

Conservation status assessment of banana crop wild relatives using species distribution modelling

Arne Mertens^{1,2}  | Rony Swennen^{1,3,4}  | Nina Rønsted^{5,6}  | Filip Vandeloos²  | Bart Panis⁴  | Gabriel Sachter-Smith⁷ | Dang Toan Vu⁸  | Steven B. Janssens²

¹Department of Biosystems, Laboratory of Tropical Crop Improvement, KU Leuven, Belgium

²Crop Wild Relatives and Useful Plants, Meise Botanic Garden, Meise, Belgium

³International Institute of Tropical Agriculture, Arusha, Tanzania

⁴Bioversity International, Heverlee, Belgium

⁵Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark

⁶Science and Conservation, National Tropical Botanical Garden, Kalaheo, HI, United States

⁷University of Hawaii, Mānoa, HI, United States

⁸Research Planning and International Department, Plant Resources Centre, Hanoi, Vietnam

Correspondence

Arne Mertens, Meise Botanic Garden, Nieuwelaan 38, 1860 Meise, Belgium.
Email: arne.mertens70@gmail.com

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Abstract

Aim: Crop wild relatives (CWR) are an essential source of genetic material for the improvement of certain traits in related crop species. Despite their importance, increasing public, scientific and political support, large gaps exist in the amount of genetic material collected and conserved of many CWR. Here, we construct a dataset on the distribution of wild banana species (*Musa* spp.) and assess their risk and conservation status. We deal with the following questions: (a) What areas are potentially suitable for wild banana species? (b) How much of the wild banana diversity is currently at risk or insufficiently conserved ex and in situ?

Location: Native distribution area of wild banana species, ranging from the north-eastern states of India to north-eastern Australia.

Methods: We assessed the potential environmental range of wild species using a species distribution modelling approach with MaxEnt. Extinction risk was evaluated following IUCN criterion B, and the ex and in situ conservation status was assessed using an indicator for biodiversity and sustainable development targets.

Results: We found that 11 out of 59 assessed species can be considered as vulnerable and nine as endangered. Highest species richness was found along the border of south China and northern Vietnam, in the north-eastern states of India and on the Malayan peninsula. Our distribution modelling approach indicates that the northern Indo-Burmese region has the highest environmental suitability for most wild banana species and that lowland rain forests in general are highly suitable for bananas. Assessment of in and ex situ conservation status indicates that 56 out of 59 assessed species are currently insufficiently conserved ex situ and that 49 are of high priority for further conservation. Additional in situ conservation is of high priority for six species and of medium priority for 40 species.

Main conclusions: To date, little of the banana CWR are sufficiently conserved both in and ex situ.

KEYWORDS

banana, conservation planning, conservation status, CWR, Musaceae, species distribution modelling

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1 | INTRODUCTION

Crop wild relatives (CWR) are wild plant species closely related or ancestral to cultivated plants. In comparison with their associated crop, CWR often contain important traits for agriculture that are new or have been lost during domestication (Fielder et al., 2015; Hajjar & Hodgkin, 2007; Heywood et al., 2007). Their genetic resources can be used to provide pest and disease resistance in crops, as well as improved crop fertility, quality, agronomic, phenological or morphological traits (Dempewolf et al., 2017). Many CWR and other wild species are at risk due to increased abiotic and biotic stress related to climate change but especially due to anthropogenic pressure caused by the increasing world population and subsequent habitat loss and/or fragmentation, improper land use and the lack of effective nature conservation strategies (Govindaraj et al., 2015; Heywood et al., 2007).

Substantial efforts have been undertaken to improve CWR conservation (Castañeda-Álvarez et al., 2016). Ex situ conservation strategies have been given most attention, and a large amount of germplasm is already stored in gene banks. Such a strategy also makes it possible to distribute genetic material to crop breeders. Nevertheless, current ex situ conservation has four major drawbacks. First, only a small proportion of the inter- and intraspecific genetic variation present in CWR is currently stored in gene banks (Castañeda-Álvarez et al., 2016; Guarino & Lobell, 2011). In Europe, only 1,095 CWR taxa (6% of CWR present in Europe) were included in the EURISCO catalogue of ex situ plant genetic resources (Ford-Lloyd et al., 2011). Second, some CWR produce recalcitrant seeds that cannot survive with traditional ex situ conservation techniques such as drying and freezing (Bonner, 1990). Third, plants conserved ex situ are not influenced by the same evolutionary selection processes as in their native environment, limiting the development of new genetic variation. As a result, accommodation to a gradually changing environment and new biotic interactions is prevented (Heywood, 2016; Meilleur & Hodgkin, 2004). Lastly, to safeguard ex situ collections from disappearing due to local natural or human-caused disasters, safety duplication of accessions is strongly encouraged. Currently, duplication of germplasm is not always documented and many accessions might not be duplicated at all (FAO, 2014).

It is thus essential to complement ex situ collections with in situ conservation strategies as a resource for future breeding strategies. Moreover, there are some species that are unable to be established or regenerated outside their natural habitat due to their complex ecosystem interactions or when seed dormancy cannot be broken by known (artificial) methods (FAO, 1997; Rasmussen et al., 2015). For example, long-term ex situ conservation of vanilla crop wild relatives is complicated due to their obligate association with mycorrhizal fungi, requiring both plant and mycobiont to be conserved simultaneously (e.g. by means of cryopreservation) (Flanagan et al., 2019; Merritt et al., 2014). In situ conservation comprises the conservation of species and their genetic variability in populations as well as the ecosystem in which they thrive. It involves many

different procedures, starting from the selection of a target species to the management and monitoring of designated areas (Hunter & Heywood, 2011).

A first step in establishing a strategy for both in and ex situ conservation is a gap analysis, that is knowing where high levels of genetic variation of a selected species might be located and to what extent these species are already represented in gene banks or protected locally. Accordingly, habitats or ecosystems that need additional protection can be readily identified (Maxted et al., 2008). In particular for species with a poorly known distribution range, a gap analysis approach often requires advanced modelling tools to overcome the need for information about species' absences and consequently demands very large datasets containing occurrence records. Modelling approaches based on presence-only data cover the lack of location data for modelling distribution ranges and can therefore aid in the establishment of conservation and management strategies of threatened species (Bosso et al., 2013; Khoury et al., 2015; Phillips et al., 2006).

With a production of over 125 million tonnes each year, bananas are considered one of the most important fruit crops in the world (FAO, 2018). However, considerably less conservation efforts and strategies exist for their wild relatives compared to rice, wheat and maize (Castañeda-Álvarez et al., 2016). Bananas belong to the genus *Musa* L. of the Musaceae, a small plant family consisting of three genera *Musa*, *Ensete* Bruce and *Musella* (Franch.) C.Y.Wu ex H.W.Li. The genus *Musa* is by far the most diverse and well-known member of this family with over 75 described species and subspecies. The majority of cultivated and edible bananas are derived from hybridization events within and between two species: *Musa acuminata* Colla and *Musa balbisiana* Colla (Häkkinen & Väre, 2008; Perrier et al., 2011). Edible bananas are diploid, triploid or tetraploid hybrids, typically containing genetic information from *M. acuminata* subspecies (the "A" genome) and from *M. balbisiana* (the "B" genome). Few cultivars also contain genetic information of *M. schizocarpa* N.W.Simmonds (the "S" genome), such as in East African Highland Bananas and genetic information from species from the *Australimusa* section (the "T" genome) (Carreel, 1994; Němečková et al., 2018). Fe'i bananas are another group of rare, edible bananas belonging to the former *Australimusa* section and are independently domesticated from *M. acuminata* and *M. balbisiana* (Ploetz et al., 2007). The presence of the *M. balbisiana* genome is often associated with drought tolerance and *Xanthomonas* resistance not found in *Musa acuminata*, but *M. balbisiana* genetic resources are currently largely underused due to incorporated sequences of the endogenous banana streak virus, a *Badnavirus* (Duroy et al., 2015). The narrow genetic basis of current cultivated bananas and their limited fertility are major constraints on further improvement through classical breeding (Brown et al., 2017). A well-known example is the collapse of the Gros Michel banana industry in Central America in the 1950s due to the Panama disease caused by an outbreak of *Fusarium oxysporum* f.sp. *cubense* E.F.Sm., W.C.Snyder & H.N.Hansen tropical race 1 (TR1) (Dita et al., 2018). In the late 1980s, a new strain of *Fusarium oxysporum* f. sp. *cubense* (TR4) started to infect cultivars of the Cavendish subgroup, which

had been selected in the past because of their resistance against TR1 (Pérez-Vicente, 2004; Ploetz, 2015). While the distribution of TR4 was restricted to East and parts of Southeast Asia for a long time, it was more recently discovered in Jordan and other banana-growing regions in Africa (Garcia-Bastidas et al., 2014; Zheng et al., 2018). Alarming, the occurrence of TR4 was recently also detected in Colombia and thus for the first time in Latin America (Garcia-Bastidas et al., 2019). Together with more extreme weather events associated with climate change, the conservation of wild bananas becomes even more important as the wild material can serve as potential source against disease resistance such as TR4 or drought tolerance (Castañeda-Álvarez et al., 2016; Heslop-Harrison & Schwarzacher, 2007; Zuo et al., 2018). Wild banana species are typically diploid and can vary in numerous traits such as height, flower and fruit shape and colour (Figure 1). They can be subdivided into two sections: the *Callimusa* section (former sections *Australimusa*, *Callimusa* and *Ingentimusa*) and the *Musa* section (former sections *Musa* and *Rhodochlamys*) (Häkkinen, 2013).

Several conservation efforts have already been made to conserve wild banana germplasm ex situ in the form of seeds, in vitro, cryopreservation or as living plants. Most of the available germplasm is kept as in vitro cultures or frozen meristems at The International Musa Germplasm Transit Centre (ITC) in Belgium (Panis et al., 2005; Van den houwe et al., 1995, 2003). Collection missions in the past mainly focussed on *Musa acuminata* subspecies, *M. balbisiana* and diploid and triploid cultivated varieties to serve as potential source of genetic resources for banana breeders. However, little is known about the natural distribution of many wild species and consequently specific collecting and in situ conservation strategies are missing for these species. Botanical knowledge to identify species correctly is rare due to the lack of good herbarium material as a result of their large, fleshy architecture and ephemeral flowers and molecular methods are often needed for a correct species distinction (Liu et al., 2002). Moreover, most wild species occur in remote and often

inaccessible areas that require substantial travelling to reach. In addition, many of the tropical and subtropical regions in Southeast Asia are heavily understudied and field missions are needed to further map the distribution of wild *Musa* species (Sardos et al., 2018).

In this study, we establish a comprehensive dataset containing georeferenced occurrence records of wild banana species and subspecies. Subsequently, potential species distributions are modelled with MaxEnt (Phillips et al., 2006) using presence-only data to overcome the need of determining and sampling the entire distribution range of a plant species. Finally, a preliminary extinction risk of wild bananas is assessed based on IUCN criterion B and their conservation status was evaluated using a recently developed indicator for biodiversity and sustainable development targets. With the evaluation of the currently known and estimated potential distribution of wild banana species and information on their conservation status, the following questions are addressed: (a) What areas are potentially suitable for wild banana species? (b) How much of the wild banana diversity is currently at risk or insufficiently conserved ex and in situ?

2 | METHODS

2.1 | Study area

The study area was limited to the native distribution area of wild banana species assessed by Janssens et al. (2016), ranging between 87.9°E–164.1°E and 31.1°N – 20.3°S. It includes the following geographical regions: north-eastern Australia, Papua New Guinea and surrounding islands, Lesser Sunda Islands, Sulawesi, Borneo, Malayan Peninsula and Sumatra, the Philippines, southern China, Taiwan, southern Indo-Burma, the north-eastern states of India and northern Indo-Burma. This area covers both subtropical-temperate and tropical areas and encloses multiple biomes and biodiversity

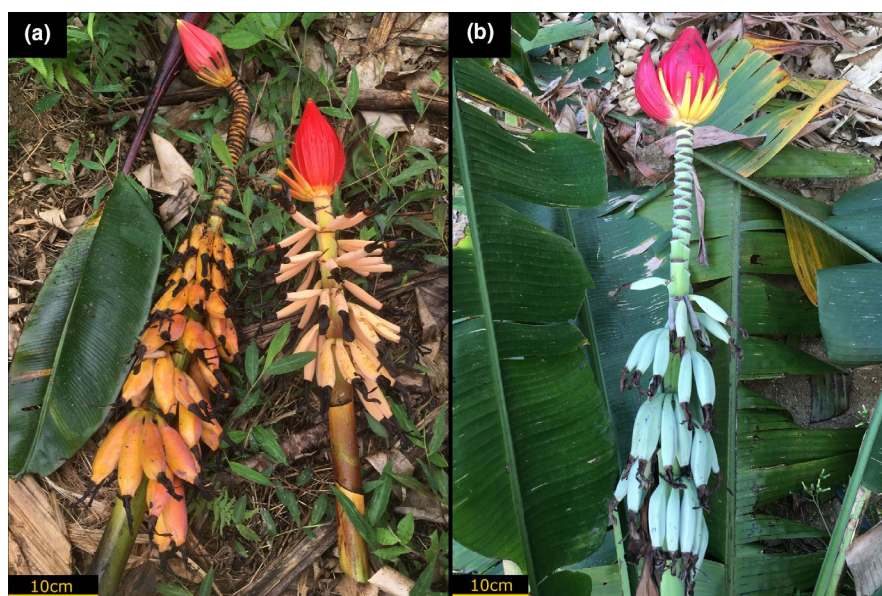


FIGURE 1 Bunch and flower bud of two closely related wild banana species. (a), *Musa lutea* R.V.Valmayor, L.D.Danh & Häkkinen; (b), *Musa paracoccinea* A.Z.Liu & D.Z.Li

hotspots of the world such as Sundaland, Indo-Burma and the Philippines (Mittermeier et al., 2011; Olson et al., 2001).

2.2 | Occurrence data

We compiled a dataset of occurrence records of wild *Musa* species and subspecies by combining information from known in situ and ex situ collections (e.g. Millennium Seed bank, The International Musa Germplasm Transit Centre) and from other well-known databases (e.g. Naturalis Biodiversity Centre, Global Biodiversity Information Facility, Genesys PGR). Presence data obtained from scientific articles and recent field missions in Vietnam, Papua New Guinea and Bougainville were also included. Accurate locality descriptions without coordinates were georeferenced using Google Earth pinpoints (Google LLC, 2018). For some taxa, occurrences were obtained at the subspecies level and are referred to as species throughout the article. Duplicate records, outliers, zero coordinates, records in centroids of provinces and countries and erroneous occurrences in the sea were removed with the online tool "CoordinateCleaner" (Zizka et al., 2019). Accession names were compared and adjusted to their currently accepted name according to the World Checklist of Selected Plant Families (WCSP, 2018). Data were trimmed to a maximum of one occurrence per species per raster cell of 30 arcseconds to avoid strong autocorrelation between environmental variables. While methods exist to identify the minimum required sample size (van Proosdij et al., 2016), we set the minimum number of records to infer relationships between species and environmental conditions for each species at five (Appendix S1—sheet 1) (Raes et al., 2014).

2.3 | Environmental data

Current climatic conditions were represented by 19 bioclimatic variables obtained from the WorldClim 2 database with a spatial resolution of 30 arcseconds. The data represent average monthly climate data for 1970–2000 (Fick & Hijmans, 2017). The Maximum Green Vegetation Fraction was downloaded at a 30 arcsecond resolution from the USGS Land Cover Institute (Broxton et al., 2014). Digital elevation models (DEM) of Asia, Southeast Asia and Australia with a 30 arcseconds spatial resolution were retrieved, subsequently combined and aligned to fit the same dimensions and number of raster cells as the layers containing bioclimatic information. Additionally, slope and aspect (i.e. slope direction) were derived from the DEM using the terrain function in the "raster" package in R (Hijmans, 2020), resulting in a final set of 23 environmental variables (Appendix S2—Table S1).

2.4 | Distribution modelling

Species-specific variable selection was carried out based on random forests with the VSURF_thres function in the package "VSURF" in R

(Genauer et al., 2019). Using 50 Random Forest runs that were built using 2,000 trees each, variables were ranked from high to low variable importance (VI). A threshold is estimated based on standard deviations of variable importance and variables with a VI lower than the threshold are eliminated. Subsequently, compared to the top five predictors and in order of importance, variables with Pearson's correlation coefficient larger than 0.7 were excluded (Appendix S1—sheet 2).

Most optimal combination of MaxEnt features (linear, quadratic, product) and regularization parameters (ranging from 0.1–10) to develop the models were selected using the ENMevaluate function in R package "ENMeval" (Muscarella et al., 2014), using the randomk-fold method to partition occurrence and background localities. As biologically meaningful thresholds are unknown or assumed, hinge and threshold features were excluded (Gomes et al., 2018; Merow et al., 2013). Considering the SDMs as a good proxy for the true species' distributions, they were transformed to binary species distribution maps using the maximized sum of sensitivity and specificity as threshold (Khoury et al., 2020; Liu et al., 2005). To model the area with suitable environmental conditions for each banana species, the values of included variables were extracted from each occurrence location together with a maximum number of background points of 5,000. We performed a species-specific background point selection method as described in Khoury et al. (2020), that is by limiting the background of each species to the ecoregion and the countries of the original occurrence locations (Khoury et al., 2020). Species distributions were modelled with the maximum entropy algorithm implemented in MaxEnt (Phillips et al., 2006) using the maxent function in R package "dismo" (Hijmans et al., 2017). This presence-background modelling software was developed to cope with presence-only (PO) data by contrasting this to a sample of background locations drawn from the study area where the presence of a species is unknown (Merow et al., 2013). It can compete with or even outperforms other methods (e.g. ANN and GLM), in particular for small sample sizes and when species have a limited distribution (Aguirre-Gutiérrez et al., 2013; Elith et al., 2006, 2011; Williams et al., 2009).

To produce and evaluate each SDM, occurrence records were split into training and testing data using a cross-validation approach with ten replicates for species with more than 10 occurrences or five replicates for species with less than 10. Distribution models were then calculated as the median of these replicates. Model evaluation was based on three different metrics: the area under the curve (AUC), the standard deviation of the AUC between replicates (SDAUC) and the proportion of the potential distribution model with a standard deviation > 0.15 (ASD15). Species with an AUC above 0.7, SDAUC < 0.15 and an ASD15 < 0.10 are considered stable (Ramírez-Villegas et al., 2010). Based on the models that passed these criteria, a species richness map was created. For species where no robust model could be generated, a buffer of 0.5 degrees (~50 km radius) was created around each occurrence record (Khoury et al., 2019).

As species distributions are not limited by ecoregion or country borders, we ran a complementary analysis without restricting the background selection to specific countries or ecoregions. Because

not all areas in the study region have been sampled to the same degree, we created a bias layer using all data records of all *Musa* species as target group (APPENDIXS2—Figure S1) (Rinnan, 2015). Sampling background points from a layer representing sampling bias has been proven to greatly improve model performance (Phillips et al., 2009; Syfert et al., 2013). This allows us to assess species richness for the study area, without excluding countries or ecoregions that had no occurrence records in our dataset. For this set of analyses, 10,000 background points were sampled and MaxEnt's standard settings were used together with a regularization parameter of one.

2.5 | Assessing the conservation status of wild banana

2.5.1 | Extinction risk assessment—IUCN criterion B

As a first measure of conservation status, we performed a preliminary risk assessment following IUCN criterion B. The general purpose of this criterion is to identify species/populations with a restricted distribution that are either fragmented or occupy few locations also taking into account continuing decline or extreme fluctuations in distribution area if this information is available (IUCN Standards & Petitions Committee, 2017). To assess the extinction risk of wild *Musa* species, we used R package “conR” (Dauby et al., 2017). The extent of occurrence (EOO), area of occupancy (AOO), number of unique coordinates, number of locations and number of locations in protected areas were calculated. A species-specific cell size was used to determine the number of different locations, and The World Database on Protected Areas (WDPA) was used to assess how many occurrences of each species were located in protected terrestrial habitats. This database consisted of both polygon (91%) and point (9%) data. For point data with information on total area, a buffer was constructed by calculating the radius of each point as suggested by the User Manual of the WDPA (UNEP-WCMC, 2015). User-defined grid cells of 2 × 2 km were used to assess AOO, as recommended by IUCN (IUCN Standards & Petitions Committee, 2017).

2.5.2 | Ex and in situ conservation status

Second, we used the “comprehensiveness of conservation of useful wild plants” indicator developed by Khoury et al. (2019) as novel gap analysis indicator methodology for an in-depth assessment of wild *Musa* species. This technique enables us to prioritize species in need for immediate conservation based on both ex situ and in situ conservation status and will allow tracking conservation progress in the future. Conservation status was determined using the first set of predicted species ranges, where the background was limited to countries and ecoregions of the evaluated species. Records that are currently kept in germplasm collections were scored as “G,” and other records from herbarium and field observation data were scored as “H.” For G records, buffers of 0.5 degrees (~50 km radius)

were made (CA50). The indicator is based on the calculation of six metrics, three for both in and ex situ [Sampling Representativeness Score (SRS), Geographical Representativeness Score (GRS) and Ecological Representativeness (ERS)] (see Appendix S2—Methods S1. for the detailed methodology).

$$SRS_{ex} = \left[\frac{\text{number of germplasm accessions (G)}}{\text{number of total reference records (H)}} \right] \times 100$$

$$GRS_{ex} = \left[\frac{\text{total area (km}^2\text{) of CA50 of all G records}}{\text{total area (km}^2\text{) of species distribution model (SDM)}} \right] \times 100$$

$$ERS_{ex} = \left[\frac{\text{number of ecoregions represented within CA50 of G records}}{\text{number of ecoregions represented within SDM}} \right] \times 100$$

$$SRS_{in} = \left[\frac{\text{number of occurrences in protected area}}{\text{total number of occurrences}} \right] \times 100$$

$$GRS_{in} = \left[\frac{\text{area (km}^2\text{) located in protected areas}}{\text{total area (km}^2\text{) of SDM}} \right] \times 100$$

$$ERS_{in} = \left[\frac{\text{number of ecoregions represented in SDM located in protected areas}}{\text{number of ecoregions represented within SDM}} \right] \times 100$$

Based on the average of these three metrics, final in and ex situ conservation scores (FCS_{in} and FCS_{ex} , respectively) were calculated. Combined conservation scores (FCS_c) were then used to determine the indicator score for the *Musa* species assessed in this study.

$$FCS_{ex} = \left[\frac{SRS + GRS_{ex} + ERS_{ex}}{3} \right]$$

$$FCS_{in} = \left[\frac{SRS_{in} + GRS_{in} + ERS_{in}}{3} \right]$$

$$FCS_c = \left[\frac{FCS_{ex} + FCS_{in}}{2} \right]$$

$$\text{Indicator} = \left(\frac{\text{number of species with } FCS_c \geq 50}{\text{total number of species}} \right) \times 100$$

In this section, we used *Musa balbisiana* var. *balbisiana* as a case study to explain in detail the assessment of the combined conservation status. Germplasm of 17 georeferenced occurrences out of 58 is currently conserved ex situ, resulting in a SRS of 29.3. Based on the 0.5 degree buffer around germplasm-collected samples, 13.7% of the predicted range of *M. balbisiana* var. *balbisiana* can be considered to be conserved ex situ (GRS_{ex}). The germplasm-collected occurrences cover six ecoregions out of the 11 ecoregions that are present in the predicted species range, resulting in an ERS_{ex} of 54.5. Based on these indices, the final ex situ conservation score (FCS_{ex}) for *M. balbisiana* var. *balbisiana* is 32.5, indicating that this species is

not sufficiently conserved ex situ and of medium priority for additional ex situ conservation. 13.8% of the occurrences and 9.7% of the predicted range are located in protected area (SRS_{in} and GRS_{in} , respectively). Nine out of 11 ecoregions within its predicted range were to some extent located in protected area, resulting in an ERS_{in} of 81.1. This results in a final in situ conservation score (FCS_{in}) of 35.1. Combining both in and ex situ conservation scores for *M. balbisiana* var. *balbisiana* resulted in a final combined conservation score of 33.8 (FCS_c), thus not sufficiently protected and of medium priority for additional conservation.

3 | RESULTS

3.1 | Distribution of wild banana

Fifty-nine wild *Musa* species with more than five observations per species were found, resulting in 1,511 georeferenced, unique records in the study area (Figure 2). A total of 147 of those are conserved ex situ. The dataset includes the species name, coordinates,

source type and unique identification numbers of each occurrence (Appendix S1, sheet 1). Five main areas with a high number of species records can be delimited: north-eastern India, south China, northern Vietnam, the Malayan Peninsula, northern Borneo and the Morobe province of Papua New Guinea. Species richness in different regions of the study area ranges from one to ten. Highest species richness (co-occurring species) is found in north-eastern India and the south China–Vietnam border.

3.2 | Distribution models

Out of the 59 species, 41 of the modelled predictions (70%) had an $AUC > 0.7$, an $STAUC < 0.10$ and an $ASD15 < 0.15$ and were considered robust. Eight out of the 18 species that did not pass these criteria had less than 10 occurrence records (Appendix S1—sheet 3). The predicted range of these 41 species and buffered maps of the species that did not pass the criteria are included in the appendix (Appendix S3). Clear differences between modelled species distributions were found. While some species models suggest a rather

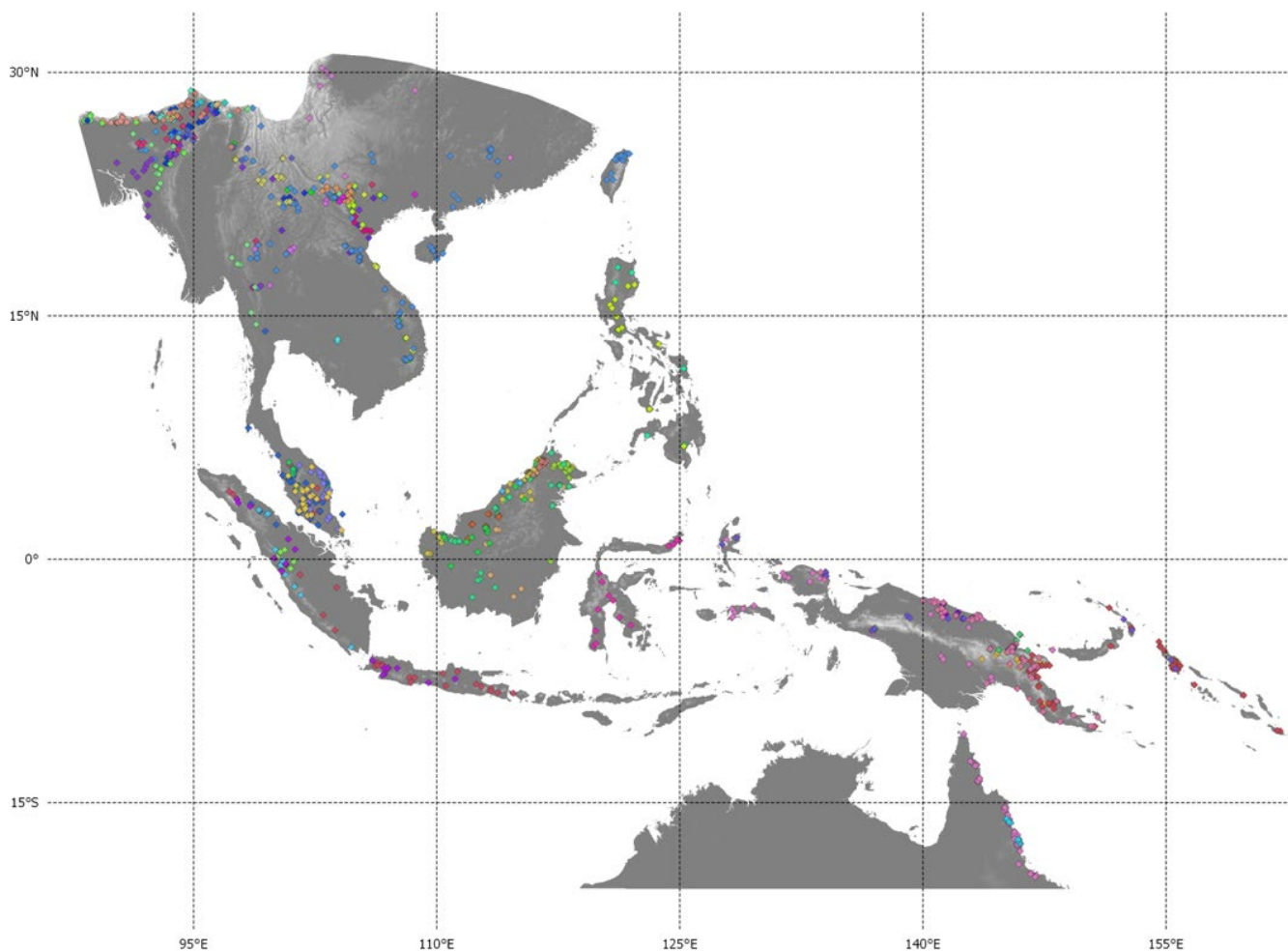


FIGURE 2 Study area, ranging from north-eastern India to Australia including all islands in between. All 1,511 occurrences of 59 *Musa* species are marked on the map in different colours. Species-specific coordinates can be found in the occurrence list (Appendix S1)

broad predicted distribution of the species, for example *M. itinerans* Cheesman, *M. banksii* F. Muell. and *M. balbisiana* var. *balbisiana*, other species models suggest a confined predicted distribution (e.g. *M. bakeri* Hook. f. and *M. bukensis* Argent). Note that we use the species name *M. bakeri* and not the currently accepted *M. balbisiana* var. *bakeri* based on molecular evidence of a recent field mission to Vietnam that placed this species closer to *Musa acuminata* than to *M. balbisiana* in the *Musa* section (personal communication S. Janssens and D. T. Vu). The species richness map based on models restricted to countries and ecoregions suggests high potential species richness in the Eastern Himalayan broadleaf forests, the Mizoram–Manipur–Kachin rain forests, the eastern part of the northern Indochina subtropical forests, the Peninsular Malaysian rain forests and the lowland rain forests of Borneo and northern New Guinea (Figure 3a). As backgrounds were restricted to countries and ecoregions of georeferenced records, many areas (including Myanmar and Laos) are excluded. In contrast, the richness map based on the full extent of the study area indicated additional areas with high predicted species richness: the Meghalaya subtropical forests, the Northern Triangle subtropical forests, the western part of the south China–Vietnam subtropical evergreen forest, the Southern Annamites montane rain forests and the lowland and montane rain forest of Sulawesi. Ecoregions with low estimated richness include the Irrawaddy dry and moist deciduous forests of central Myanmar, the dry and swamp forests of Central Indochina, the Yunnan Plateau subtropical and Changjiang Plain evergreen forests, and the freshwater swamp forests and Trans Fly savanna and grasslands of Southern New Guinea (Figure 3b) (Olson et al., 2001).

3.3 | Risk assessment

Preliminary risk assessment with “conR” based on IUCN criterion B indicated that 11 out of 59 *Musa* species are currently vulnerable while 9 species are currently endangered. Most *Musa* species analysed in this study were considered as of least concern for future conservation efforts or as near-threatened (i.e. could become threatened in the near future). Occurrence in protected area greatly varied between different species and ranged from 0 for 11 species to 60% for *Musa exotica* R.V.Valmayor, with an average of 13.9% for the genus (Table 1).

3.4 | Conservation status

Forty-six out of 59 species did not have any georeferenced records that were conserved ex situ, resulting in a final ex situ conservation score of 0. For the remaining 13 species, final ex situ conservation scores varied from 16.01 for *M. acuminata* subsp. *microcarpa* (Becc.) N.W.Simmonds to 94.44 for *M. bakeri*. Final in situ conservation scores ranged from 0 for *M. bukensis* to 74.66 for *M. jackeyi* W.Hill. Combined conservation score (FCS_c) varied between 0 and 70.6, indicating that no banana species is sufficiently conserved ($FCS_c > 75$).

Only three (*M. acuminata* subsp. *truncata* (Ridl.), *M. gracilis* Holttum and *M. bakeri*) out of 59 species had an $FCS_c \geq 50$ and are of low priority for future conservation efforts, resulting in a “comprehensiveness of conservation of useful wild plants” indicator score of 5.08 for the assessed *Musa* species. Nineteen species are of medium priority ($25 < FCS_c < 50$) and there is a high priority ($FCS_c < 25$) for additional conservation effort for 36 species (Table 2; Figure 4). All intermediate values for calculating the indicator score can be found in Appendix S2–Table S2.

4 | DISCUSSION

4.1 | Data collection

Out of 81 accepted *Musa* species and subspecies summarized by the WCSP (WCSP, 2018), 22 species had less than five observed or georeferenced occurrences after data cleaning (>25%), resulting in 59 species with an average of 26 occurrence records per species, already indicating that more fieldwork is still needed on this group of wild relatives. Moreover, the taxonomy of wild *Musa* species is not well resolved and a large number of new species have been described in the past decade (Chen et al., 2014; Gogoi & Borah, 2013; Gogoi & Häkkinen, 2013; Häkkinen et al., 2014). Lumping different species is also frequently proposed (Hareesh et al., 2017; Joe et al., 2016; Liu et al., 2002), highlighting the necessity of more field missions combined with molecular research to resolve these taxonomic issues (Christelová et al., 2017). While many surveys are standardized and record important data such as date, locality and geographical coordinates, such data are often missing in literature, making them only partially usable in modelling studies.

North-eastern India, the south China–northern Vietnam border as well as northern Borneo and the Morobe province show a high number of occurrence records and high species richness. This pattern is likely influenced by higher sampling efforts and habitat heterogeneity in these regions. For example, high number of records in Papua New Guinea can be explained by a series of field missions that were carried out in 1988 and 1989 by the International Board for Plant Genetic Resources (IBPGR) and the Queensland Department of Agriculture and Fisheries (QDPI) (Arnaud & Horry, 1989). In 2016, 61 more accessions were collected from Papua New Guinea on the Autonomous Region of Bougainville by NARI, Bioversity International and Meise Botanic Garden (Sardos et al., 2018). A series of field missions to the northern provinces of Vietnam in 2018 and 2019 contributed to the high number records observed here (personal communication S. Janssens and D. T. Vu).

4.2 | Suitable area

Species richness maps produced with SDMs that passed the evaluation criteria suggest large differences in environmental suitability throughout the study area. Next to the high number of different

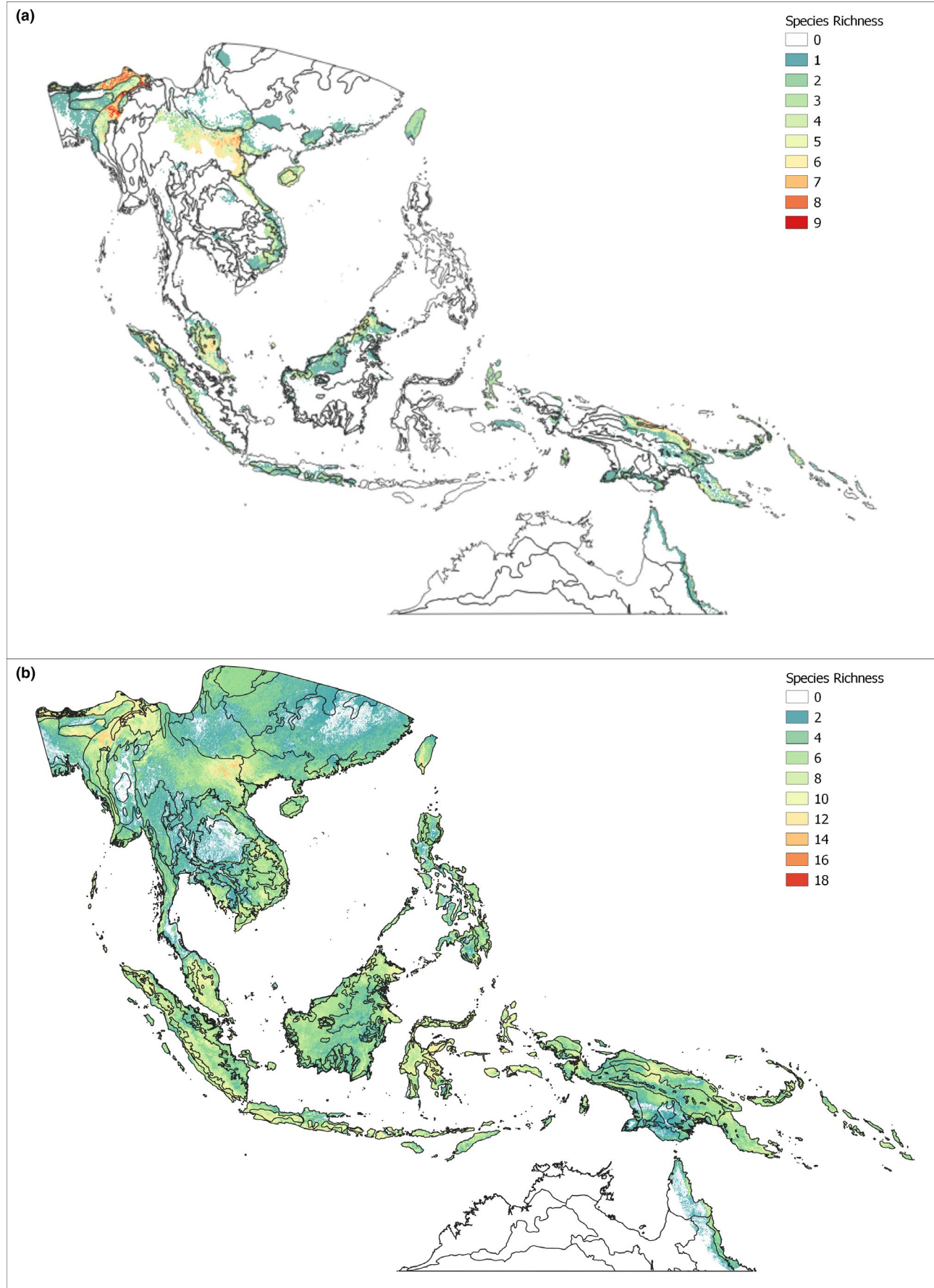


FIGURE 3 Species richness maps based on species that passed the criteria. (a), species richness with background points constricted to countries and ecoregions in which occurrence records were present; (b), species richness based on analyses using the full study area as background

TABLE 1 Partial assessment of conservation status of wild bananas based on IUCN criterion B. EOO, extent of occurrence; AOO, area of occupancy. IUCN categories are determined and designated as follows: LC or NT, least concern or near-threatened; VU, vulnerable; EN, endangered

| Taxon | EOO | EOO Category | AOO | AOO Category | % in protected area | Criterion B Category |
|--------------------------------------------------|-----------|--------------|-----|--------------|---------------------|----------------------|
| <i>Musa acuminata</i> subsp. <i>acuminata</i> | 515140.8 | LC or NT | 160 | LC or NT | 12.82 | LC or NT |
| <i>Musa acuminata</i> subsp. <i>burmannica</i> | 455130.6 | LC or NT | 84 | LC or NT | 18.75 | LC or NT |
| <i>Musa acuminata</i> subsp. <i>errans</i> | 141381.5 | LC or NT | 44 | VU | 40.00 | VU |
| <i>Musa acuminata</i> subsp. <i>halabanensis</i> | 14369.8 | VU | 32 | VU | 25.00 | VU |
| <i>Musa acuminata</i> subsp. <i>malaccensis</i> | 220033.2 | LC or NT | 196 | LC or NT | 21.95 | LC or NT |
| <i>Musa acuminata</i> subsp. <i>microcarpa</i> | 470674.8 | LC or NT | 204 | LC or NT | 23.68 | LC or NT |
| <i>Musa acuminata</i> subsp. <i>siamea</i> | 106821.4 | LC or NT | 48 | LC or NT | 36.36 | LC or NT |
| <i>Musa acuminata</i> subsp. <i>truncata</i> | 35854.6 | LC or NT | 88 | LC or NT | 40.00 | LC or NT |
| <i>Musa acuminata</i> var. <i>sumatrana</i> | 87994.5 | LC or NT | 56 | LC or NT | 23.08 | LC or NT |
| <i>Musa acuminata</i> var. <i>tomentosa</i> | 95077 | LC or NT | 56 | LC or NT | 14.29 | LC or NT |
| <i>Musa aurantiaca</i> | 49253.2 | LC or NT | 80 | LC or NT | 13.33 | LC or NT |
| <i>Musa bakeri</i> | 8488.3 | LC or NT | 60 | LC or NT | 9.09 | LC or NT |
| <i>Musa balbisiana</i> var. <i>balbisiana</i> | 1109163.2 | LC or NT | 208 | LC or NT | 11.11 | LC or NT |
| <i>Musa banksii</i> | 997835.5 | LC or NT | 592 | LC or NT | 16.82 | LC or NT |
| <i>Musa basjoo</i> | 1043474.3 | LC or NT | 60 | LC or NT | 0.00 | LC or NT |
| <i>Musa beccarii</i> | 83512.1 | LC or NT | 92 | LC or NT | 30.00 | LC or NT |
| <i>Musa boman</i> | 5603.1 | VU | 28 | VU | 0.00 | VU |
| <i>Musa borneensis</i> | 377728.7 | LC or NT | 192 | LC or NT | 15.38 | LC or NT |
| <i>Musa bukenis</i> | 1762.5 | VU | 56 | VU | 0.00 | VU |
| <i>Musa campestris</i> | 109055.2 | LC or NT | 188 | LC or NT | 23.53 | LC or NT |
| <i>Musa cheesmanii</i> | 100348 | LC or NT | 104 | LC or NT | 7.69 | LC or NT |
| <i>Musa coccinea</i> | 157475.6 | LC or NT | 28 | VU | 28.57 | VU |
| <i>Musa exotica</i> | 3455.4 | EN | 20 | EN | 60.00 | EN |
| <i>Musa flaviflora</i> | 64796.9 | LC or NT | 68 | LC or NT | 0.00 | LC or NT |
| <i>Musa gracilis</i> | 62028 | LC or NT | 120 | LC or NT | 37.04 | LC or NT |
| <i>Musa griersonii</i> | 6400.8 | LC or NT | 60 | LC or NT | 27.27 | LC or NT |
| <i>Musa hirta</i> | 23862.6 | LC or NT | 56 | LC or NT | 8.33 | LC or NT |
| <i>Musa ingens</i> | 67236.3 | LC or NT | 56 | LC or NT | 0.00 | LC or NT |
| <i>Musa itinerans</i> | 2269688.1 | LC or NT | 524 | LC or NT | 13.59 | LC or NT |
| <i>Musa jackeyi</i> | 1852.9 | VU | 52 | VU | 50.00 | VU |
| <i>Musa johnsii</i> | 52.6 | EN | 20 | EN | 0.00 | EN |
| <i>Musa kamengensis</i> | 1247.7 | VU | 28 | VU | 16.67 | VU |
| <i>Musa laterita</i> | 892676.6 | LC or NT | 132 | LC or NT | 13.33 | LC or NT |
| <i>Musa lawitiensis</i> | 135679 | LC or NT | 64 | LC or NT | 12.50 | LC or NT |
| <i>Musa lolodensis</i> | 191355.1 | LC or NT | 60 | LC or NT | 13.33 | LC or NT |
| <i>Musa lutea</i> | 28194.9 | LC or NT | 36 | VU | 12.50 | VU |
| <i>Musa maclayi</i> | 146308.6 | LC or NT | 264 | LC or NT | 1.75 | LC or NT |
| <i>Musa markkuana</i> | 10987.8 | VU | 20 | EN | 0.00 | EN |
| <i>Musa markkui</i> | 46 | EN | 20 | EN | 50.00 | EN |
| <i>Musa monticola</i> | 1632.4 | VU | 52 | VU | 25.00 | VU |
| <i>Musa nagensium</i> | 195887.9 | LC or NT | 56 | LC or NT | 7.69 | LC or NT |
| <i>Musa ornata</i> | 352670.1 | LC or NT | 80 | LC or NT | 10.53 | LC or NT |
| <i>Musa paracoccinea</i> | 12854.8 | LC or NT | 76 | LC or NT | 0.00 | LC or NT |

(Continues)

TABLE 1 (Continued)

| Taxon | EOO | EOO Category | AOO | AOO Category | % in protected area | Criterion B Category |
|-------------------------------------------------|----------|--------------|-----|--------------|---------------------|----------------------|
| <i>Musa peekelii</i> subsp. <i>angustigemma</i> | 9794.1 | LC or NT | 68 | LC or NT | 0.00 | LC or NT |
| <i>Musa peekelii</i> subsp. <i>peekelii</i> | 37670.7 | LC or NT | 20 | EN | 0.00 | EN |
| <i>Musa puspanjalae</i> | 1729.9 | EN | 16 | EN | 0.00 | EN |
| <i>Musa rosea</i> | 30.4 | EN | 20 | EN | 50.00 | EN |
| <i>Musa rubra</i> | 994752.6 | LC or NT | 80 | LC or NT | 27.78 | LC or NT |
| <i>Musa salaccensis</i> | 285796.4 | LC or NT | 76 | LC or NT | 35.29 | LC or NT |
| <i>Musa sanguinea</i> | 211793.9 | LC or NT | 64 | LC or NT | 14.29 | LC or NT |
| <i>Musa schizocarpa</i> | 427144.4 | LC or NT | 284 | LC or NT | 3.64 | LC or NT |
| <i>Musa sikkimensis</i> | 87827.1 | LC or NT | 44 | VU | 11.11 | VU |
| <i>Musa splendida</i> | 7126.9 | VU | 16 | EN | 33.33 | EN |
| <i>Musa textilis</i> | 76191.3 | LC or NT | 56 | LC or NT | 36.36 | LC or NT |
| <i>Musa thomsonii</i> | 284888.5 | LC or NT | 24 | VU | 16.67 | VU |
| <i>Musa tuberculata</i> | 521.4 | EN | 16 | EN | 25.00 | EN |
| <i>Musa velutina</i> | 104846.3 | LC or NT | 76 | LC or NT | 11.76 | LC or NT |
| <i>Musa violascens</i> | 76338.5 | LC or NT | 108 | LC or NT | 25.00 | LC or NT |
| <i>Musa yunnanensis</i> | 94316 | LC or NT | 68 | LC or NT | 7.14 | LC or NT |

species and species records recorded in the northern Indo-Burmese region, this region is also indicated as environmentally most suitable for most banana species both in the full and in the restricted background analyses. Especially areas within the Eastern Himalayan broadleaf forests and Mizoram–Manipur–Kachin rain forest ecoregions of northeast India are highly suitable. Interestingly, the northern Indo-Burmese region was previously marked as area of origin of the genus *Musa* (Janssens et al., 2016), a pattern that was also found in *Impatiens* L. species (Janssens et al., 2009) and likely applies for many other genera. This biodiversity hotspot is in general characterized by a high species richness and is believed to contain the sixth most endemic genera and species in the world (Mittermeier et al., 2011). A drawback of restricting the background to countries where occurrences have been found is that countries that might have a suitable environment are completely ignored. Therefore, we did an additional analysis using the full study area as background. This resulted in similar patterns but shows additional regions where banana species are likely to be found. Northern Myanmar, parts of Laos and Sulawesi are indicated as environmentally highly suitable areas. Interestingly, several banana species can be found in these areas but were either not georeferenced or were just recently recorded and not included yet in this study (personal communication G. Sachter-Smith). These distribution models are based on environmental suitability across the full study area and do not include the dispersal limitation and might thus lead to an overestimation of its real distribution. For both restricted and full background approaches, potential distribution might be further impeded by other variables not included in this study (e.g. soil type, soil characteristics, habitat degradation, solar radiation). Because the geological history of the study area only allowed members of the Musaceae to colonize the region east of Wallace's line in the late Miocene, species might likely not have colonized some

areas yet, even though the environment is highly suitable (Janssens et al., 2016). Considering climate change, areas that are climatically suitable for wild bananas might shift or completely disappear in the future. Using projections of future climate can give an indication of expansion or reduction of suitable areas for wild banana species, further improving the efficacy of distribution models as tool for conservation planning. Similar analyses have been done on *Coffea arabica* L., for example, and the models showed that climate change might result in a reduction in suitable area of up to almost 100% of indigenous *Arabica* by 2080 (Davis et al., 2012).

While differences in environmental tolerance exist between species, *Musa* species occupy a rather limited range of temperatures in subtropical and tropical areas (BIO2). Day temperatures of above 37°C can damage the plant (BIO5), no species is tolerant for long periods of frost (BIO6) and cold temperatures cease growth, normal fruit development, and can induce chilling damage and necrosis of tissues (Nelson et al., 2006; Office of the Gene Technology Regulator, 2016; Salau et al., 2016). Drought is considered to be a major limiting abiotic factor in banana production (van Asten et al., 2011; Carr, 2009). Bananas require a high amount of annual precipitation ranging between 1,100 and 2,690 mm evenly distribution throughout the year (BIO12) (van Asten et al., 2011; Robinson & Alberts, 1986). Longer periods of dry soil might lead to root tip death and increased susceptibility to pathogens (BIO14, BIO18) (Nelson et al., 2006; Ochola et al., 2015; Turner et al., 2007). These requirements largely coincide with these of lowland tropical rain forests that are here confirmed to be most environmentally suitable for most bananas in this study. However, highland areas (>900 m) should not be ignored as some wild and cultivated species are typically found there (e.g. *M. cheesmanii* N.W.Simmonds, *M. sikkimensis* Kurz, *M. ingens* N.W.Simmonds, *M. nagensium* Prain, East African Highland Bananas).

TABLE 2 Conservation gap analysis results. FCS_{ex} , final conservation score ex situ; FCS_{in} , final conservation score in situ. FCS_c , combined final conservation score. Priorities range from low, LP ($FCS_c > 50$) to medium, MP ($25 < FCS_c < 50$) to high, HP ($FCS_c < 25$)

| Taxon | Total records | Total ex situ germplasm (G) | Total reference (H) | FCS_{ex} | FCS_{in} | FCS_c | Priority category |
|--------------------------------------------------|---------------|-----------------------------|---------------------|------------|------------|---------|-------------------|
| <i>Musa acuminata</i> subsp. <i>acuminata</i> | 46.00 | 13.00 | 33.00 | 23.99 | 41.00 | 32.49 | MP |
| <i>Musa acuminata</i> subsp. <i>burmannica</i> | 25.00 | 1.00 | 24.00 | 38.66 | 40.64 | 39.65 | MP |
| <i>Musa acuminata</i> subsp. <i>errans</i> | 11.00 | | 11.00 | 0.00 | 51.46 | 25.73 | MP |
| <i>Musa acuminata</i> subsp. <i>halabanensis</i> | 8.00 | | 8.00 | 0.00 | 49.78 | 24.89 | HP |
| <i>Musa acuminata</i> subsp. <i>malaccensis</i> | 52.00 | 11.00 | 41.00 | 28.45 | 37.60 | 33.03 | MP |
| <i>Musa acuminata</i> subsp. <i>microcarpa</i> | 51.00 | 4.00 | 47.00 | 16.01 | 43.17 | 29.59 | MP |
| <i>Musa acuminata</i> subsp. <i>siamea</i> | 12.00 | 1.00 | 11.00 | 26.92 | 57.45 | 42.19 | MP |
| <i>Musa acuminata</i> subsp. <i>truncata</i> | 25.00 | 8.00 | 17.00 | 59.87 | 56.52 | 58.20 | LP |
| <i>Musa acuminata</i> var. <i>sumatrana</i> | 14.00 | | 14.00 | 0.00 | 47.45 | 23.73 | HP |
| <i>Musa acuminata</i> var. <i>tomentosa</i> | 14.00 | | 14.00 | 0.00 | 41.77 | 20.88 | HP |
| <i>Musa aurantiaca</i> | 20.00 | | 20.00 | 0.00 | 42.19 | 21.10 | HP |
| <i>Musa bakeri</i> | 30.00 | 25.00 | 5.00 | 94.44 | 46.67 | 70.56 | LP |
| <i>Musa balbisiana</i> var. <i>balbisiana</i> | 58.00 | 17.00 | 41.00 | 32.50 | 35.11 | 33.81 | MP |
| <i>Musa banksii</i> | 164.00 | | 164.00 | 0.00 | 45.39 | 22.70 | HP |
| <i>Musa basjoo</i> | 15.00 | | 15.00 | 0.00 | 23.92 | 11.96 | HP |
| <i>Musa beccarii</i> | 24.00 | | 24.00 | 0.00 | 50.94 | 25.47 | MP |
| <i>Musa boman</i> | 8.00 | | 8.00 | 0.00 | 16.76 | 8.38 | HP |
| <i>Musa borneensis</i> | 49.00 | 4.00 | 45.00 | 46.58 | 42.97 | 44.78 | MP |
| <i>Musa bukenis</i> | 15.00 | | 15.00 | 0.00 | 0.00 | 0.00 | HP |
| <i>Musa campestris</i> | 48.00 | | 48.00 | 0.00 | 46.37 | 23.19 | HP |
| <i>Musa cheesmanii</i> | 26.00 | | 26.00 | 0.00 | 40.13 | 20.07 | HP |
| <i>Musa coccinea</i> | 7.00 | 1.00 | 6.00 | 26.35 | 44.65 | 35.50 | MP |
| <i>Musa exotica</i> | 5.00 | | 5.00 | 0.00 | 63.75 | 31.87 | MP |
| <i>Musa flaviflora</i> | 17.00 | | 17.00 | 0.00 | 30.49 | 15.25 | HP |
| <i>Musa gracilis</i> | 31.00 | 11.00 | 20.00 | 74.80 | 42.13 | 58.46 | LP |
| <i>Musa griersonii</i> | 16.00 | | 16.00 | 0.00 | 49.71 | 24.86 | HP |
| <i>Musa hirta</i> | 14.00 | | 14.00 | 0.00 | 33.56 | 16.78 | HP |
| <i>Musa ingens</i> | 14.00 | | 14.00 | 0.00 | 25.45 | 12.73 | HP |
| <i>Musa itinerans</i> | 157.00 | 38.00 | 119.00 | 24.77 | 42.56 | 33.66 | MP |
| <i>Musa jackeyi</i> | 13.00 | | 13.00 | 0.00 | 74.66 | 37.33 | MP |
| <i>Musa johnsii</i> | 5.00 | | 5.00 | 0.00 | 59.25 | 29.63 | MP |
| <i>Musa kamengensis</i> | 7.00 | | 7.00 | 0.00 | 46.15 | 23.08 | HP |
| <i>Musa laterita</i> | 33.00 | | 33.00 | 0.00 | 29.36 | 14.68 | HP |
| <i>Musa lawitiensis</i> | 16.00 | | 16.00 | 0.00 | 44.14 | 22.07 | HP |
| <i>Musa lolodensis</i> | 16.00 | | 16.00 | 0.00 | 33.01 | 16.50 | HP |
| <i>Musa lutea</i> | 10.00 | | 10.00 | 0.00 | 38.83 | 19.41 | HP |
| <i>Musa maclayi</i> | 71.00 | | 71.00 | 0.00 | 27.67 | 13.83 | HP |
| <i>Musa markkuana</i> | 5.00 | | 5.00 | 0.00 | 65.69 | 32.84 | MP |
| <i>Musa markkui</i> | 5.00 | | 5.00 | 0.00 | 61.27 | 30.63 | MP |
| <i>Musa monticola</i> | 13.00 | | 13.00 | 0.00 | 43.11 | 21.55 | HP |
| <i>Musa nagensium</i> | 16.00 | | 16.00 | 0.00 | 52.71 | 26.35 | MP |
| <i>Musa ornata</i> | 20.00 | | 20.00 | 0.00 | 47.69 | 23.84 | HP |
| <i>Musa paracoccinea</i> | 22.00 | | 22.00 | 0.00 | 50.47 | 25.24 | MP |

(Continues)

TABLE 2 (Continued)

| Taxon | Total records | Total ex situ germplasm (G) | Total reference (H) | FCSex | FCSin | FCSc | Priority category |
|-------------------------------------------------|---------------|-----------------------------|---------------------|-------|-------|-------|-------------------|
| <i>Musa peekelii</i> subsp. <i>angustigemma</i> | 21.00 | | 21.00 | 0.00 | 17.89 | 8.94 | HP |
| <i>Musa peekelii</i> subsp. <i>peekelii</i> | 5.00 | | 5.00 | 0.00 | 45.53 | 22.77 | HP |
| <i>Musa puspanjaliae</i> | 5.00 | | 5.00 | 0.00 | 27.41 | 13.70 | HP |
| <i>Musa rosea</i> | 6.00 | | 6.00 | 0.00 | 53.27 | 26.63 | MP |
| <i>Musa rubra</i> | 20.00 | | 20.00 | 0.00 | 49.18 | 24.59 | HP |
| <i>Musa salaccensis</i> | 19.00 | | 19.00 | 0.00 | 42.35 | 21.18 | HP |
| <i>Musa sanguinea</i> | 16.00 | | 16.00 | 0.00 | 40.65 | 20.33 | HP |
| <i>Musa schizocarpa</i> | 78.00 | | 78.00 | 0.00 | 27.17 | 13.59 | HP |
| <i>Musa sikkimensis</i> | 13.00 | | 13.00 | 0.00 | 55.30 | 27.65 | MP |
| <i>Musa splendida</i> | 5.00 | | 5.00 | 0.00 | 24.79 | 12.40 | HP |
| <i>Musa textilis</i> | 16.00 | | 16.00 | 0.00 | 39.47 | 19.73 | HP |
| <i>Musa thomsonii</i> | 6.00 | | 6.00 | 0.00 | 38.33 | 19.17 | HP |
| <i>Musa tuberculata</i> | 5.00 | | 5.00 | 0.00 | 35.97 | 17.98 | HP |
| <i>Musa velutina</i> | 19.00 | | 19.00 | 0.00 | 37.51 | 18.76 | HP |
| <i>Musa violascens</i> | 30.00 | 13.00 | 17.00 | 47.42 | 40.57 | 43.99 | MP |
| <i>Musa yunnanensis</i> | 19.00 | | 19.00 | 0.00 | 17.46 | 8.73 | HP |

Based on occurrences, our results suggest that some wild species might be more drought tolerant than others. Especially *M. acuminata* subsp. *siamea* seems to occur in more dry areas, with a minimum annual rainfall of 907 mm and an average annual rainfall of 1,205 mm. Some *M. yunnanensis* Häkkinen & H.Wang and *M. itinerans* occurrences were also located in more dry areas, with an average annual rainfall of 1,380 mm and 1,825 mm and a minimum annual rainfall of 952 and 907 mm, respectively (Appendix S1—sheet 4). In the light of climate change and the quest for searching superior alleles against drought stress, these results suggest areas where these species occur should be further explored and where more germplasm should be collected from. In these cases, central parts of the Northern Indochina subtropical forests, the montane rain forests and parts of dry forests of northern Thailand and western Laos.

4.3 | Risk assessment and conservation status

Our extinction risk assessment with ConR suggests that nine wild *Musa* species are currently endangered while 11 are vulnerable and should be prioritized for conservation. For a proper assessment, information on a continuous decrease in time in the extent of occurrence (EOO), the area of occupancy (AOO) and the number of mature individuals and locations are necessary in combination with information of habitat fragmentation rate and decline in habitat quality (IUCN Standards & Petitions Committee, 2017). This information is often unavailable and consequently not implemented in the “conR” package (Dauby et al., 2017). While many of the occurrence records included in this study were sampled in the last two to three decennia, others were collected much earlier (e.g. Argent, 1976; Hotta, 1947; Simmonds, 1956). Including older occurrence records might lead to

an overestimation of the current distribution, as these populations are more likely to have gone extinct in contrast to more recently sampled populations.

To date, at least one wild banana native to north-eastern Queensland, *Musa fitzalanii* F.Muell., has been reported as extinct or critically endangered in the wild. It has only been reported from a type specimen in the herbarium of Queensland (Pollefeys et al., 2004). Another example is *M. mannii* H.Wendl. ex Baker, which was thought to be extinct for over 120 years but was recently rediscovered in north-eastern India, collected ex situ and listed as critically endangered in the wild (Häkkinen & Väre, 2008; Joe et al., 2014).

The extinction risk assessment (IUCN criterion B) suggests that, based on the size of their distribution, 39 wild species are currently listed as of least concern or as near-threatened. As only 5% of wild banana species were indicated as sufficiently conserved or of low priority for additional in and ex situ conservation, these species are prone to become threatened in the near future. Eleven out of 20 species that were classified as endangered (EN) or vulnerable (VU) in the risk assessment were marked as high priority for further conservation in the gap analysis based on their final conservation score. Additionally, none of these species except *M. coccinea* Andrews had georeferenced records that are conserved ex situ, making higher conservation efforts even more critical for those species. Especially because assessment of in situ conservation status assumes that plants in protected areas are effectively protected, occurrence in protected area does not necessarily mean that the taxon of interest is being protected. The level of in situ conservation priority is therefore likely an underestimation compared to the reality as protected areas include both strictly and less strictly protected areas, as well as multiuse protected areas with zones of integrated management where some species—bananas in this case—are not actively protected (Ferraro

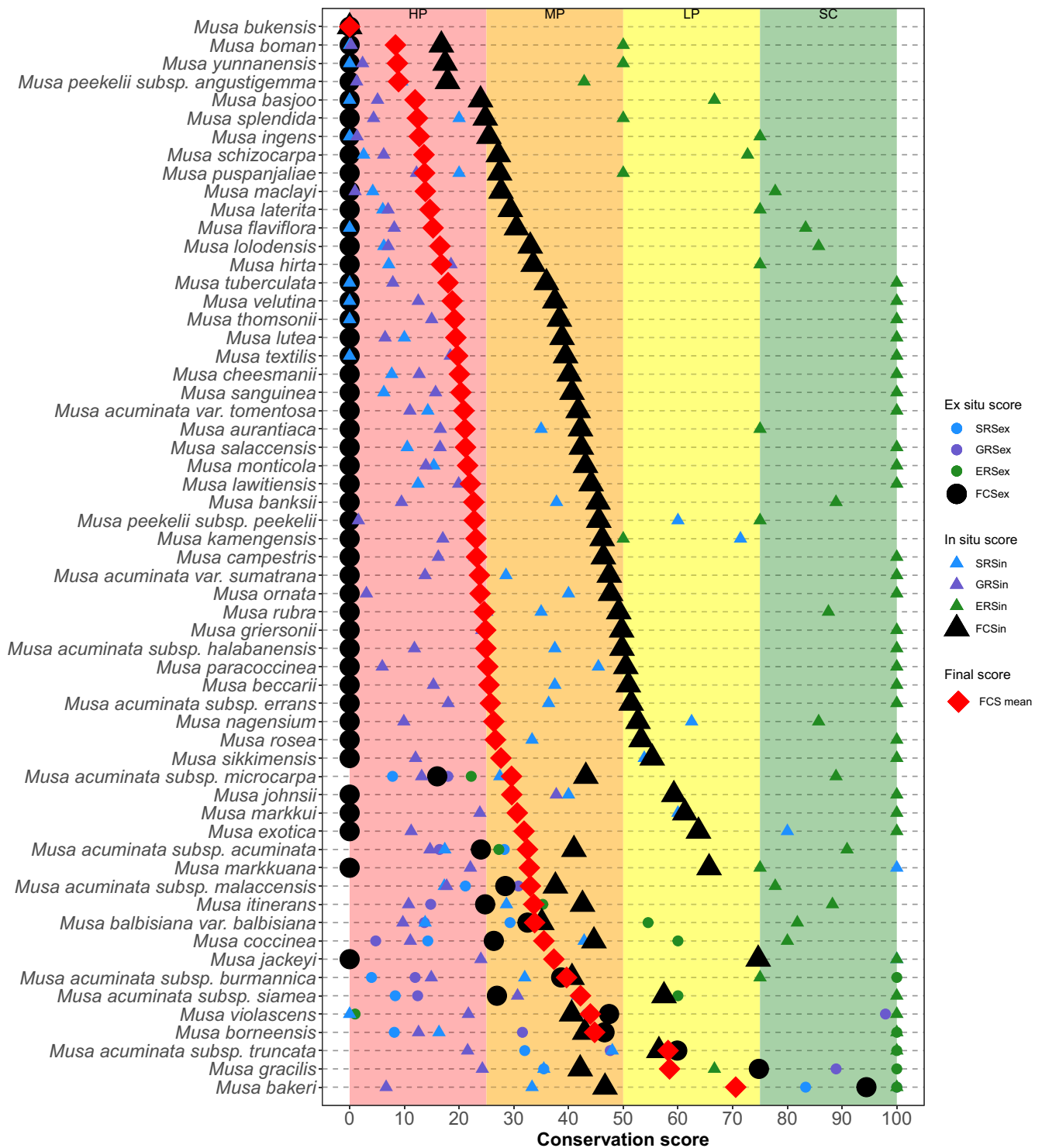


FIGURE 4 Conservation score assessment of wild *Musa* species. SRS_{ex} , sampling representativeness score ex situ; GRS_{ex} , geographical representativeness score ex situ; ERS_{ex} , ecological representativeness score ex situ; FCS_{ex} , final conservation score ex situ; SRS_{in} , sampling representativeness score in situ; GRS_{in} , geographical representativeness score in situ; ERS_{in} , ecological representativeness score in situ; FCS_{in} , final conservation score in situ; FCS_{mean} , combined final conservation score

et al., 2013). The distribution area of the species that are of high priority for additional in situ conservation could be indicative for areas that require additional in situ conservation plans. In Oceania, two species (*M. boman* Argent, *M. peekelii* subsp. *angustigemma* (N.W.Simmonds) Argent) from the Northern New Guinea rain forests and one (*M.*

bukensis) from the Solomon island rain forest are currently not or barely conserved in situ. High priority for additional in situ conservation was also found for *Musa splendida* A.Chev. (Lai Chau province, Vietnam) and *M. yunnanensis* (Yunnan province, China), both situated in the Northern Indochina subtropical forests ecoregion.

While not all ex situ collections (and coordinates) are currently available in online databases for many species (Khoury et al., 2019), we had access to the information of the International *Musa* germplasm Transit Centre (ITC), the largest *Musa* germplasm collection in the world. Still, there are big differences in ex and in situ conservation scores (9.17 vs 41.63, respectively), suggesting that many wild banana species, and this also accounts for other CWR, are in need for additional ex situ conservation (Castañeda-Álvarez et al., 2016). There are many local banana collections in the world (Bioversity International, 2019), but most focus on preserving cultivars in their collections rather than wild species. While a high number of wild accessions are present in some collections (e.g. UPLB in the Philippines, RIF in Indonesia, NTBG in Hawaii), collection-specific information and georeferenced localities are either unknown or unavailable for the public.

4.4 | Considerations on species importance for crop improvement

Because wild banana species belong to the same genus as the crop, they can all be considered as CWR. However, it is unlikely that all have the same value for crop improvement. As cultivated bananas are vegetatively propagated and typically have seedless fruits, breeding effort, time and intensive resources are required to develop more resistant varieties (Batte et al., 2019; Brown et al., 2017; Ortiz, 2013; Ortiz & Swennen, 2014). For this reason, the use of CWR has been more successful in conventional breeding programmes for crops such as maize, rice and wheat that are not limited to clonal propagation (Dempewolf et al., 2017). However, new molecular techniques such as genomic prediction in banana might facilitate the process and will further increase the importance of banana CWR (Nyine et al., 2018). Moreover, cultivated bananas are derived from hybridization between *Musa acuminata* subspecies (A genome) and *M. balbisiana* (B genome), *M. schizocarpa* in some cultivars (S genome) and some *Australimusa* species (T genome) (D'Hont et al., 2000). This indicates that some species might be more interesting for breeding programmes than others. For example, cross-compatibility has been assessed between *M. acuminata* subspecies, *M. balbisiana* and species with the same number of chromosomes (sections *Musa* and *Rhodochlamys*, $2n = 22$), such as *M. ornata* Roxb., *M. laterita* Cheesman and *M. velutina* H.Wendl. & Drude, and very limited cross-compatibility was found with species from the *Australimusa* section (Andersson & de Vicente, 2010; D'Hont et al., 2000; Shepherd, 1999).

In this study, we assessed 25 species of the former *Musa* section, including 10 *M. acuminata* subspecies, *M. banksii* and *M. balbisiana* that have contributed to modern breeding programmes (Brown et al., 2017). On average, *M. acuminata* subspecies, *M. banksii* and *M. balbisiana* had a conservation score of 32.24, indicating that conservation efforts have been already successful but still need to be intensified. Nine members of the former *Rhodochlamys* section were included and seven are of high priority for further conservation (with an average FCS_c of 23.71). Because

of their high tolerance to drought and resistance to *Fusarium* wilt and leaf spot disease, more attention needs to be given to their conservation (Uma et al., 2006). Members of the *Australimusa* section and potential progenitors of the Fe'i bananas are insufficiently conserved (FCS_c of 18.38 for the section) and 10 out of 13 included species are of high priority for further conservation. Here, *M. bukensis* is indicated to be absent in germplasm collections and in protected area. Seeds of this species were, however, recently collected and conserved ex situ at Meise Botanic Garden (Sardos et al., 2018).

5 | CONCLUSION

While bananas are one of the most important fruit crops and many efforts exist in conserving large numbers of varieties, both in and ex situ conservation of their wild relatives is limited. With a less stable future climate and large deforestation, collection needs to be accelerated for the conservation of species and important adaptive traits for crop improvement. We find that highest *Musa* species richness is likely found in the north-eastern states of India and the south China–northern Vietnam border. Based on a partial IUCN assessment, 20 out of 59 assessed wild species are considered vulnerable or endangered. The ex situ conservation assessment indicated that three species are of low priority for further conservation while 48 are of high priority because they are in need for further collecting or completely absent in germplasm collections. Thirteen out of 59 species are of low priority for additional in situ conservation, though it is hard to assess whether bananas are actively being protected and whether the conserved plants are good representatives of the gene pool of their species. Little is still known about many wild banana species and specific information on their distribution (e.g. georeferenced localities) is often scarce or insufficient for generating reliable SDMs. Hence, there is a great need for supplementary field missions. Based on the species distribution and species richness maps that are provided, researchers have an indication where new individuals could be located. Therefore, our approach forms a basis for developing a proper collecting strategy. In the context of climate change, a follow-up study assessing the effect of different climate scenarios (according to the IPCC) on distribution of wild *Musa* species might provide additional information on their conservation threat.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Appendix S1 is deposited in the online repository, and it can be accessed through the link <https://doi.org/10.5061/dryad.xpnvx0kbs>.

ORCID

Arne Mertens  <https://orcid.org/0000-0003-3272-9464>
 Rony Swennen  <https://orcid.org/0000-0002-5258-9043>
 Nina Rønsted  <https://orcid.org/0000-0002-2002-5809>
 Filip Vandeloos  <https://orcid.org/0000-0003-4591-5557>
 Bart Panis  <https://orcid.org/0000-0001-6717-947X>
 Dang Toan Vu  <https://orcid.org/0000-0003-3589-6428>

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Biosketch

Arne's research focuses on wild species of banana (*Musa* spp.). With global change and the increasing world population, breeding and cultivation of bananas have been put under serious pressure. More research is needed to discover novel alleles in wild species as they hold the key to resistance against various diseases and abiotic stresses. They look at the native distribution area of wild species with a focus on *Musa balbisiana* and evaluate the genetic resources available in ex situ conservation programmes. Arne is additionally interested and involved in projects that assess the impact of mating system, floral morphology and pollinators on diversification.

<https://www.biw.kuleuven.be/biosyst/plantenbiotechniek/tropical>

<https://www.plantentuinmeise.be/en/pQw2QCQ/plants-for-society>

Author contributions: S.R., V.F., V.D.T. and J.S.B. conceived the idea of the study; M.A., P.B., S.G., V.D.T. and J.S.B. collected the data; M.A. analysed the data; M.A. wrote the manuscript with continuous support and critical feedback from S.R., V.F. and J.S.B. and additional input from R.N., P.B., S.G. and V.D.T.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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