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ORIGINAL PAPER

From keystone species to conservation: conservation genetics of wax palm *Ceroxylon quindiuense* in the largest wild populations of Colombia and selected neighboring *ex situ* plant collections

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Abstract

The cloud forest of the Andean Region contains a high biodiversity. Unfortunately, human land use has caused most of the forest to become fragmented, negatively impacting many species due to the reduction of and constant change within the local habitat. In Colombia, these fragmentation triggers can include agriculture, livestock, and corridors for tourism. Conservation strategies focusing on keystone species could have more impact and better results to recover ecosystem dynamics. The wax palm *Ceroxylon quindiuense* (*C. quindiuense*) is an endemic and keystone species in cloud forests with a distribution across the three cordilleras of Colombia. Despite its ecological, economic and social importance, most forests of *C. quindiuense* are endangered; the most severely affected residing in small isolated populations in Central Cordillera. Nevertheless, these populations seem to retain a high genetic diversity. Because of this, the goal of conservation strategies should focus on retaining genetic diversity instead of increasing it. Because it can take as long as 80 years for *C. quindiuense* to reach maturity, our approach entails the introduction of juveniles (around 30 years) with genetic profiles similar to wild populations in order to augment population size, connect isolated populations, and avoid outbreeding. We evaluated the genetic makeup of three neighboring *ex situ* collections of living palms and compared them with the genetic profile of three wild populations of Central Cordillera. Multivariate analysis was used to assess patterns of genetic similarity and assign individuals to infer genetic clusters between collections and wild populations. Expected heterozygosity (He) of *ex situ* collections was lower (0.56) than wild populations (0.63), and the percentage of private alleles was higher in the wild populations (25%) than *ex situ* collections (10%). Collections Milan and Botanic Garden show genetic similarity with the Cocora and La Linea populations while the Toche and Roso collections were the most genetically distinct among the

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Extended author information available on the last page of the article

ones studied. Our results are that conservation programs should consider each population as a different evolutionary unit and protect them as such.

Keywords *Ceroxylon quindiuense* · Conservation genetics · *Ex situ* collections · Augmentation · Wild populations

Introduction

The damaging effects of human activities on wild populations such as reduction of habitat, poaching and deforestation are well-known and strategies to mitigate these effects are in progress for many of the species (Santos et al. 2016). One such strategy along with habitat restoration, is the recovery and maintenance of the genetic diversity of individual populations (Kashimshetty et al. 2015; Mijangos et al. 2015; Santos et al. 2016). In order to preserve the adaptive potential of species to changing environments such as in tropical regions a powerful conservation strategy is to focus on maintaining the genetic diversity of such species. (Ruber et al. 2001; Mijangos et al. 2015; Santos et al. 2016). However, there could be some pitfalls to this approach if implemented without knowledge of the ecological and biological characteristics of each individual species. These include (1) Introducing different genetic profiles that could lead to contamination with foreign alleles and (2) Introducing closely related individuals which could lead to increased endogamy (Kashimshetty et al. 2015). One of the reasons why most conservation strategies have failed is when implemented broadly without taking into account the underlying differences in life history traits (LHT) between distinct species. Therefore, programs which include species LHT, ecological status and preservation of genetic diversity are needed to improve conservation practices.

The tropical mountain cloud forest is the ecosystem with the highest biodiversity globally (Brummit and Lughada 2003). The cloud forest encompasses 11.7% of mountain tropical forests and represents 2.5% of the area of forests globally (Bubb et al. 2004). In the 1980s, the highly endangered central American and Caribbean cloud forests were disappearing more rapidly than any other type of forest (LaBastille and Pool 1978; Bruijnzeel et al. 2010; Armenteras et al. 2017). Colombia has been known as one of the most megadiverse countries in the world, and economic activities have centered in the Andean region where cloud forests subsist. Since pre-Colombian times, this area has undergone large transformations of the natural ecosystem primarily due to exponential human population growth and extensive land use occurring throughout the eighteenth and nineteenth centuries (Etter and Van Wyngaarden 2000). The demands of the growing economic market have transformed over 90% of the habitats into pastures and crops, and in later decades, this came along with lowered governability and the expansion of illicit crops (Etter and Van Wyngaarden 2000; Doumenge et al. 1995; Armenteras et al. 2007, 2017). Despite being poorly studied, the effects of deforestation in the tropical mountain cloud forests have been shown to be highly detrimental (Svenning 1998; Goerner et al. 2007; Svenning et al. 2009). Even though, the landscape of the Colombian Andes still contains small resilient fragments of forest that could hold the specific genetic pool from which modern repopulation strategies could derive.

Ceroxylon quindiuense (*C. quindiuense*), the Colombian national tree, is an endemic and umbrella species in cloud forests of the Tropical Andes of Colombia and Peru and grows in dense but isolated populations along the three cordilleras of Colombia (Sanín and Galeano 2011; Sanín et al. 2013). Unfortunately, threats to this species are numerous and the conservation status is endangered (EN) according to the IUCN criteria (IUCN 1987; Galeano and Bernal 2005).

The leaves are used for many religious celebrations, the stems for constructions and extracting wax and the juveniles are used as food for live-stock among many other uses. Pastures and crop plantation have taken over the landscape, replacing natural forest and leading to reduced wild populations and exposing juveniles to direct light which causes the leaves to burn. Additionally, a more recent threat to the successful growth of these habitats is the massive increase in local tourism (Bernal et al. 2015). The remaining individuals have challenging conditions for growth, including this species' long-life cycle. First, it takes around 3 years for seedlings to emerge and produce the first leaves; this is a small plant with a height no larger than 20 cm which are easily confused with grass. This can mean a higher susceptibility to herbivory and damaging direct light exposure. Second, individuals expand around 30 years to become juveniles with a height between 12 and 19 m (Bernal and Sanín 2013). Although this is large enough for the plant to survive and grow, it takes another 50 years to achieve the reproductive adult stage (Bernal and Sanín 2013; Sanín et al. 2013). Third, although *C. quindiuense* still retains a high genetic diversity in many populations found within the three Cordilleras, these forests remain isolated and highly structured (i.e. discrete populations) which could represent a drastic loss of genetic diversity in the future (Sanín et al. 2013; Bernal et al. 2015).

Our working model includes the *C. quindiuense* populations in the Cocora-Quindio region of Colombia (Quindío wax palm). Cocora holds one of the most fragile populations of *C. quindiuense.* After colonization and up to the mid-twentieth century approximately, the distribution of the species became scattered throughout Central Cordillera. Nevertheless, the Cocora population today possesses a high genetic diversity despite the high structure, reproductive isolation, small remaining populations and reduction of gene flow among populations, but still the persistence of the species is threatened (Sanín 2013; Sanín et al. 2017). Despite the ecological and economic importance of *C. quindiuense*, only a few conservation studies have approach strategies that take into account the current ecological status of the species. Wild populations contain a high percentage of older adults and smaller populations of juveniles and seedlings that could continue with the generational replacement (Bernal and Sanín 2013).

Several populations of *C. quindiuense* found within natural forest regions, including Cocora, have been declared protected under government protection, preventing more habitat degradation. Despite this, the extremely small and highly isolated populations are still at high risk for becoming endangered or extinct. First, isolated wild populations do not have enough juveniles that could replace older plants, so small populations are already at risk of endogamy. Second, due to the species' long-life cycle, connections between populations and recovery of habitat would be slow. Lastly, although the introduction of individuals could accelerate the recovery process, it may take a long time before any positive or negative results could even be evaluated.

An increasing concern remains for the fate of *C. quindiuense*, especially the Quindío wax palm, but several conservation strategies have been suggested, such as regeneration sites. Juveniles and adults are resilient to intermediate disturbance and can grow well under moderate shade, therefore a vast and intensive repopulation program could improve the current status of *C. quindiuense* (Anthelme et al. 2011; Bernal and Sanín 2013; Sanín et al. 2013; Bernal et al. 2015). Specifically, conservation strategies point to augmentation of the wild populations supplemented with juveniles from near nurseries (Bernal et al. 2015). These private *ex situ* collections are a source of seed and seedling, and most of them are formed by individuals from Cocora, Toche and Linea, wild populations in the Central Cordillera.

The genetic characterization of the populations and the *ex situ* juveniles to be introduced to these wild populations should be a priority before augmentation programs initiate (Hoban and Schlarbaum 2014; Mijangos et al. 2015). For this reason, the current study focuses on two main goals: (1) Restore the original genetic profile of Cocora by the introduction of individuals that resemble the original genetic diversity and genetic profile of the natural population. This would aim to accelerate the recovery process of wild populations by the introduction and establishment of juveniles closer to a reproductive state and reduce the chances of introducing genetic material that could lead to outbreeding depression. (2) Evaluate *ex situ* private collections in terms of allele capture and the effects of kinship in collection composition. Due to the vast distribution of *C. quindiuense* and the fact that collections do not have a conservation purpose, individuals from living *ex situ* collections are likely to come from the same parental line. Hence, results from this study could not only lead to better practices for establishment of ex situ collections (i.e. kinship reduction) and also act as a bridge between the community and environment by the use of local and private nurseries. Together, results of this analysis will be used to provide conservation management recommendations that both protect the local gene pools of wild populations and enhance diversity within ex situ collections.

Materials and methods

Sampling and PCR conditions

Sampling consisted of 142 individuals, divided into two main groups. The first group included three wild populations from Central Cordillera of Colombia: (1) Cocora Valley, Quindío at 2300 to 2900 masl, an area of 600 ha of which nearly 360 ha have been converted to pastures (N = 30); (2) Toche, Tolima at 2160 to 3000 masl, an area of 4500 ha consisting mostly of pastures (N = 26); (3) La Línea, Tolima at 2500 to 2700 masl, that underwent total deforestation (N = 29) (Fig. 1). The second group included three local ex situ plant collections: (1) Quindío Botanical Garden (N = 30) and (2) two commercial ex situ plant collections Milan (N = 11), and Roso (N = 16).

We collected 10 g of young leaf tissue of juvenile individuals and the material was saved and dried in silica gel. The DNA was extracted by using Qiagen DNeasy Plant Mini Kit (Qiagen, Ltd.) following the manufacturer's instructions. DNA quality was checked in 1.5% agarose gels and quantified by using a NanoDrop 1000 Spectrophotometer V3.

Ten microsatellite loci previously developed for *C. alpinum* and *C. sasaimae* (Gaitán 2003) were amplified in 142 individuals, which were CA7, CA16, CA17, CS24, CA25, CA20, CA30, CS30, CS5, and CS3. Polymerase Chain reaction (PCR) were 25 μl in volume, consisting of 5 μl of DNA (5 ng/μl), 12.5 μl of GoTaq® Green Master Mix (Promega, Ltd.), 1 μl of each primer and 5.5 μl of free nuclease water (Promega, Ltd.) The PCR program was 94 °C (4 min), [94 °C (15 s), AT °C (15 s), 72 °C (5 min)] for 35 cycles, 72 °C (5 min), 10 °C (∞), as described in Sanín (2013). The PCR products were visualized in polyacrylamide gels (4%) with positive and negative controls. To identify the size of the

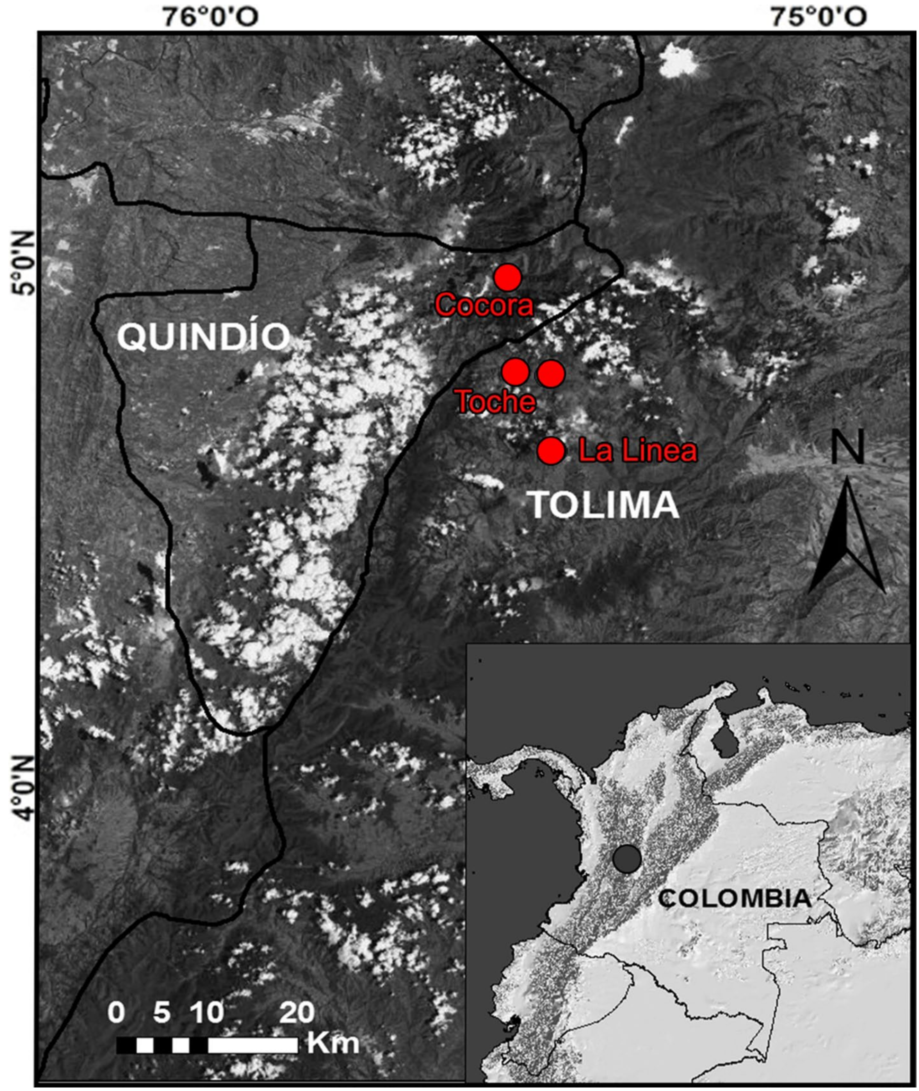

Fig. 1 Map of the wild populations. Lower corner shows a map of Colombia and the three Cordilleras of the Andes. Dark circle shows the location on the central Cordillera of the three populations evaluated in this study. Red circles show the location of the wild population Cocora, Toche and La Linea in a bigger scale

fragments, we used a Thermo Fisher 10-bp DNA ladder, and score reads were carried out by two independent operators to generate the allele profile per sample.

Analysis for genetic diversity for wild and *ex situ* populations

The restoration strategy through augmentation of the wild populations focuses primary in the Cocora region. Nevertheless, individuals from the collections expected to be introduced could come from any population across the Central Cordillera in Colombia. We evaluated the genetic profile of three wild populations of the Central Cordillera, including Cocora, and three *ex situ* collections from the area, two of them belonging to a private party (Milan and Roso) and one to a public botanical garden. Genetic diversity statistics were compared for every population. We calculated deviations from Hardy–Weinberg equilibrium (HWE), heterozygote deficiency, and linkage disequilibrium were computed in GENEPOP on the Web (Rousset 1995, 2008). Markov chain parameters were set to 5000 iterations, according to Gou and Thompson (1992). Standard molecular diversity indices were estimated in Arlequin v.3.5 (Excoffier and Lischer 2010) including number of alleles per population and per locus (Ap, Al respectively), effective number of alleles (Ae), Allelic richness (Ar), number of rare alleles (alleles with frequency < 0.01), private alleles (alleles found in only in one population), observed heterozygosity (Ho) and expected heterozygosity (He), genetic diversity (H). Allele frequencies were calculated in GenAlEx v.6.4.1 (Peakall and Smouse 2006) and diveRsity package (Keenan et al. 2013).

Genetic structure analysis of wild populations and *ex situ* plant collections

The Discriminant Analysis of Principal Components (DAPC) was used to identify the number of clusters or gene pools and identify the genetic profile of the *ex situ* collections that could resemble the genetic profile of wild populations, focusing primarily on Cocora (Pritchard et al. 2000; Jombart et al. 2010). DAPC analysis was performed as an individual assignment and infer implied genetic clusters based on k-means clustering. DAPC analysis was done in R (R development Core Team 2013), with the Adegenet package (Jombart et al. 2010). DAPC analysis does not rely on a particular population genetics model and is tolerant of deviations from HWE, linkage equilibrium, and null alleles (Jombart et al. 2010). The *find.clusters* function was used to run k-means clustering to select the best-supported number of clusters using the Bayesian Information Criterion (BIC) for values of *K*. Additionally, automated clustering was performed using a fix cluster number of 5 based on BIC and a cross-validation to select the correct number of PCs to retain. Assignment probabilities were based on the retained discriminant functions as indicators of how clear-cut genetic clusters were.

We separated the data into two groups: wild populations and *ex situ* collections. To validate the genetic variation components among, within, and between groups, an Analysis of Molecular Variance (AMOVA) was performed using F_{ST}-like statistics in Arlequin program (Excoffier and Heckel 2006; Excoffier and Lischer 2010). To elucidate relationships between groups, two different approaches were used to estimate genetic differentiation, F_{ST} (Wright 1969; Weir and Cockerham 1984) and D_{ST} (Jost 2008, 2009). Pairwise F_{ST} was tested with log likelihood ratio (test G) to assess population differentiation by Markov chains algorithms in the GENEPOP software and pairwise D_{ST} was performed in DEMEtics package in R (Gerlach et al. 2010). Both statistics were assumed under a significance of 95% bootstrap confidence intervals (1000 iterations).

Assignment test based on ten microsatellite loci

To infer the origin of the *ex situ* plant collections, we performed an assignment test using Bayesian method Rannala and Mountain (1997) criterion with the 'leave one out' procedure on the basis of microsatellite variation with the program GeneClass2 (Piry et al. 2004). This test calculates the probability that an individual's multilocus genotype occurs on each reference population. Here we took each wild population as a reference and compared them with each *ex situ* collection. After we found the population with highest probability, we evaluated rejection and acceptance of membership of the genotype to the population by the Monte Carlo resampling Frequency method of Paetkau et al. (2004). The probability of given individual multilocus genotype was compared to the distribution of probabilities of multilocus genotypes (10,000 replicates) generated based on the allele frequencies of the population, and if the value was below $\alpha < 0.01$, the individual was rejected from the population. Such a combination of an assignment test and exclusion-method is used for other studies (Manel et al. 2005; Frantz et al. 2006; Hare et al. 2006). Additionally, we used likelihood values to test for presence of first-generation migrants on each sample. We used L_home criteria which is the likelihood of individual genotype from the population where it was sample (Paetkau et al. 2004).

Evaluation of relatedness analysis and eligible material for augmentation programs

Kinship analysis was performed using Nei genetic distances (Nei and Feldman 1972). Values were obtained with the *dist.genpop* function in the Adegenet package. Analysis of hierarchical clustering was performed with bootstrap confidence intervals of 1000 interactions and plotted in R with the Dendextend package (Galili 2015). To assess relatedness among individuals as a proxy of intrapopulation genetic diversity, we used the Demerelate package (Kraemer and Gerlach 2013) in R to evaluate the levels of half and full siblings based on the model of shared genotypes (Mxy) (Blouin et al. 1996), and 1000 iterations. Subsequently, individuals with a genetic profile similar to wild populations were taken as eligible material for a restoration program.

Results

All ten loci were amplified in all populations, and all sampled loci were polymorphic. 136 alleles were found in the ten loci, ranging from 2 to 21 alleles per locus. Significant deviations from the Hardy–Weinberg equilibrium were found in all populations, but no evidence of linkage disequilibrium, $p < 0.001$. Cocora had the highest values for expected heterozygosity and allelic richness among all population, and levels of expected heterozygosity among collections were similar to each other (Table 1). Botanical Garden and Milan were very similar in their diversity measures. Roso, La Linea, Toche and Cocora harbored larger and similar amounts of expected heterozygosity. However, both groups differ in their observed heterozygosity levels. Total number of alleles, rare alleles and private alleles were

Table 1 Summary of diversity statistics for microsatellite data for wild populations and *ex situ* collections

	Botanical Garden	Collections			Wild	
		Roso	Milan	Cocora	Toche	La Linea
Sample size (N)	30	16	11	31	26	29
Expected heterozygosity (He)	0.51	0.69	0.50	0.68	0.63	0.60
Observed heterozygosity (Ho)	0.58	0.83	0.62	0.47	0.62	0.59
Allelic richness (Ar)	3.16	4.52	2.67	5.61	4.22	3.73
Fixation index Fis	1.000	0.392	1.000	0.351	0.052	−0.014

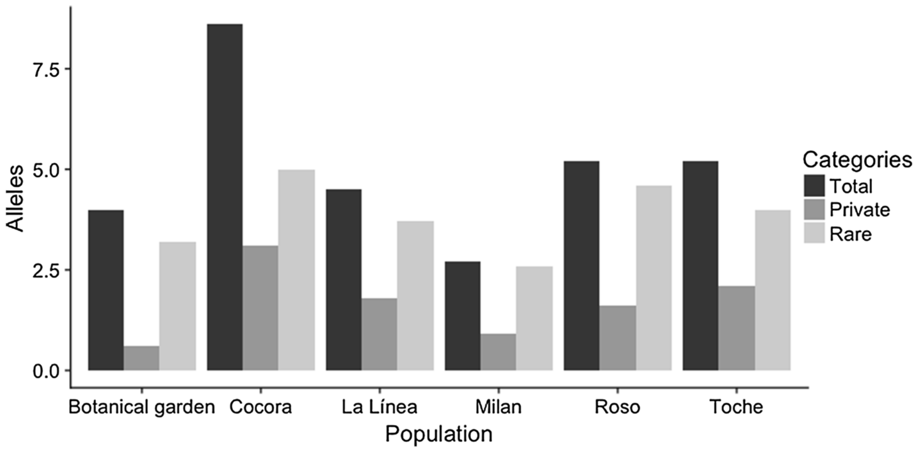

Fig. 2 Alleles categories recovered in wild populations and *ex situ* collections. Allele categories are defined as: Private alleles, total number of alleles and rare alleles

measured. Between wild populations, Cocora had the highest number of total, private, and rare alleles, while among *ex situ* collections, Roso had the highest number in all previous categories (Fig. 2). In general, wild populations showed a higher number of alleles (total, rare and private) compared to collections. Although a Chi square test suggests that all categories are homogeneous across populations, it does not imply a similar genetic makeup between wild and *ex situ* collections.

Pairwise comparisons with both F_{ST} and D_{ST} among wild populations and *ex situ* collections showed significant levels of differentiation. F_{ST} was 0.30 and D_{ST} was 0.76, both with a $p<0.001$ (Table 2). Genetic differentiation between the two groups (wild populations and *ex situ* collections) was also reflected in the AMOVA results, indicating that 34.85% of the variation was among populations within groups ($F_{IT}=0.35$, $p<0.001$), 3.07% among individuals within populations ($F_{IS}=0.04$, $p<0.001$) and 64.56% within individuals ($F_{SC}=0.34$, $p<0.001$). The variation among groups was not significant (−2.49% $p>0.05$). Multivariate DAPC analysis indicated that populations of *C. quindiuense* from wild and *ex situ* collections were divided into three distinct clusters identified by *k-means clustering* (Fig. 3). Botanical Garden, Milan, La Linea and Cocora are very close, suggesting potential admixture. Conversely, Toche and Roso are each genetically distinct, and none of the *ex situ* collections appears to capture the diversity from Toche with limited evidence of admixtures (Fig. 3). A second DAPC encompassing just wild populations showed a high

Table 2 Pairwise values of Fst (upper level) and Dst (lower level) differentiation

	BG	Mi	Ro	Co
BG	*	0.327	0.224	0.137
Mi	0.901	*	0.210	0.250
Ro	0.822	0.757	*	0.140
Co	0.611	0.792	0.549	*

Evaluated collections: *BG* Botanic Garden, *Mi* Milan, *Ro* Roso, Evaluated wild population: *Co* Cocora. All values in this table were significant with $p<0.001$

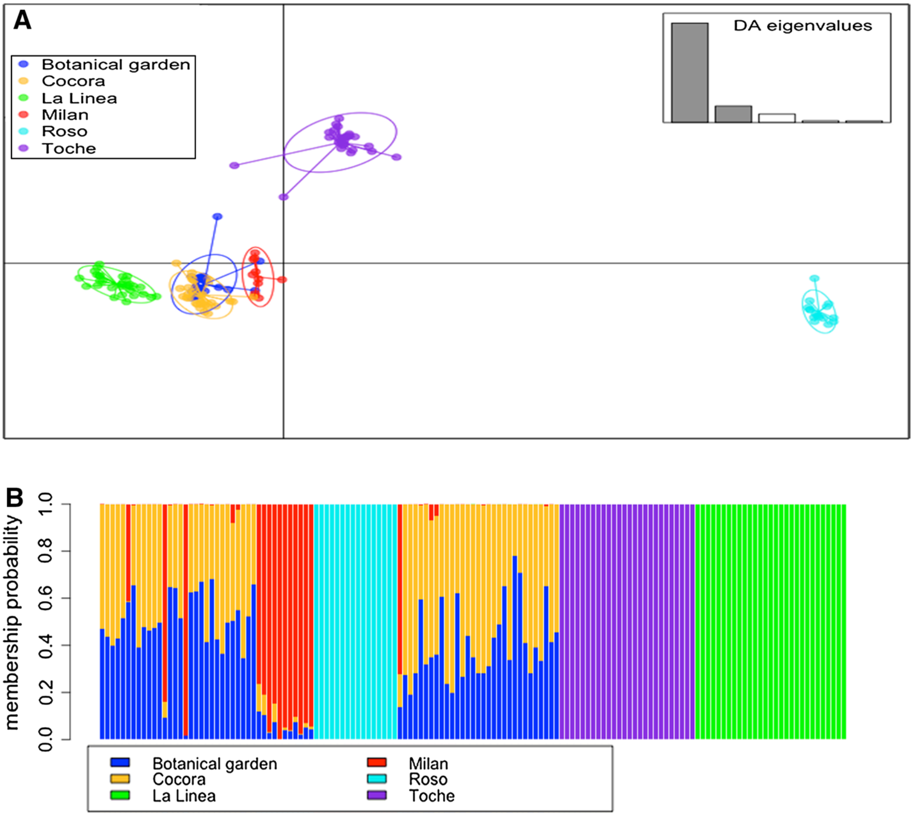

Fig. 3 Assignment analysis of *C. quindiuense* individuals. **a** Discriminant analysis of principal components (DAPC) with 4 K-mean clusters. Confidence interval (95%) represented by the ellipses. Each line represents and individual and the shapes represent its assigned genetic cluster. Eigenvalues show the genetic information of each component. Axis X and Y correspond to the first and second principal component respectively. **b** Membership probabilities of individual wax palm for all individuals. Each line represents and individual and the colors represent genetic clusters. Color segments for each individual are proportional to the probability of assignment to a genetically unique cluster

genetic structure between populations (Supplementary Fig. 1). Additionally, GeneClass2 results based on Bayesian methods assigned each individual to the population from which they were sampled with a 100% score (Supplementary Table 1). Frequency-based method (Paetkau et al. 2004) using L_home provide no evidence of first-generation migrants among any of the groups we sampled (*p* value > 0.01). Only three individuals from Cocora, one from Toche, two from Roso, and three from Botanic Garden were below threshold of 0.01 (Supplementary Table 2).

The Nei genetic distance showed a close relation among the Botanical Garden, Milan, and the group from Cocora and Toche also with low genetic distance. On the other hand, Roso was the most distant from the rest of the wild population and the other two collections (Fig. 4). Results of kinship analysis indicated that collections had significant levels of full-siblings ($p < 0.001$); Milan and Botanical Garden levels are over 50%, different from Roso with equal percentages of full and half-siblings. Wild populations had lower levels of full-siblings than collections, and Cocora had the lowest percentage of full siblings (5%,

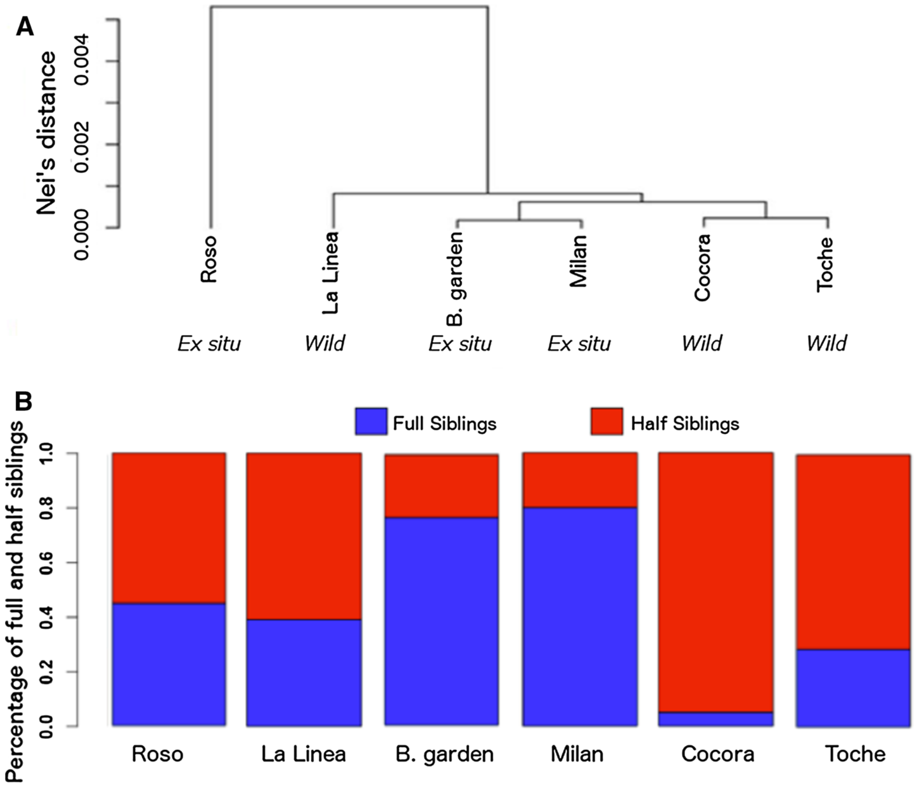

Fig. 4 **a** Hierarchical clustering between wild populations and *ex situ* collections of *C. quindiuense* in the Central Cordillera of Colombia evaluated by Nei distances. All nodes are supported by bootstrap > 75. Kinship analysis. **b** Bars represent the percentage of full (blue) and half siblings (red) for each population. Kinship values were calculated using 1000 randomizations by population ($p < 0.001$). Wild populations present a lower percentage of full siblings when compared to collections

$p < 0.001$) (Fig. 4). A negative correlation ($R^2 = -0.82$) was obtained between genetic diversity and percentage of full-siblings in each population and collection evaluated ($p < 0.005$).

Discussion

The microsatellites used in this analysis were polymorphic and informative and allowed us to characterize both *ex situ* and wild populations. As expected, these suggest significant genetic structure between the three wild populations (Cocora, La Línea, Toche) in the Central Cordillera of Colombia. Regarding genetic provenance and representativeness, the *ex situ* plant collections Botanical Garden and Milan showed genetic similarity only with Cocora, and the collection Roso did not show genetic concordance with any of the three wild populations. The topics presented in this study will focus on (1) conservation state of the wild populations Cocora, La Linea, Toche and (2) the use of the evaluated *ex situ* plant collections for augmentation of these wild populations and (3) the effectiveness of *ex situ* plant collections for conservation purposes.

Conservation status of wax palm (*C. quindiuense*) in the Andean region

Wax palms in general, and *C. quindiuense* in particular, face several conservation problems. Total population extension and connectivity is lost to deforestation by cattle raising and crops, areas in which ecological population structure is lost (Sanín et al. 2013). Secondly, even when deforestation took place decades before, the low tolerance of seedlings to radiation in open areas, limited seed dispersal, and the destruction of seeds and seedlings by trampling and livestock grazing prevent generation replacement (Anthelme et al. 2011). The establishment of these forest systems imposes long time lapses with no seed recruitment and leads to an inevitable population scenario wherein all large wax palm forests are solely composed of very old adults (Bernal and Sanín 2013). The resilience of these old adults and the longevity of the species provide a conservation opportunity. As a standing generation derived from better forests, these old adults hold high genetic diversity and continue to reproduce massively. However, their seeds and seedlings have to be protected within areas where human activities prevail or should be taken to protected areas where seeds may develop into the more resilient juveniles (rosette fase, see Sanín et al. 2013).

Evidence of a high level of genetic diversity was found across the three populations and agrees with previous findings showing that populations in this region have the highest level of diversity across the entire distribution (Sanín et al. 2017). Evidence of genetic structuring and inbreeding was found within wild populations, although, few studies have evaluated the genetic diversity and population structure of *C. quindiuense*, it has been shown that Cocora and Toche have some level of structure compare to other wild populations (Sanín et al. 2017; González-Rivillas et al. 2018). This structure pattern could potentially reduce genetic diversity of the already isolate populations creating a worse scenario for *C. quindiuense* persistence.

Small, close and isolate populations are more susceptible to inbreeding and loss of genetic diversity (Wright 1969; Frankham et al. 2014). Anthropogenic impacts have reduced the connectivity between populations, thus, genetic composition is based on chance and forged by inbreeding and drift. There is generally a tradeoff between genetic diversity and local population fitness, and both are correlated with population size (Leimu et al. 2006; Reed and Frankham 2003; Szczecińska et al. 2016). Additionally, for this species, dispersion is carry on by small/medium mammals (i.e. bats) or by air (Bernal et al. 2015), nevertheless, in disturbed habitats the dispersal ability is reduced, and this correlates negatively with F_{ST} values (Leimu et al. 2006; Frankham et al. 2014).

In the Central Cordillera, *C. quindiuense* populations are small and isolated which means they may become more susceptible to inbreeding (Fis values Table 1). Although inbreeding is not very strong, and the genetic diversity still high wild population remain at risk. These results are screenshots of old generations of palms which could differ from new generations (juveniles and seedlings) which are more affected by habitat reduction and isolation. Future studies that explore genetic diversity differences between the three palm generations (adults, juveniles, seedings) are needed. Genetic rescue could be an optimal management strategy for *C. quindiuense* conservation. Augmenting population size with material that resembles the original genetic makeup of the populations and connecting isolated populations would provide a low risk for outbreeding depression within the crosses and an increase of gene flow, respectively (Frankham et al. 2011; Frankham 2015; Ralls et al. 2017). Although genetic rescue might be a sound strategy for species with a marked reduction in local genetic diversity, all populations that were investigated here and previously studied by Sanín et al. (2017) show high levels of genetic diversity despite the apparent isolation. Also, fruit production and germination remain high, even in extremely small populations suggesting sexual reproduction from local material is still an option. Moreover, historical population divergence was found between wild populations (Sanín et al. 2017) which could entail local adaptation, but this has not yet been studied. Therefore, we believe the key issue is population size as a consequence of habitat availability and that genetic diversity is still there to support population growth and permanence.

Use of *ex situ* plant collections for augmentation of the studied wild populations

Aiming at the conservation of natural habitats and of natural biological interactions, (re) introduction has become important for the restoration of endangered plant species that require augmentation of existing populations (Robert et al. 2007; Godefroid et al. 2011; Maschinski et al. 2012; Menges et al. 2016). In an ideal scenario, individuals for reintroduction are available in *ex situ* plant collections that are enrolled in conservation projects. These are especially important in cases where it is difficult or impractical to employ *ex situ* strategies through standard methods (i.e. seed or tissue banks; Namoff et al. 2010; Pence 2011; Griffith et al. 2015). Introducing juveniles from these collections (Fig. 5) would save a quarter to half a decade for conservation efforts which takes into account that wax palms are long-lived and only reach maturity at about 80-year-old according to developmental age estimates from Sanín et al. (2013).

Given the marked genetic structuring between wild populations and *ex situ* collections, material for reintroduction programs should be locally sourced. A high level of genetic diversity is advantageous for conservation, but the introduction of non-local genotypes to enrich genetic diversity could lead to increased non-adapted characteristics as a result of exogamic depression or expression of intermediate genotypes not favored locally (Mckay et al. 2005; Menges 2008). Even if two populations are similar phenotypically and experience similar selection pressures, crosses between these populations can produce unfit hybrids from the breakup of the complex of genes (Fenster and Galloway 2000; Mckay et al. 2005), which is a disadvantage especially for species with long generation times, represented by small and isolated populations (Hufford and Mazer 2003; Rice and Emery 2003).

Both the genetic distance and multivariate analyses show that Botanical Garden and Milan collections can be unambiguously traced to Cocora rather than Toche or La Linea wild populations. However, collections are established from only certain genotypes, and genetic relatedness can be even closer than observed (Etisham-Ul-Haq et al. 2001; Li YY et al. 2005). Furthermore, the provenance of Roso collection could not be traced to any of the studied populations. Using genetic assignment methods based in Bayesian, Frequency and multivariate analysis, we have demonstrated clear discrimination between *ex situ* plant collections and wild populations despite relatively small sample sizes. GeneClass2 using Bayesian approach (Rannala and Mountain 1997) and a Frequency approach (Paetkau et al. 2004) suggested that wild populations were highly unlikely to be source population of any of the collections. Although, no evidence of first-generation migrants on the collections was found, assignation of individuals to the different groups by DAPC showed similar genetic profiles between Cocora Milan and Botanical Garden. Based on these results we suggest that individuals from the collections could be introduce in the wild population Cocora but not on any of the other two wild populations Toche or La Linea. Finally, Roso

Fig. 5 Life stages of *C. quindiuense* individuals taking from Sanín et al. (2013): Seedling, Juvenile 1, Juvenile 2, Juvenile 3 and Adult. The bottom left number point the estimated age by the end of that developmental phase. Photograph on the right shows a juvenile from Botanical Garden collection

genetic profile does not match any of the wild populations which suggest unknown wild population source from any of the Cordilleras. Interestingly, this match with few exceptions found by GeneClass2 on Roso, Cocora, Toche and La Linea where few individuals appear to be first generation migrants from unknown sources.

Effectiveness of collections for conservation purposes

Taking into account that the materials from Botanical Garden and Milan collections were unambiguously traced to Cocora wild population, the comparison between *ex situ* collections and their wild source could also be used to assess the effectiveness of collections in capturing and representing wild genetic diversity (Griffith et al. 2011). Changes in wild populations are also important for the future direction of collections, as the effect of inbreeding on and the reduction of genetic diversity in wild populations would indirectly affect collections. This would mean that genetic information saved in living collections now may not reflect the genetic composition of future wax palm generations (Li-Q et al. 2005; Liu et al. 2008; Yokogawa et al. 2013).

Ex situ plant collections are normally established in the studied area with commercial purposes where a sampling plan is not considered. Some collections, as is the case for Botanical Garden, are not established for business purposes, but their relevance for conservation research is not an issue when the material is retrieved from the source population. Values of genetic diversity were significantly different ($p<0.05$). Roso with a small collection size showed high diversity (potentially representative of a wild population), while Milan and Botanical Garden, with a small and big collection size respectively, showed lower genetic diversity and redundant alleles. These results suggest that a high number of full siblings may be an indication of poor management strategies (Li et al. 2005; Yokogawa et al. 2013), whereas a large size or genetically diverse source do not translate into high captured diversity. In all cases collections were developed without a sampling scheme focusing on allelic capture of the wild genetic pool, nonetheless, Roso was the only collection where the material came from distant geographic parents whereas Milan and Botanic Garden material were from the same individual in many cases.

Nevertheless, in general, allelic diversity and heterozygosity are positively correlated with population size, (e.g., Leimu et al. 2006) and one valuable estimate approximation might be to increase the size of collections in terms of half-siblings to enhance allelic capture. Collectors should not exclusively rely on the quantity of individuals but on the sample, these represent (Walters 2004; Namoff et al. 2010). Strategies that intend to improve allelic capture in *ex situ* plant collections can change depending on the species life history traits (i.e. pollination and dispersal of seeds), demographic history, relevant threats or on their distribution (Namoff et al. 2010; Godefroid et al. 2011; Griffith et al. 2011; Menges et al. 2016; Griffith et al. 2015).

Based on the previous analysis, we could assume that the material from *ex situ* collections, specifically Botanical Garden and Milan, came mostly from Cocora. Nevertheless, these collections did not recover a high genetic diversity from the wild population. The high percentage of private alleles in the wild population indicates that several alleles were missing from *ex situ* collections. This is explained by a common practice whereby material for collections (seedlings) is retrieved from a few parentals (i.e. many seeds or seedlings collect from a single female palm). Seed and seedling selection should be scattered to cover the vicinities of many female palms in order to increase the number of half siblings. Otherwise, artificial selection can affect and reduce genetic diversity in collections which would generate genetic differences between them and wild populations (Abbo et al. 2003; Yokogawa et al. 2013; Miao et al. 2015).

In general, Botanic Gardens have progressively focused on *ex situ* conservation (Raven and Havens 2014), and several works have established guidelines for creating effective and genetically diverse *ex situ* collections (Namoff et al. 2010; Godefroid et al. 2011; Griffith et al. 2011, 2015; Guerrant et al. 2014). This would help to implement a protocol for high allelic capture in Botanical Garden collections based on the information that we discuss before. Even though sampling protocols may differ from one species to another, we can build from studies in other palms. In studies focusing on *Leucothrinax morrisii* (Namoff et al. 2010; Griffith et al. 2011), results suggested that collections with 59 plants were able to capture more than 90% of the genetic diversity of a single population and that a collection of 15 plants from three accessions was sufficient to recover a mean of 83% of alleles in the population. Here we found a good example where collections built with different material sources are more efficient to capture wild diversity than collection built with few sources and a higher number of individuals. For our case, 16 individuals in the collection were sufficient to capture a high genetic diversity as long as the parental sources were different.

More important than collection number is a collection procedure that follows general recommendations established by and cited textually from Griffith et al. (2015): (1) use the species biology to inform the collecting strategy; (2) manage each population separately; (3) collect and maintain multiple accessions; and (4) collect over multiple years. Also, guidelines for collection management in Krishnan et al. (2013) for coffee and Cibrian-Jaramillo et al. (2010, 2013) for cycads highlight the way to represent the full range of wild genetic diversity. Wax palm populations from the Central Cordillera are markedly structured and behave as different evolutionary units and should therefore be represented in independent *ex situ* collections.

Conclusions

Similar to previous studies, we have found that populations of *C. quindiuense* from the Central Cordillera cover restricted areas but host high genetic diversity (see Sanín et al. 2013; Bernal et al. 2015). This diversity is highly structured, and conservation programs should consider each population as a different evolutionary unit (Sanín et al. 2017) to be genetically represented and protected as such. Genetic rescue could be an ideal plan for small and isolated populations since there is limited evidence of inbreeding, however *C. quindiuense* still remains at risk if it continues solely within small and isolated populations. Consequently, we propose ecological rescue, focusing on the augmentation of current populations using *ex situ* living collections ensuring genetic fidelity to source populations. From the three studied *ex situ* plant collections, only Botanical Garden and Milan represent part of the wild gene pool of Cocora and can be potentially used for restorations programs. Nevertheless, neither of the collections cover the total diversity of the wild population especially concerning private alleles. Furthermore, collection strategies that specify better practices regarding seed and seedling retrieval are needed. Juveniles should be retrieved from distant parental to minimize the probability of obtaining full-siblings. At the time of introduction to the wild, genetic mixture between populations should be avoided, and juveniles should be shuffled within the palm stand to avoid proximity between full siblings.

Although these strategies focus within a local context, we believe the development of new strategies that link conservation and genetic and population analysis are required to optimize conservation strategies. Especially if the strategies have a social impact that could involve local communities that already hold commercial collections by including them in restoration programs where they can contribute with seed, seedlings or juveniles. This would also promote awareness in which people are economically favored and contribute to the conservation of the entire cloud forest ecosystem. As a final and more regional perspective, these practices are feasible within the current socioeconomic context of the region. Colombia has entered a post-conflict period after 76 years of armed conflict, and many possibilities open up for conservation actions in previously inaccessible areas (Castro-Nuñez et al. 2017). Under this new context, the Quindio wax palm becomes a flagship species (Bernal and Sanín 2013) to address new conservation challenges under scientific criteria.

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