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Distribution, diversity and environmental adaptation of highland papayas (*Vasconcellea* spp.) in tropical and subtropical America

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Abstract *Vasconcellea* species, often referred to as highland papayas, consist of a group of fruit species that are closely related to the common papaya (*Carica papaya*). The genus deserves special attention as a number of species show potential as raw material in the tropical fruit industry, fresh or in processed products, or as genetic resources in papaya breeding programs. Some species show a very restricted

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distribution and are included in the IUCN Red List. This study on *Vasconcellea* distribution and diversity compiled collection data from five *Vasconcellea* projects and retrieved data from 62 herbaria, resulting in a total of 1,553 georeferenced collection sites, in 16 countries, including all 21 currently known *Vasconcellea* species. Spatial analysis of species richness clearly shows that Ecuador, Colombia and Peru are areas of high *Vasconcellea* diversity. Combination of species occurrence data with climatic data delimitates the potential distribution of each species and allows the modeling of potential richness at continent level. Based on these modeled richness maps, Ecuador appears to be the country with the highest potential *Vasconcellea* diversity. Despite differences in sampling densities, its neighboring countries, Peru and Colombia, possess high modeled species richness as well. A combination of observed richness maps and modeled potential richness maps makes it possible to identify important collection gaps. A Principal Component Analysis (PCA) of climate data at the collection sites allows us to define climatic preferences and adaptability of the different *Vasconcellea* species and to compare them with those of the common papaya.

Keywords Americas · Biodiversity mapping · Caricaceae · Climatic modeling · GIS · Plant genetic resources · Richness · Tropical fruits

Introduction

Nowadays, less than 5% of all edible fruit species native to tropical areas are cultivated and marketed on a commercial basis (Wijeratnam 2000). Five species alone, banana, mango, pineapple, avocado and papaya, account for over 90% of fruit exports. As their demand is even expected to increase by 8% in the period 2000–2010 (FAO 2003) and as in recent years there has been a growing trend to identify and develop new crops for export and domestic markets (Padulosi et al. 1999), it is clear that a rise in demand for new tropical fruit species can be anticipated. A common constraint in answering this potential demand is a lack of knowledge on the nature and potential of many of these fruit species. The latter problem can be addressed by assessing existing diversity of new species and analyzing their climatic requirements. One of the promising tropical fruit families are the Caricaceae.

Caricaceae is a small family of six genera and 35 species, most of which originated in the Americas. The only non-American genus is *Cylicomorpha*, with two West African tree species. *Horovitzia* is a monotypic genus of hairy herbaceous plants that occur around Oaxaca, Mexico. The genus *Jarilla has* three herbaceous species in southern Mexico and Guatemala. *Jacaratia* has seven tree species that are widely spread in tropical climates. *Carica* is monotypic and includes the economically most important representative of the family, the common papaya (*Carica papaya* L.) (Badillo 1971, 1993, 2000, 2001). This species, which gives a large, bland, juicy fruit, is extensively cultivated throughout the tropics. Indeed, with a total annual world production of more than 6.5 Mt, covering nearly 400,000 ha (FAOSTAT 2005) the common papaya is considered the fourth most important tropical fruit crop. *Vasconcellea* was established as a genus by Saint Hilaire in 1837 and later treated as a section within the genus *Carica*. Recently it has been restored as a genus by Badillo (2000), and the genus*Vasconcellea* is now the largest within the family, holding 21 species. The present study focuses on this relatively unknown genus, *Vasconcellea*, using papaya as a reference for climate studies.

Vasconcellea species are often collectively called 'highland papayas' or 'mountain papayas' (National Research Council 1989) because many of them occur at higher altitudes. Compared to their better-known lowland cousin, *Carica papaya*, highland papaya fruits are generally smaller and have distinct texture, taste and aroma. In the Andes, they are consumed fresh, roasted, processed in juices, marmalades, preserves or dairy products or even prepared in sauces, pie fillings and pickles (National - Research Council 1989; CAF 1992; Van den Eynden et al. 1999, 2003). Most *Vasconcellea* fruits and processed products are consumed at household level or, less frequently, sold on local markets. Only the largest mountain papaya, the babaco (*V.* × *heilbornii*), has been commercially developed, albeit on a small scale, outside of its region of origin. It was introduced as a crop in New Zealand in 1973 (Endt 1981; Harman 1983) from where it spread during the eighties to Australia (Cossio 1988), Italy (Cossio and Bassi 1987; Ferrara et al. 1993), Spain (Merino Merino 1989), France (CTIFL 1992), South Africa (Wiid 1994) and even Switzerland (Evéquoz 1990, 1994), Canada (Kempler and Kabaluk 1996) and the Netherlands (Heij 1989) where greenhouse trials have been done. *Vasconcellea cundinamarcensis* is marketed locally in Ecuador, Colombia and Peru and has been successfully introduced in northern Chile (National Research Council 1989) where it has gained some local importance and from where some preserves are exported to Europe and the US. Other *Vasconcellea* species such as *V. candicans*, *V. crassipetala*, *V. goudotiana*, *V. microcarpa*, *V. monoica*, *V. palandensis*, *V. parviflora*, *V. quercifolia*, *V. sphaerocarpa* and *V. stipulata* are consumed locally (Badillo 1993, Van den Eynden et al. 1999; Scheldeman 2002). In addition to their existing use, highland papayas show potential (1) as a source of papain (Baeza et al. 1990; Dhuique Mayer et al. 2001; Scheldeman et al. 2002), a proteolytic enzyme complex used in pharmaceutical and food industries; and (2) as genetic resources for improvement of the common papaya. *Vasconcellea* carry resistance genes, particularly for the most severe and widespread disease, the papaya ringspot virus (Manshardt and Wenslaff 1989a, b; Magdalita et al. 1997; Drew et al. 1998), cold tolerance and organoleptic characteristics (Manshardt and Wenslaff 1989b). Improvement breeding is, however, hampered because interspecific gene flow between *Carica papaya* and *Vasconcellea* species faces considerable postzygotic barriers (Mekako and Nakasone 1975; Drew et al. 1998).

Five of the 21 described *Vasconcellea* species (*V. horovitziana*, *V. omnilingua*, *V. palandensis*, *V. pulchra*, *V. sprucei*) are included in the IUCN Red List of Threatened Species (IUCN 2004a) and require special monitoring attention for their conservation. A better knowledge of these threatened species could therefore contribute to their conservation. For example, *V. palandensis*, was, despite its local importance (Van den Eynden et al. 1999), only described as new to science in 2000 by Badillo et al. (2000). Agricultural extension and intensification causes genetic erosion in all *Vasconcellea* species, including the cultivated and tolerated forms. Their distribution has been declining with a concomitant loss of traditional knowledge (Scheldeman 2002). A detailed study on their distribution, diversity and environmental adaptability will undoubtedly generate valuable information for future conservation actions.

Indeed, in spite of its importance, *Vasconcellea* crop ecology and distribution have been little studied. The present study is looking for general answers to these questions based on spatial information. Spatial analyses based on georeferenced herbarium or collecting data, often in combination with environmental spatial information, have previously generated valuable information in diversity studies (Skov 2000; Guarino et al. 2002; Vargas et al. 2004; Rodríguez et al. 2005). Such studies allow a clearer understanding of distribution of specific taxa and definition of areas of high diversity (Hijmans and Spooner 2001), on evolutionary origin (Jarvis et al. 2002), on defining sampling strategies and collection gaps (Jones et al. 1997; Greene et al. 1999a, b), on sampling biases (Reddy and Davalos 2003), on climatic adaptation (Berger et al. 2003), and on prioritization and definition of conservation areas (Kress et al. 1998; Funk et al. 1999; Bystriakova *et al*., 2003; Jarvis et al. 2003).

The main objectives of the presented study were: (1) to summarize the distribution of all 21 *Vasconcellea* species using collection data as well as herbarium specimen data; (2) to identify areas of high diversity and (3) collection gaps; and (4) to describe climatic and altitude preferences for *Vasconcellea* species.

Materials and methods

Data collection

Biogeographic data were obtained from collecting trips organized in the framework of five research projects (see Acknowledgements), complemented by herbarium records extracted from label data provided by the following herbaria: A, AAU, AMD, ASU, AWH, B, BIGU, BM, BR, BRIT, CAY, CAUP, CHAPA, CLEMS, COL, CONC, CPUN, CR, CSAT, CTES, CUVC, DAV, DS, F, FAUC, GB, GENT, HUA, HNMN, HULE, HUMO, HUT, JAUM, JEPS, JVR, K, LP, LZ, M, MAD, MEDEL, MFA, MPU, MO, MU, MY, NY, P, PSO, QCA, QPLS, S, SEL, SSUC, TEFH, U, ULM, ULS, UPS, USCG, USJ, VALLE, VT (acronyms based on Index Herbariorum, Holmgren et al. 1990). Species collected were identified using the taxonomic keys developed by Badillo (1993) applying the nomenclature as revised by the same author (Badillo 2000, 2001).

All data points were entered into the Geographic Information System DIVA-GIS 4.1 (Hijmans et al. 2001, 2003), chosen to carry out spatial analysis. Georeferenced data were checked for inconsistencies. Data points without coordinates were assigned coordinates where possible while duplicate or doubtful data were removed. To define the altitude for each collection point, elevation data provided with collection site information were used where possible. In other cases, altitude was extracted from the $2.5 \times 2.5'$ (approximately 4.5×4.5 km at the equator) Worldclim data available at the DIVA-GIS website (http://www.diva-gis.org/).

Diversity and distribution

The measurement of diversity and distribution of *Vasconcellea* species was addressed in several ways. Firstly, the number of observations was tabulated per species and per country. Secondly, the area of occupancy (AOO), defined by IUCN (IUCN 2001, 2004b) as the total area occupied by a specific taxon, was selected as an indicator of abundance or rarity of a particular species. IUCN recommends the use of a 2×2 km (4 km^2) grid to define this parameter (IUCN 2004b). Thus, AOO was calculated by superposing a 2×2 km grid (based on a Lambert Equal Area

Azimuthal projection with central meridian 0 and reference latitude – 80) over the study area, followed by determining the number of grid cells occupied by each species (using the DIVA-GIS histogram tool) and by converting these to an effective area by multiplying the number of occupied cells by 4 km^2. Thirdly, the extent of the distribution area for each species was also estimated by determining the average distance between all possible pairs of collection points of each species. Finally, observed species richness was mapped using the point-to-grid richness analysis tool in DIVA-GIS, using a $1 \times 1°$ grid (corresponding to 111×111 km at the equator). The circular neighborhood option, with a 2° diameter (Hijmans and Spooner 2001), was applied to eliminate border effects due to the assignation of the grid origin.

Modeled richness and collecting gaps

Potential area of distribution of each species was modeled based on climatic preferences using the Bioclim model (Nix 1986; Busby 1991) in DIVA-GIS, using a $10 \times 10'$ Worldclim climate data set. In the Bioclim model, a site is considered suitable for a particular species if its climate data fall within the range prevalent at the sites where the species occurs (Hijmans et al. 2003). In this study, all 19 available climatic parameters were used (see Table 3). For each climatic parameter, the lower and upper 2.5 percentile of the total range were excluded from the suitability range to avoid the influence of extreme values. In order to prevent modeling outside the natural distribution area, a buffer zone with a radius of 3° (Jarvis et al. 2003) around all collection sites of each species was applied to limit the modeled richness. This climatic modeling resulted in 21 modeled distribution maps, one per *Vasconcellea* species. The sum of these 21 maps resulted in a map that indicates modeled potential species richness at a $10 \times 10'$ grid. Subtracting modeled species richness with the observed richness allowed detection of possible collection gaps.

Climatic requirements and adaptability

For each collection site, values for the 19 climatic parameters were extracted from the $2.5 \times 2.5'$ Worldclim data set and species collection points within the same grid cell were removed. Principal component analysis (PCA) was carried out on all 19 climatic parameters, applying a varimax normalized rotation, with the Statistica® package. To promote visibility, the centroid, i.e., the arithmetic average of the factor scores for each species, was used to represent each species' general climatic preferences. Standard deviation of factor scores was used to represent variation around the centroid to give an indication of the adaptability of each species for each climatic principal component. The well-known *Carica papaya* served as a reference in the *Vasconcellea* climate study.

Results and discussion

Diversity and distribution

The total dataset included 1,702 records representing all 21 *Vasconcellea* species (1,553) and *Carica papaya* (149). Table 1 presents a synthesis for the different species and countries of collection. *Vasconcellea cauliflora*, *V. cundinamarcensis*,

Table 1 List of all known *Vasconcellea* and *Carica* species and the countries where they were collected

Species (Red list Cat.**)	Country* (with respective number of collections)	Total number of collections	AOO (km^2)	Average Distance (km)
V. cundinamarcensis	Col(163), Ecu(75), Ven(14), Per(5), Bol(4), Pan(3), Chl(1), Cri(1)	266	856	705
V. microcarpa	Ecu(110), Per(46), Col(35), Ven(14), Bra(12), Bol(3), Cri(1), Pan(1),	222	792	872
V. stipulata	Ecu(180)	180	424	50
V. × heilbornii	Ecu(164), Per(4)	168	420	116
C. papaya	Col(49), Nic(37), Ecu(18), Bol(8), Blz(6), Cri(6), Per(4), Ven(4), Pan(3), Dma(2), Guf(2), Mex(2), Pry(2), Slv(2), Bra(1), Dom(1), Hnd(1), Pri(1)	149	600	1,584
V. quercifolia	Arg(78), Bol(19), Bra(17), Pry(11), Per(1)	126	464	842
V. cauliflora	Col(54), Cri(25), Ven (11), Nic(8), Pan(7), Gtm(5), Mex(5), Hnd(4), Slv(4)	123	456	985
V. goudotiana	Col(108), Ecu(7) Ven(1)	116	372	318
V. parviflora	Ecu(63), Per(18)	81	288	241
V. chilensis	Chl(62)	62	244	147
V. glandulosa	Bol(17), Arg(17), Per(12), Bra(1)	47	168	1,039
V. monoica	Ecu(17), Bol(6), Per(3), Col(2)	28	100	863
V. crassipetala	Col(21), Ecu(3)	24	68	286
V. candicans	Ecu(13), Per(9)	22	72	618
V. pulchra (Nt)	Ecu(18), Col(1)	19	68	82
V. sphaerocarpa	Col(18)	18	68	318
V. longiflora	Ecu(8), Col(4)	12	44	231
V. weberbaueri	Ecu(11), Per(1)	12	36	102
V. horovitziana (En)	Ecu(8)	8	32	222
V. sprucei (Nt)	Ecu(8)	8	32	109
V. palandensis (Vu)	Ecu(6)	6	8	7
V. omnilingua (En)	Ecu(5)	5	20	23

*Country Codes: Arg: Argentina; Bra: Brazil; Blz: Belize; Bol: Bolivia; Chl: Chile; Col: Colombia; Cri: Costa Rica; Dma: Dominica; Dom: Dominican Republic; Ecu: Ecuador; Gtm: Guatemala; Guf: French Guyana; Hnd: Honduras; Mex: Mexico; Nic: Nicaragua; Pan: Panama; Per: Peru; Pri: Puerto Rico; Pry: Paraguay; Slv: El Salvador; Ven: Venezuela

**Red List Categories: En: endangered; Vu: vulnerable; Nt: Near threatened

V. goudotiana, *V. microcarpa*, *V. quercifolia*,*V. stipulata* and *V.* × *heilbornii*, are the species that were most commonly collected as evidenced by number of specimens as well as number of countries, while the Red List species *V. horovitziana*, *V. omnilingua*, *V. palandensis*, *V. pulchra* and *V. sprucei* together with *V. longiflora*, mostly from Ecuador, are the least collected and should therefore be regarded as rare. The AOO confirms this sharp contrast in distribution extent between these two groups of common and rare species. *Vasconcellea cundinamarcensis* is the species with the widest distribution, covering mountainous zones from Costa Rica to Chile. *Vasconcellea microcarpa* has a similar AOO with an area ranging from Colombia to Brazil and Bolivia. *Vasconcellea quercifolia* is widespread in the south of the continent whereas *V. cauliflora* has an ample distribution in the northern part, ranging from Mexico southwards to Colombia and Venezuela. All species mentioned in the IUCN Red List show both a limited AOO and short distances between collection sites, confirming their status. The analyses presented indicate that both *V. longiflora* and *V. weberbaueri* are very rare species as well, and their possible inclusion in the Red List should be considered, after a more detailed analysis. *Vasconcellea palandensis*, which has the lowest values for both AOO and average distance, should be regarded as the rarest species in the genus.

Figure 1 gives a more detailed view of the geographic distribution of each *Vasconcellea* species. Ecuador, where 16 of the 21 *Vasconcellea* species have been recorded, is without any doubt the country with the highest richness for *Vasconcellea*, with its neighbor countries Colombia and Peru coming in second place with nine species. In all other countries, five or less species have been collected. The Andes of northwestern South America clearly constitute the center of diversity of *Vasconcellea* (Fig. 2). Ecuador has the highest diversity, and southern Ecuador (provinces El Oro, Loja and Zamora-Chinchipe) alone accounts for 12 of the 21 species, whereas southern Colombia (Nariño Department), where all nine Colombian species have been recorded, is another area with high *Vasconcellea* diversity.

Despite the size of the dataset, the study faces some methodological difficulties to precisely assess the extent of the distribution area and the rarity of a species, particularly when using a large, continent scale. The use of average distance between collection sites does not give a good indication of local abundance while the AOO does not constitute a direct indicator of abundance either. Considering that the dataset reflects the distribution at continent level, the combination of both indicators allows obtaining a better insight in the abundance of highland papayas in tropical America. Some species, e.g., *V. stipulata* and *V.* × *heilbornii*, show a rather wide AOO but a small average distance between collection points. They are very common in their area of origin (Loja Province, Ecuador; Badillo, 1993), but are rarely found outside this restricted area. Opposed to this, *V. monoica* and *V. candicans* show a small AOO but have a large distance between collection points, which indicates that they are never very abundant where they occur. The latter situation can however also be caused by undercollection of a species, highlighting the importance of a complete trustworthy dataset in this type of analysis. In fact, only cautious (and iterative) field verification of potential distribution maps, allows one to distinguish rarity from incomplete collecting. Despite these possible methodological shortcomings, our spatial analyses provide useful indications on the rarity of *Vasconcellea* species.

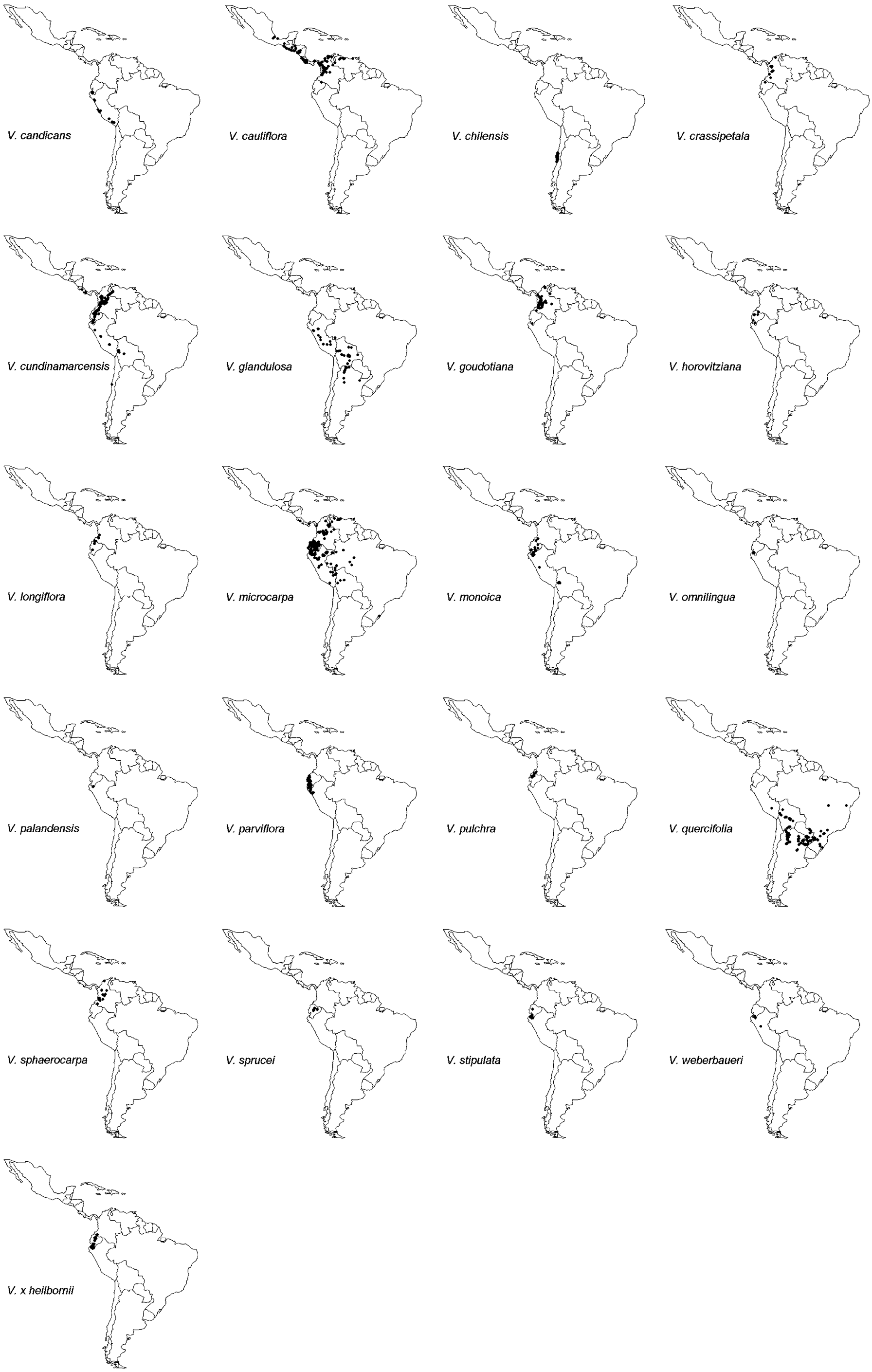

Fig. 1 Collection sites of the 21 *Vasconcellea* species within tropical America

Fig. 2 Observed *Vasconcellea* species richness in Latin America on a $1 \times 1°$ grid using 1,553 *Vasconcellea* observations. The darker areas indicate the highest richness (maximum value: 12 species per grid cell)

Modeled richness and collection gaps

The sum of the modeled potential distribution maps of the 21 *Vasconcellea* species resulted in a map indicating the modeled species richness in tropical America (Fig. 3). This map, which is based on the species climatic preferences, gives a slightly different view on *Vasconcellea* diversity. The Andean region of northern Ecuador and southern Colombia are now identified as those areas that posses the most favorable climate for *Vasconcellea* diversity and that therefore have the highest potential richness. Comparing, at country level, the observed richness with the modeled richness (Table 2), Ecuador, with a potential of 18 species, is confirmed as the most important center of *Vasconcellea* diversity. Its neighboring countries, Peru and Colombia are obviously also countries where a relatively high number of species occur, confirming the importance of the northern Andes for *Vasconcellea* diversity.

The sampled species richness map (Fig. 2), based on collection data, can be compared to the modeled potential species richness map (Fig. 3) to identify collection gaps. Figure 4 shows the areas where the discrepancy between observed and modeled richness is highest for *Vasconcellea*. The most important collection gaps are located in Colombia, where the higher parts of the departments of Nariño, Putumayo, Cauca, Valle de Cauca, Huila, Tolima, Caquetá and Meta should be given top priority for future collecting. Less important, but still significant, gaps are located in

Fig. 3 Modeled *Vasconcellea* species richness in Latin America on a 1 × 1° grid using the sum of the modeled distribution maps of the 21 *Vasconcellea* species. The darker areas indicate the highest potential richness (maximum value: 11 species)

Table 2 Sampled *Vasconcellea* species richness versus modeled species richness in key countries

Country	Sampled species richness	Modeled species richness
Ecuador	16	18
Colombia	9	12
Peru	9	12
Bolivia	5	5
Venezuela	4	5
Brazil	3	3
Costa Rica	3	3
Panama	3	5
Argentina	2	2
Chile	2	1
Guatemala	1	1
Mexico	1	1
Paraguay	1	2
Nicaragua	1	2
Uruguay	0	2

eastern Venezuela (Zulia, Portuguesa, Trujillo, Barinas), in northeastern Colombia (Cundinamarca, Boyacá, Santander, Norte de Santander, Cesar and Bolivar), in northern Ecuador (Imbabura, Pichincha and Esmeraldas), in Central Peru (Cajamarca, San Martin, Amazonas, Huánuco, Pasco, Junín, Ucayali) and in eastern

Fig. 4 *Vasconcellea* collection gaps in northwestern South America based on an overlay of the sampled richness map and the modeled richness map (on a 1 × 1° grid). The darker areas indicate those zones were a high *Vasconcellea* richness is likely to occur, but where up to this moment no or only a limited number of specimens have been collected

Bolivia (La Paz). These are all highly suitable zones where only a limited number of *Vasconcellea* species have been collected so far. Figure 4 also shows that Ecuador, the country with the highest diversity, generally appears well-sampled as few undercollected areas could be identified.

Diversity studies often face the risk of a bias related to uneven collection intensity, particularly oversampling in areas of high species richness and in easily accessible areas (Hijmans et al. 2000; Reddy et al. 2003). This is illustrated clearly in a comparison between Ecuador and Colombia, both located in the center of highland papaya diversity. From the observed richness map (Fig. 2) Ecuador is identified as the country with the highest species number. It is also a country where environmental and political conditions make it easy to sample, as proven by the numerous herbaria records. Colombia on the other hand, has less observed diversity, but the modeled richness (Fig. 3) shows that, especially in the southern part, species richness is equal or higher than in Ecuador. These areas are often difficult to access due to security problems. Extrapolation of species ranges using environmental data, as shown in Fig. 3, is generally acknowledged to counter the sampling bias (Jarvis et al. 2003; Sommer et al. 2003). One could therefore wonder whether the fact that Ecuador is considered more diverse in highland papayas than Colombia could be partly due to a different sampling intensity.

Climatic requirements and adaptability

The extraction of climatic data on the 1,702 collection sites, covering 1,278 grid cells, resulted in a matrix of more than 24,000 values. The PCA allowed the identification of climatic conditions governing the distribution of the 21 *Vasconcellea* species and permitted a comparison of the climatic preferences of all these species, together with those of the better-known *Carica papaya*.

Taking into account only factors with eigenvalues superior or equal to one, four principal components were retained (Table 3). The first one, representing 44% of the observed variance, is a temperature factor differentiating warm climate species from cool climate species. The second factor shows a positive correlation with precipitation in the driest period and a negative correlation with precipitation seasonality. Thus, it differentiates species found in areas with year-round precipitation from those found in areas with a marked precipitation seasonality. Similarly, factor 3 is related to temperature seasonality, separating species found at higher latitudes, where monthly temperatures vary according to seasons, from the species living near the equator. Finally, the fourth factor shows a high correlation with precipitation and separates dry climate species from humid climate species. These four factors together accounted for 88.73% of total variance.

Figure 5 shows the centroids of the PCA factor scores for each *Vasconcellea* species and for papaya. Figure 5a places them in the plan of the two temperature-related factors (1 and 3) whereas Fig. 5b places them in the plan of the precipitation-

Table 3 Factor loadings, eigenvalues and percentages of variance for the first four axes, resulting from the PCA analysis of 19 climatic parameters for the 1,702 collection points (*Vasconcellea* and *Carica*)

	Factor 1	Factor 2	Factor 3	Factor 4
Eigenvalue	8.30	4.86	2.31	1.39
Percentage of variance	43.66	25.59	12.16	7.32
Description bioclim parameter				
Annual mean temperature	**0.98**	0.04	– 0.03	0.19
Mean monthly temperature range	– 0.19	– 0.51	– 0.48	0.26
Isothermality	– 0.14	0.07	**0.85**	0.25
Temperature seasonality	0.06	– 0.05	– **0.95**	– 0.20
Max. temperature of warmest month	**0.91**	– 0.06	– 0.34	0.17
Min. temperature of coldest month	**0.90**	0.17	0.36	0.16
Temp. annual range	– 0.06	– 0.31	– **0.93**	0.00
Mean temperature of wettest quarter	**0.93**	0.00	– 0.19	0.21
Mean temperature of driest quarter	**0.95**	0.07	0.18	0.15
Mean temperature of warmest quarter	**0.95**	0.02	– 0.27	0.13
Mean temperature of coldest quarter	**0.93**	0.05	0.24	0.24
Annual precipitation	0.26	0.58	0.15	**0.73**
Precipitation of wettest month	0.34	0.17	0.17	**0.88**
Precipitation of driest month	0.05	**0.90**	0.04	0.30
Precipitation seasonality	0.11	– **0.82**	– 0.16	– 0.09
Precipitation of wettest quarter	0.33	0.18	0.17	**0.88**
Precipitation of driest quarter	0.05	**0.91**	0.06	0.33
Precipitation of warmest quarter	0.23	0.36	– 0.02	0.66
Precipitation of coldest quarter	0.09	0.60	0.26	0.46

The climatic parameters that have a high (> 0.7) contribution are highlighted in bold

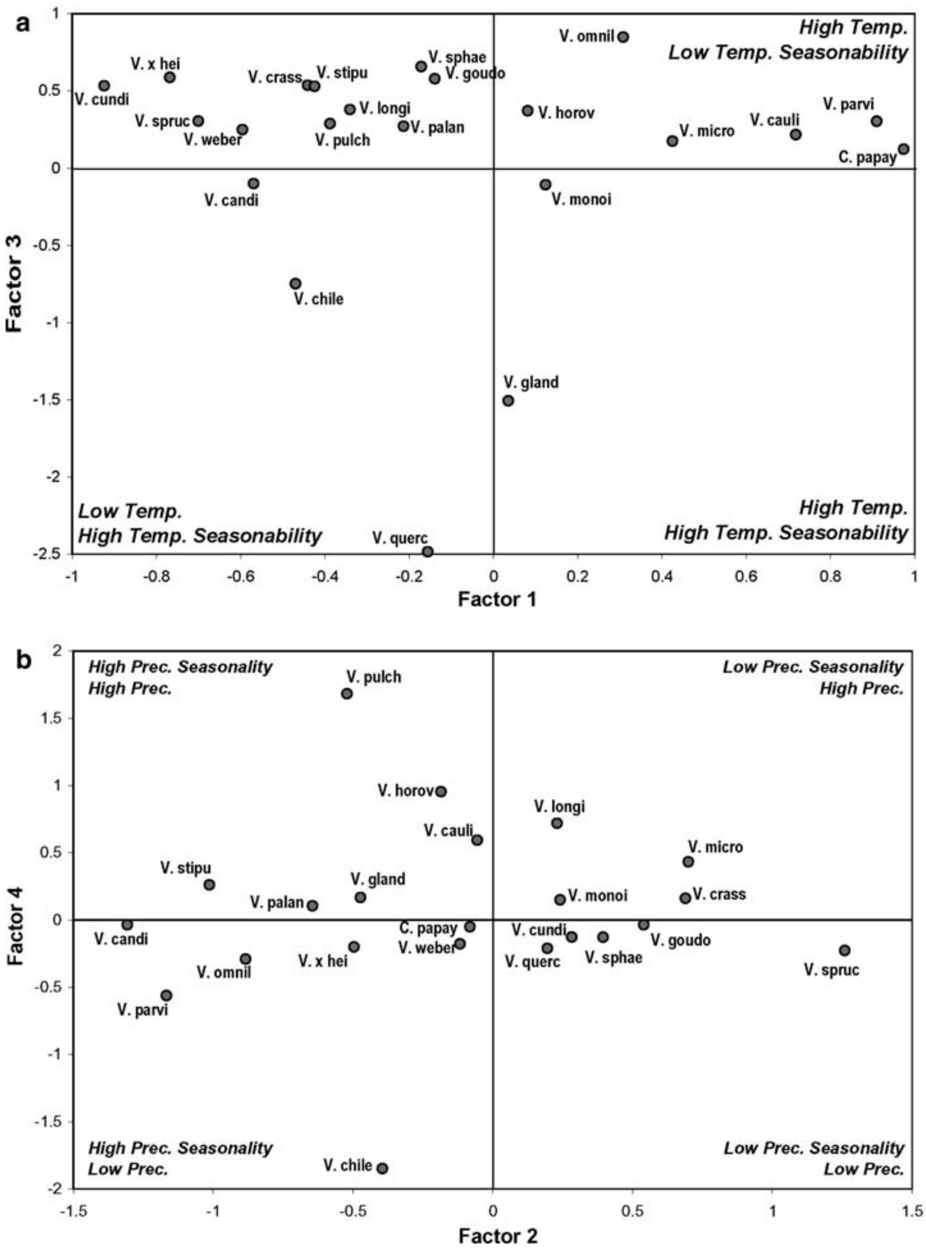

Fig. 5 Distribution of the species centroids for the first four PCA axes, for 1,702 *Vasconcellea* and *Carica* collection sites in Latin America and 19 climatic parameters. **a**: temperature-related axes (1 and 3). **b**: precipitation-related axes (2 and 4)

related factors (2 and 4). As expected, factor 1 allows a clear distinction between typical lowland species, *C. papaya*, *V. parviflora*, *V. cauliflora* and *V. microcarpa*, and highland species as *V. cundinamarcensis*, *V.* × *heilbornii* and *V. weberbaueri*, whereas factor 3 allows to distinguish the three species found at higher latitudes, i.e., *V. quercifolia*, *V. glandulosa* and *V. chilensis*, from the majority of species most commonly found around the equator. In Fig. 5b, factor 4 clearly separates *V. chilensis*, a species with adaptation to a marked dry season whereas factor 2 ranks species according to their general humidity requirements. Thus, species such as *V. candicans*, *V. parviflora* and *V. stipulata*, from drier regions like southern Ecuador and northern Peru, are logically placed on the left side of the plan, while species adapted to the humid Amazon region, such as *V. monoica V. microcarpa*, and *V. sprucei* appear grouped on the right side, together with species of the humid forests of the Colombian Andes, such as *V. crassipetala*, *V. goudotiana* and *V. sphaerocarpa*.

Table 4 gives the standard deviation around the centroids for each species, and for each of the four main axes. Very low deviations for *V. chilensis* reflect its narrow geographic distribution, probably in relation with very strict climatic adaptations, whereas large values for *V. microcarpa* reveal a very wide adaptability, especially for precipitation. Comparing the deviations for the four factor scores across species, the standard deviation of Factor 3 generally shows the lowest value, reflecting the essentially tropical distribution of *Vasconcellea*. Indeed, only the three species distributed well beyond the equator up to subtropical latitudes, show a high (*V. glandulosa* and *V. quercifolia*) or relatively high (*V. chilensis*) adaptability for temperature seasonality.

Of all the species studied, *Carica papaya* is the one that is found in the warmest zones, with a mean annual temperature of 24.2°C, with little seasonal temperature variations. From a precipitation perspective it nearly falls in the center of the precipitation plan (Fig. 5b) indicating that is occurs at average precipitations (annual

Table 4 Climatic adaptability indicated by the standard deviation of the mean factor scores for each species

Species	Factor 1	Factor 2	Factor 3	Factor 4
V. candicans	1.01	0.54	0.59	1.22
V. cauliflora	0.67	0.86	0.55	1.41
V. chilensis	0.28	0.10	0.39	0.39
V. crassipetala	1.00	0.80	0.16	0.46
V. cundinamarcensis	0.73	0.56	0.37	0.76
V. glandulosa	0.94	0.58	1.11	0.58
V. goudotiana	0.86	0.50	0.21	0.70
V. horovitziana	1.24	0.98	0.21	1.82
V. longiflora	0.68	0.97	0.22	0.68
V. microcarpa	0.90	1.28	0.41	1.05
V. monoica	0.82	1.32	0.54	0.41
V. omnilingua	0.64	0.28	0.11	0.22
V. palandensis	0.53	0.16	0.10	0.08
V. parviflora	0.73	0.39	0.42	0.87
V. pulchra	0.96	0.41	0.21	0.93
V. quercifolia	0.82	1.08	0.79	0.58
V. sphaerocarpa	1.07	0.50	0.24	0.64
V. sprucei	0.97	0.84	0.21	0.74
V. stipulata	0.45	0.56	0.21	0.58
V. weberbaueri	0.75	0.33	0.49	0.55
V. × heilbornii	0.48	0.66	0.27	0.62
C. papaya	0.71	0.86	0.68	0.81

precipitation 1,830 mm) in areas without extreme precipitation seasonality. These values correspond very well with values given in literature, i.e., 24.5°C and 1,920 mm for mean annual temperature and annual precipitation respectively (Duke 1983). Compared to *Vasconcellea* species, *Carica papaya* shows a more constant standard deviation among the four factors (Table 4), which is in general very close to the overall average (0.64) of the four axes for all species, indicating a similar and average adaptability for both temperature and precipitation. Most *Vasconcellea* species show a low standard variation for one of the four factors, which indicates a more limited adaptability for a specific climatic environment.

Altitude

Figure 6 presents an analysis of the relation between elevation and species richness. An average of 14 species can be found at altitudes up to 2,500 m. Above this elevation, species richness gradually decreases, as shown by the second order regression.

The *Vasconcellea* richness map (Fig. 2) illustrates a clear relation between *Vasconcellea* diversity and the Andes. Even lowland species are mostly confined to the Andean foothills. *Vasconcellea cauliflora*, also found in Central America, *V. quercifolia*, also present in southern Brazil, southern Paraguay and northern Argentina and *V. microcarpa*, also collected in the Brazilian Amazon, are only partial exceptions to this link between *Vasconcellea* species and the Andes. Thus, even though several *Vasconcellea* species can be found at sea level, the use of the term ''highland papayas'' or ''mountain papayas'' as a collective term for *Vasconcellea* species appears justified.

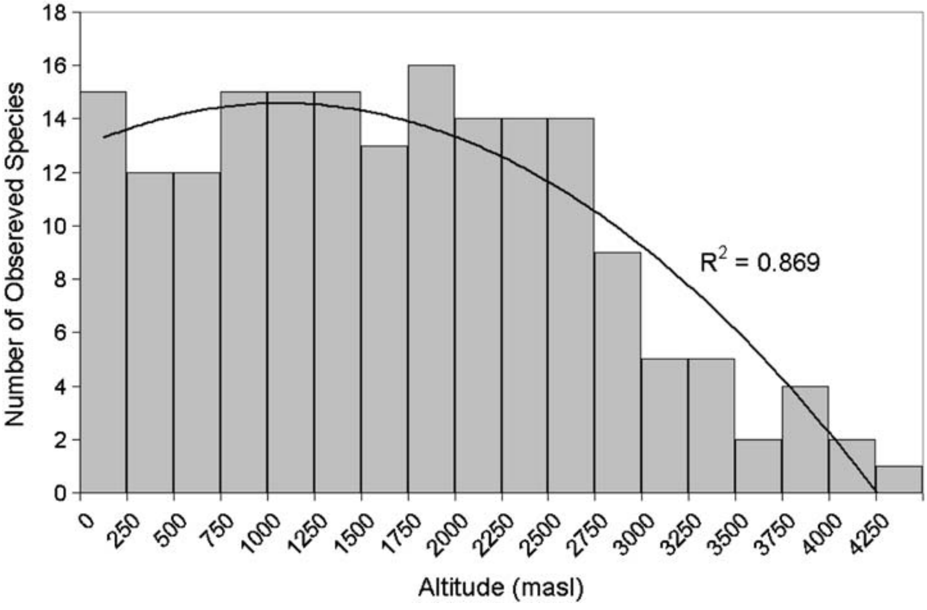

Fig. 6 Relation between altitude and number of observed *Vasconcellea* species using 1,553 *Vasconcellea* observations in Latin America. The solid line represents a second order regression

Conclusions

This study, based on the most complete *Vasconcellea* collection data set compiled so far, provides an overview of distribution, diversity and climatic preferences of 21 *Vasconcellea* species. It is therefore an important addition to the monographs on Caricaceae by Badillo (Badillo 1971, 1993). Despite their wide distribution in tropical America, ranging from Mexico down to Argentina and Chile, the majority of the *Vasconcellea* species are confined to the northern Andean region (Colombia, Ecuador and Peru). This is also reflected in their temperature preferences, generally cooler climates with limited seasonality, as prevalent in the equatorial Andes.

Although some highland papaya species are commonly grown in backyard gardens to be consumed and/or marketed locally, other species such as *V. horovitziana*, *V. omnilingua*, *V. palandensis*, *V. pulchra* and *V. sprucei* are only found in the wild within a very limited distribution range, and are included in the IUCN Red List. Results of the analysis of the distribution results suggest that two more *Vasconcellea* species, *V. longiflora* and *V. weberbaueri*, should be considered for inclusion in the Red List as well.

This study shows that by combining georeferenced species collection data together with available detailed climate data, the use of GIS can add significant value and knowledge to the existing information sources. This study is also a clear illustration of the importance of trustworthy collection data and its sharing, which might allow a better understanding of many other potential neglected and underutilized species to enhance their conservation and use.

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