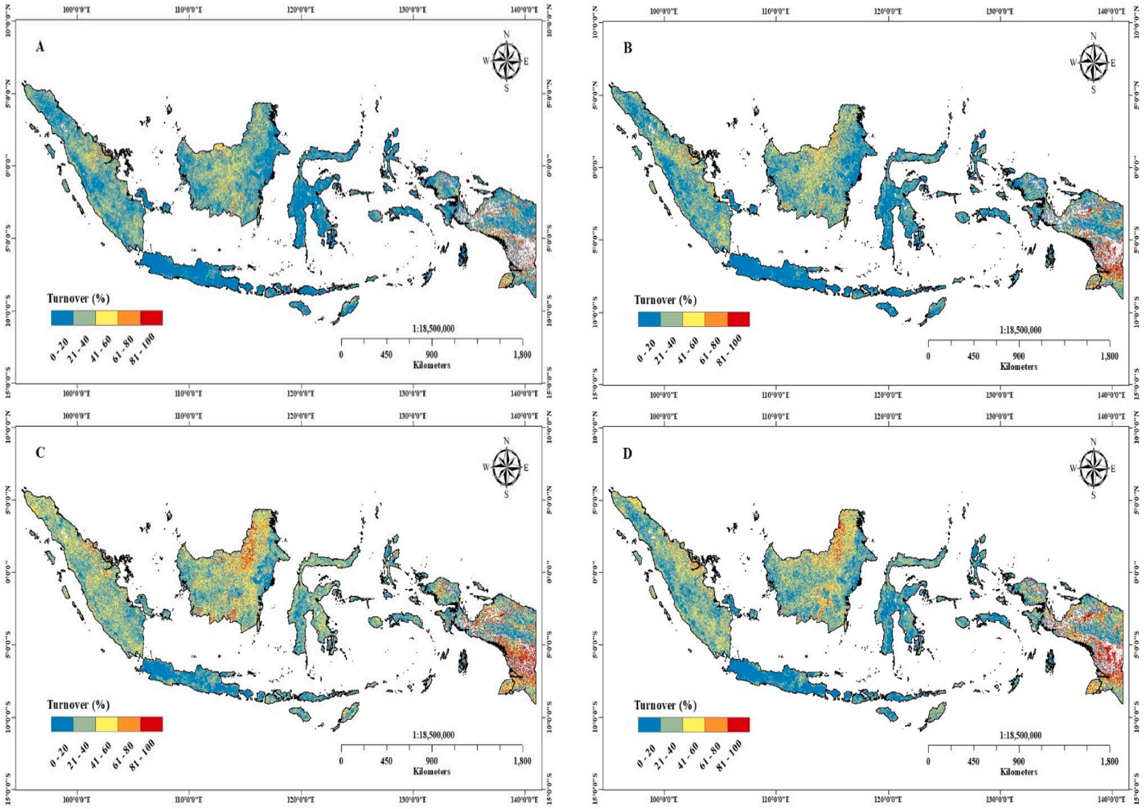

Fig. 6. Species turnover (%) based on unlimited dispersal scenario of 55 priority CWR taxa A. RCP 4.5 in year 2050, B. RCP 4.5 in year 2080, C. RCP 8.5 in year 2050, D. RCP 8.5 in year 2080.

Table 4
The average number of PAs as climate refugia for priority crops genepool for all scenarios.

Crop Genepool	No CWR	The average number of PAs as refugia								
		Current	RCP 4.5–2050		RCP 4.5–2080		RCP 8.5–2050		RCP 8.5–2080	
			Unlimited	No Dispersal	Unlimited	No Dispersal	Unlimited	No Dispersal	Unlimited	No Dispersal
Archidendron	**5**	262	267	248	264	248	264	234	269	246
Aubergine	**1**	304	302	295	306	299	302	292	309	296
Banana	**1**	267	265	259	263	256	241	230	274	260
BlackPalmSugar	**1**	325	305	305	310	309	319	304	321	311
Breadfruit	**8**	222	243	208	222	210	220	198	220	204
Coconut	**1**	300	304	290	271	268	256	238	267	254
Durian	**1**	304	309	269	300	283	347	292	302	278
Fig	**7**	200	197	190	192	183	192	175	188	181
Gnetum	**1**	312	316	302	307	299	330	301	317	300
Ipomoea	**4**	339	334	325	333	322	323	308	336	322
Longan	**1**	198	213	175	206	183	168	156	208	177
Mangoes	**3**	263	259	253	262	253	251	238	262	248
Mangosteen	**1**	371	369	359	364	357	370	346	370	348
Mungbean	**1**	250	258	238	271	243	252	238	293	245
Parkia	**1**	237	231	215	232	218	201	195	228	218
Pigeon_pea	**1**	173	192	168	189	169	198	171	158	139
Rambutans	**1**	334	308	305	333	320	318	310	330	319
Raspberry	**4**	144	138	134	140	136	130	122	135	131
Rice	**4**	239	232	217	238	219	263	213	227	209
Sorghum	**2**	331	326	318	325	314	322	300	302	296
Starfruit	**1**	310	303	293	310	299	272	267	301	288
Sugarcane	**2**	176	168	164	173	168	177	162	172	163
Taro	**1**	337	343	330	325	322	327	311	327	318
Yam	**2**	288	279	258	285	257	223	214	292	253

Table 5
The average number of PAs containing significant holdouts for priority crops genepool for all scenarios.

Crop Genepool	No CWR	The average number of PAs contain significant holdouts							
		RCP 4.5–2050		RCP 4.5–2080		RCP 8.5–2050		RCP 8.5–2080	
		Unlimited	No Dispersal	Unlimited	No Dispersal	Unlimited	No Dispersal	Unlimited	No Dispersal
Archidendron	**5**	59	79	71	85	84	114	74	92
Aubergine	**1**	55	65	46	50	65	72	44	55
Banana	**1**	69	86	66	79	111	131	72	86
BlackPalmSugar	**1**	142	149	157	163	127	152	99	122
Breadfruit	**8**	65	84	64	81	89	116	71	86
Coconut	**1**	78	85	148	152	171	196	146	153
Durian	**1**	84	122	111	129	29	68	103	125
Fig	**7**	56	64	71	78	82	98	83	90
Gnetum	**1**	68	85	99	113	62	131	84	104
Ipomoea	**4**	81	95	89	103	124	161	81	99
Longan	**1**	34	65	44	63	111	133	57	86
Mangoes	**3**	69	79	59	71	85	118	57	70
Mangosteen	**1**	122	149	138	169	138	188	166	187
Mungbean	**1**	42	65	34	55	49	77	20	40
Parkia	**1**	83	99	86	95	130	142	80	89
Pigeon_pea	**1**	11	17	7	14	5	8	65	80
Rambutans	**1**	146	167	101	126	135	155	105	134
Raspberry	**4**	49	54	43	51	63	78	60	64
Rice	**4**	69	85	67	84	72	102	83	98
Sorghum	**2**	78	98	98	115	146	175	157	169
Starfruit	**1**	120	126	100	107	154	178	121	132
Sugarcane	**2**	62	76	55	65	71	88	59	72
Taro	**1**	23	61	131	140	86	135	118	133
Yam	**2**	86	95	83	90	168	178	90	97

et al., 2008; Maxted et al., 2020).

5. Conclusion

Only 23.5 % of 234 priority CWR taxa in Indonesia are included in the current analysis. Most taxa require more field surveys to fulfil the need for occurrence data. Forty-six taxa are national endemics and should be a conservation priority for both *in situ* and *ex situ* programs. The impact of climate change on the distribution of 55 priority CWR in Indonesia is species-specific. RCP and dispersal scenarios influence the future distribution of priority taxa. However, actual future distribution will fall between those scenarios in different places and times, depending on their ability to cope with the future adverse climate. However, those scenarios could guide future climate refugia conservation planning for priority CWR. Holdout populations of priority CWR are important to consider to maximize genetic diversity for *ex situ* conservation and assisted dispersal. The network of PAs is the ultimate key to reducing the impact of climate change on the distribution range shift of CWR. Identification of refugia sites, holdout populations and non-analogue community assemblages based on the PAs network will make the conservation planning more precise and easy to understand, evaluate and practice by the practitioner of *in situ* and *ex situ* management. Establishing new formal protected areas and non-formal local communities' protected land is suggested to facilitate non-analogue community assemblages and the long-term conservation program. The national germplasm commission, the research institute, the Ministry of agriculture, and the Ministry of forestry should be major players in mainstreaming the conservation of CWR as part of biodiversity conservation in national development programmes. It will be easier for all stakeholders to include the CWR conservation program in their management plans when it has a legal framework. Only recently, conservation plans have yet to be practised for CWR in Indonesia. Implementation of this recommendation will enhance the effectiveness of the biodiversity conservation program and support mandated national responsibilities for global agendas such as CBD and SDGs.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

We acknowledge The RISET-PRO program of Ministry of Research, Technology and Higher Education of Indonesia for the scholarship to W. Rahman.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jnc.2023.126368.

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