Disentangling morphologically similar species of the Andean forest: integrating results from multivariate morphometric analyses, niche modelling and climatic space comparison in *Kaunia* (Eupatorieae: Asteraceae)

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Six subtropical montane forest *Kaunia* spp. are remarkable for their superficial morphological similarity. We aim to explore different sources of data to clarify species delimitation in this complex of *Kaunia*. Morphological variation and environmental data of the species of the complex were assessed by using multivariate morphometric analyses. We performed a species distribution modelling approach applying BIOMOD2. Morphological quantitative traits allowed discrimination of some species in the complex. These *Kaunia* spp. have statistically different potential distributions, although some similarities between species in terms of climatic space were found. The species with the most similar climatic space were *K. saltensis* and *K. lasiophthalma*. The biogeographical context that could have affected the distribution of these two species is discussed. The results of our integrative study confirm the discrimination of three species, *K. lasiophthalma*, *K. rufescens* and *K. saltensis*, but the other three, *K. arbuscularis*, *K. longipetiolata* and *K. uber*, are here regarded as a single entity.

ADDITIONAL KEYWORDS: montane forest – morphological traits – multivariate analyses – Oxylobinae – species complex – species distribution modelling (SDM).

INTRODUCTION

Kaunia is a small genus of 13 species in Eupatorieae, Asteraceae (King & Robinson, 1980; Jørgensen, Nee & Beck, 2010). *Kaunia* spp. are shrubs with showy cymose–corymbose capitulescences; they are important ecological constituents of Andean subtropical montane forest and montane scrublands from north-western Argentina to Ecuador. *Kaunia* inhabits variable environments especially in the shrubby layer or often as elements of secondary forests (Liberman Cruz & Pedrotti, 2006). *Kaunia* spp. play a key role in Andean ecosystems by dominating or co-dominating specific vegetation units in the montane forest (Seibert, 1993; Liberman Cruz & Pedrotti, 2006).

Six subtropical montane forest species of *Kaunia* [*K. arbuscularis* (B.L.Rob.) R.M.King & H.Rob., *K. lasiophthalma* (Griseb.) R.M.King & H.Rob., *K. longipetiolata* (Sch.Bip. ex Rusby) R.M.King & H.Rob., *K. rufescens* (P.W.Lund ex DC.) R.M.King & H.Rob., *K. saltensis* (Hieron.) R.M.King & H.Rob. and

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K. uber (B.L.Rob.) R.M.King & H.Rob.; see Appendix]
are remarkable for their superficial morphological
similarity (Hieronymus, 1897; Robinson & Holmes,
2008; Novara, 2009). From a molecular point of view,
three species of this complex have been recovered
as monophyletic (*K. rufescens*, *K. lasiophthalma* and
K. saltensis; Rivera *et al.*, 2016). The sampling of
Kaunia, however, was scarce and low.

The six species of the complex, although somewhat
overlapping, show a continuous distribution along a
latitudinal gradient of subtropical montane forest from
Ecuador to Argentina. In the Andes, as in other regions
worldwide, disentangling species delimitation has
implications in defining species richness, conservancy
strategies and elucidating the biogeographical history
of the ecosystem component units. On the other
hand, some recent studies have explored the role of
climatic niche attributes in species diversification
(e.g. Kozak & Wiens, 2010; Schnitzler *et al.*, 2012;
Kostikova, Salamin & Pearman, 2014). Studying the
environmental conditions affecting the distribution of
Kaunia spp. and the variation in morphological traits
could provide an integrative approach to help in species
delimitation. In addition, these studies could provide
the first knowledge of the spatio-temporal paths of
diversification of *Kaunia* in the Andes.

As suggested by Blundo *et al.* (2012) and Malizia *et al.*
(2012), to understand the environmental conditions
affecting the distribution of *Kaunia* and other species in
the Andean montane forest, latitudinal and elevational
gradients and regional environmental factors in the
Andes need to be considered. A species with a wide
latitudinal range of distribution (from Bolivia to
Ecuador) in this complex, *K. longipetiolata*, has been
treated either as a polymorphic species (Robinson &
Holmes, 2008) or as three different, more geographically
restricted species (King & Robinson, 1980; Hind, 2011).
Indeed, the confusing circumscription of this species
led to misinterpretations of its distributional range
with the consequent regional and taxonomic biases
in the diversity estimates (Brako & Zarucchi, 1993;
Jørgensen & León-Yáñez, 1999; Robinson & Holmes,
2008; Jørgensen *et al.*, 2010).

Elevational gradient also appears to influence the
distribution of some species in this complex of *Kaunia*
(Blundo *et al.*, 2012; Malizia *et al.* 2012). In the Andes
of Argentina, for instance, *Kaunia* spp., although found
throughout almost the whole elevational gradient of
subtropical forest, apparently prefer environments
1600–2100 m a.s.l. (Blundo *et al.*, 2012; Malizia *et al.*,
2012). Elevational gradients in the Andes and the
changing environmental conditions are crucial in the
definition of vegetation types and its constituents.
According to Malizia, Blundo & Pacheco (2006) and
Malizia *et al.* (2012), elevation has dramatic effects
on vegetation types of the subtropical montane forest,
including shifts in species richness, tree height and
tree top surface. Additionally, regional environmental
factors, such as climate, also vary along sites in the
montane forest and may also be significant for its
species composition (Blundo *et al.*, 2012), probably
impacting on the distribution of *Kaunia*.

From the preliminary evidence, a context of
morphologically similar traits and somewhat
overlapping distributional patterns obscures the
species distinction in this Andean complex of six *Kaunia*
spp. We aim to explore different sources of data to
clarify species delimitation in this complex. To this end,
morphological and environmental data of the species
of the complex were assessed using multivariate and
species distribution modelling (SDM) approaches.

We expect that climatic niche and quantitative
characters allow the identification of morphologically
similar Andean *Kaunia* spp. Otherwise, only one
species rather than six may be considered. We
hypothesize that the species in this complex of *Kaunia*
have different climatic niches, which may have acted
in promoting its diversification.

MATERIAL AND METHODS

MORPHOMETRIC ANALYSES

Plant material and morphological characters

A complex of six morphologically similar *Kaunia* spp.
was selected for this study. In total, 229 herbarium
specimens from CORD, CTES, F, GH, LP, LPB, MO and
NY (abbreviations from Thiers, 2013) were examined
and from which 75 were selected and measured for
their inclusion in the statistical analyses (Appendix).
Thirty-one vegetative and floral characters were
investigated (Table 1), including those regarded here
to be reliable for the identification of species and those
known to be diagnostic in *Kaunia* (De Candolle, 1836;
Grisebach, 1874; Hieronymus, 1897; Rusby, 1893;
Robinson, 1920; Cabrera, 1978; Cabrera & Klein, 1989;
Ariza Espinar, 1994; Vega & Dematteis, 2008; Novara,
2009). Invariant and nearly invariant characters were
excluded from the analyses. Twenty-seven characters
were used in the final analyses (Table 1).

When the availability of specimens made it possible,
replicates of three measurements for each character
were obtained and the average was used in the ensuing
statistical analyses.

Statistical analyses

Statistical analyses were performed using PAST v.3.06
(Hammer, Harper & Ryan, 2001) and XLSTAT v.2.01
software (Addinsoft, Paris, France). We standardized

Table 1. Table of morphological traits measured for the morphological analyses of *Kaunia arbuscularis*, *K. lasiophthalma*, *K. longipetiolata*, *K. rufescens*, *K. saltensis* and *K. uber*

Character	Description
INTLEN15 #	Internode length: measured at 15 cm of capitulescence base (cm)
INTLEN0 #	Internode length: measured at capitulescence base (cm)
LEPELE15 #	Petiole length: measured on leaves at 15 cm of capitulescence base (cm)
LEPELE0 #	Petiole length: measured on leaves at the capitulescence base (cm)
LMTOL	Length of leaf margin tooth: measured on an equatorial tooth (mm)
LMTOW	Width of leaf margin tooth: measured on an equatorial tooth (mm)
NUMT/LL	Number of teeth of leaf margin/leaf blade length (cm)
NUMTDT/LL	Number of teeth of leaf margin (distal third)/leaf blade length (cm)
NUMTMT/LL	Number of teeth of leaf margin (middle third)/leaf blade length (cm)
NUMTPT/LL	Number of teeth of leaf margin (proximal third)/leaf blade length (cm)
LMBLBFP	Midvein length: measured between leaf base and the divergence point of the first pair of secondary veins (mm)
LMBLFPS	Midvein length: measured between the divergence point of first pair of secondary veins and the divergence point of second pair of secondary veins (mm)
HPV/HM +	Height of midvein/height of mesophyll: measured in cross-section
WL/ LL	Leaf blade width: measured at its widest point/leaf blade length (cm)
LLBT	Length of leaf blade: measured from the base to the widest point (cm)
WDT*	Maximum leaf width (distal third) (cm)
CASHLS	Area of abaxial leaf surface covered by simple trichomes (%): observations with a stereoscopic microscope (magnification 4×)
PGLH +	Presence of glandular trichomes on abaxial leaf surface
CASHUS	Area of adaxial leaf surface covered by simple trichomes (%): observations with a stereoscopic microscope (magnification 4×)
PUGH*	Presence of glandular trichomes on adaxial leaf surface
CAGHP	Area of phyllaries covered by glandular trichomes (%): observations with a stereoscopic microscope (magnification 4×)
LCAPT	Capitulescence length (cm)
LFIC*	Length of the capitulescence first internode (cm)
LEPED*	Length of capitulum peduncle (mm)
NUMFLO*	Number of florets per head
NUMPHY*	Number of phyllaries per head
LEINV*	Involucre height (mm)
LECOR*	Corolla length (mm)
NGHPCL*	Number of glandular trichomes per corolla lobe
NUMPBR*	Number of pappus bristles
CYPLEN*	Cypsela length (mm)

Traits indicated with a numeral (#) were not included in analyses because measurements were scarce. Traits with an asterisk (*) were not included in analyses because they were correlated with other traits. Traits with a plus (+) symbol were not included in analyses because they were not informative when *K. saltensis* was excluded.

variables prior to all analyses with $\log_{10}$ transformation. The character value was transformed through the addition of a constant value of 1 to ensure positive values for all characters.

Morphological variation within and among taxa was assessed first using univariate statistics (mean, SD, variance) and multivariate morphometric analyses [principal component analysis (PCA) and discriminant analysis (DA)].

To explore correlations and dependencies among characters, a pairwise Pearson correlation matrix was created. One trait of each pair with a correlation value > 0.6 was excluded. A preliminary matrix of 16 traits was used in all analyses. We performed PCA based on a variance–covariance matrix and the results were plotted in two-dimensional scatter plots.

DA of quantitative morphological variables was used to determine statistically significant differences among a priori groups (the six *Kaunia* spp.). Wilk's lambda, Pillai's trace and Hotelling-Lawley trace tests for equality of group centroids were carried out based on Mahalanobis distances between coordinates in

N-dimensional hyperspace and the F statistics on the distances (Cook, Semple & Baum, 2009).

Preliminary analyses (PCA and DA) showed all the specimens of *K. saltensis* as a clearly separated group respect to the other samples. To explore deeper distinction among the other species, we excluded the specimens of *K. saltensis* from a second round of analyses. When *K. saltensis* was excluded, two traits became invariant [presence of glandular trichomes on abaxial leaf surface (PGLH) and height of midvein/height of mesophyll (HPV/HM; Supporting Information, Appendix S1, Table S1], and thus they were excluded from the data matrix. The final analyses were carried out based on 60 specimens and 14 traits.

SPECIES DISTRIBUTION AND CLIMATE NICHE ANALYSIS

An SDM approach (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005; Araújo *et al.*, 2013) was used to define the potential distribution and compare climatic space between the species of this *Kaunia* complex in South America. The BIOMOD2 package (Thuiller *et al.*, 2016) in R (R Core Team, 2017) was used to develop the SDM framework. BIOMOD2 allows the user to run a set of different modelling techniques and to define an ensemble of model projections. The ensemble modelling approach allows us to deal with uncertainties related to SDM methodology, for example the sensibility of techniques to the definition of pseudo-absences (Lobo, Jiménez-Valverde & Hortal, 2010) and the number of occurrences used (Hernandez *et al.*, 2006). In our study, four techniques were selected to define the ensemble for current projection of *Kaunia* spp. in this complex: generalized linear model (GLM), generalized boosting model (GBM), random forest (RF) and maximum entropy (Maxent). The selected techniques represent the main two families of models (statistical and machine-learning methods) and showed good performance under different assessment of SDM techniques (Elith *et al.*, 2006).

Occurrence data were obtained from specimens in nine herbaria (CORD, CTES, F, GH, LP, LPB, MO, NY, SI) completing a database of 229 records for the six species of the *Kaunia* complex. To obtain accurate and comparable SDM models, two species were excluded from the SDM analysis (*K. arbuscularis*, *K. uber*) because they have a low number of occurrences (<10), making it impossible to calibrate and project a reliable SDM model. The final selected species occurrences were filtered to avoid spatial autocorrelation using the rarefaction procedure present in SDMtools (Brown, 2014). This procedure allows us to deal with close distance effects between occurrences and spatial autocorrelation of variables. In Table 2 we show the total number of occurrences per species and the different selection procedures to define the final number of occurrences used with BIOMOD2.

Climatic variables for species distribution modelling were obtained from Worldclim (Hijmans *et al.*, 2005). As a procedure for variable selection we apply a correlation pairwise analysis (Pearson's product moment correlation coefficient) for all the 19 current bioclimatic variables for South America present in Worldclim, which are been widely used for plant distribution modelling. The results allow discrimination of those variables with high correlation (> 0.8) in the pairwise analysis. We obtained a final set of seven variables with low correlation to use in BIOMOD2: annual mean temperature, minimum temperature of the coldest month, temperature annual range, annual precipitation, precipitation of wettest month, precipitation of driest month and precipitation of warmest quarter.

Two repetitions and one pseudoabsence approach (10 000 random points around the whole study area) was carried out for each of the four techniques run under the BIOMOD2 framework, selecting a calibration set with the 20% of initial occurrences. Performance was tested using TSS (true skill statistics). A final binary ensemble was obtained using a TSS binary transformation for each full model of the four techniques. The binary ensemble

Table 2. Total number of records per species of *Kaunia* and selection procedures to define the final number of records used in the species distribution modelling (SDM)

	Total number of records	Number of unique records	Records removed by rarefaction	Records used in modelling
*K. arbuscularis**	5	5		
K. lasiophthalma	104	83	11	72
K. longipetiolata	38	34	5	29
K. rufescens	26	26	4	22
K. saltensis	112	72	12	60
*K. uber**	9	9		
Total	294	229	32	183

*Species not modelled.

for each species was used to establish climatically suitable areas in the climatic niche comparisons.

We follow the framework proposed by Broennimann *et al.* (2012) for niche analysis, calculating climatic niche overlaps between species and estimating similarity and identity indices. This framework allows the analysis of species–climate relationships using the availability of different environmental (climatic) variables within niche space. It has been used to explore niche dynamics, for example between native and invaded ranges (Liu *et al.*, 2017), and to track climate change (Ralston *et al.*, 2017).

RESULTS

MORPHOMETRIC ANALYSES

Univariate analysis

The means, SDs and ranges of the 27 traits initially scored were calculated for 75 specimens of *Kaunia* (Supporting Information, Appendix S1, Table S1). The ranges of variation in each trait overlap to such an extent that none of them can be used individually to provide reliable delimitation, with the exception of six characters (CAGHP, CASHLS, CASHUS, LMBLBFP, PGLH, PUGH), which clearly allow *K. saltensis* to be distinguished.

Principal component analysis

According to our results (in the analyses excluding *K. saltensis*), in the scatter plot showing PC1 vs. PC2 (Fig. 1A) one group of specimens belonging to *K. lasiophthalma* could be discriminated to some extent. The remaining specimens are distributed in one undifferentiated cloud, with the possible exception of some specimens of *K. rufescens*. Less resolution was obtained by comparing PC1 vs. PC3 (Fig. 1B). In the PCA of the data matrix excluding *K. saltensis*, the first three principal components (PCs) accounted for 66.8% of the total variance of the data (34.98, 16.43 and 15.39%, respectively) (Fig. 1A, B). In decreasing order, PC1 has the highest loadings for area of adaxial leaf surface covered by simple trichomes (CASHUS; eigenvector: 0.73), area of abaxial leaf surface covered by simple trichomes (CASHLS; 0.54) and number of teeth of leaf margin/leaf blade length (NUMT/LL; –0.19). PC2 has the highest loadings for area of phyllaries covered by glandular trichomes (CAGHP; eigenvector: 0.82) and area of adaxial leaf surface covered by simple trichomes (CASHUS; –0.21). PC3 has the highest loadings for area of phyllaries covered by glandular trichomes (CAGHP; 0.46), number of teeth of leaf margin/leaf blade length (NUMT/LL; 0.45) and area of adaxial leaf surface covered by simple trichomes (CASHUS; 0.39).

Discriminant analysis

The results of the DA more clearly discriminated groups of specimens than those of the PCA (*K. lasiophthalma*, *K. rufescens*, and another group with *K. arbuscularis*, *K. longipetiolata* and *K. uber*). As a first result of DA, the eigenvalue for the first canonical axis (14.09) accounted for 70.24% of the variation, the eigenvalue for the second (4.63) for 23.08% of the variation (Fig. 1C) and the eigenvalue for the third (0.84) for 4.19% of the total dispersion of the specimens. The most discriminating characters for the first axis were, in decreasing order: area of adaxial leaf surface covered by simple trichomes (CASHUS; loading = 0.08), area of abaxial leaf surface covered by simple trichomes (CASHLS; 0.04) and area of phyllaries covered by glandular trichomes (CAGHP; –0.02). For the second axis, the most discriminant characters were area of abaxial leaf surface covered by simple trichomes (CASHLS; –0.11), midvein length: measured between the divergence point of the first pair of secondary veins and the divergence point of the second pair of secondary veins (LMBLFPS; –0.06), and area of adaxial leaf surface covered by simple trichomes (CASHUS; -0.05). For the third canonical axis the values were: leaf blade width: measured at its widest point/leaf blade length (WL/LL; 0.09) and area of phyllaries covered by glandular trichomes (CAGHP; 0.07). The probabilities for Wilk's lambda [Value (v) = 0.004; F value (Fv) = 8.72; d.f. = 56], Pillai's trace (v = 2.529; Fv = 5.405; d.f. = 56) and Hotelling-Lawley trace (v = 19.763; Fv = 14.015, d.f. = 56) indicated significant differences at least between one group centroid and the others (P < 0.0001). F values based on Mahalanobis distances indicate significant differences between most pairs of group centroids (*P* < 0.0001). Separation between the group centroids of *K. arbuscularis* and *K. uber* were less well supported (*P* = 0.011).

SPECIES DISTRIBUTION AND CLIMATE NICHE ANALYSIS

Species distribution modelling

The results of the SDM approach are presented in Figure 2 where we show the final binary model obtained for the ensemble of modelling techniques carried out with BIOMOD2. The importance of climatic variables used for the definition of potential distributions models (Fig. 3, Supporting Information, Appendix S2, Fig. S1) reveals overall similar results, annual mean temperature being the most relevant variable, with the exception of *K. longipetiolata* for which minimum temperature of the coldest month was the most important. In *K. rufescens*, precipitation of the warmest quarter was relevant in indicating a difference with the other three species.
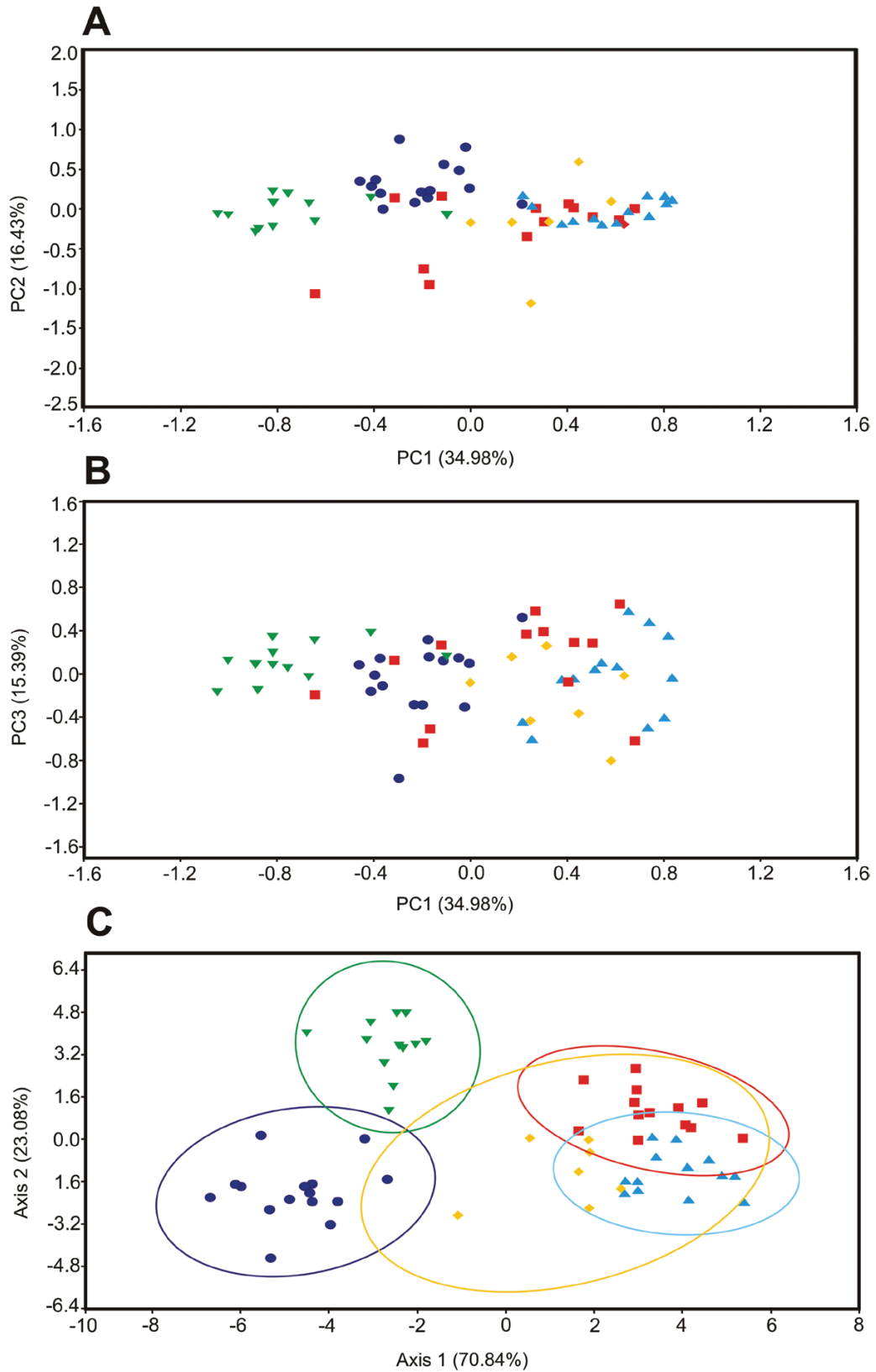
Comparison of climatic spaces

Climatic spaces obtained from the final binary ensemble model were compared for the four species using the equivalence test, Schoener's niche overlap index (*D*) and identity index (*I*) (Fig. 4 and Table 3). The first overall results show that the potential species distribution is statistically different because of the similarity simulations. The four species show geographically separated distributions, and thus the equivalence test is not statistically supported among all species, and this is finally reflected in the results for overlap and identity indices. The results indicate closer relationships in terms of climatic space similarity between *K. lasiophthalma* and *K. saltensis* (*D*: 0, 57, *I*: 0, 68) and *K. longipetiolata* and *K. saltensis* (*D*: 0, 44, *I*: 0, 62). Finally, *K. rufescens* presents lower values for both indices in all the pairwise comparisons (Table 3, Supporting Information, Appendix S2, Fig. S2).

DISCUSSION

Our morphometric analyses provided clear identification of *K. saltensis*, although discrimination of the other five species was less conclusive. Overall, our results showed that this Andean complex of *Kaunia* spp. has statistically different potential distributions, although some similarities between species in terms of climatic space were obtained. The results of our integrative study confirm the discrimination of three species (*K. lasiophthalma*, *K. rufescens* and *K. saltensis*), whereas *K. arbuscularis*, *K. longipetiolata* and *K. uber* are regarded here as a single entity. With the evidence obtained here, we discuss the biogeographical context that could have affected the distribution of these two species.

MORPHOMETRIC ANALYSES

From the six species in this Andean complex of *Kaunia*, *K. saltensis* was clearly discriminated in all morphometric analyses. *Kaunia saltensis* is a species of Andean forests from northern Argentina to central Bolivia and has distinguishing glabrous leaves and phyllaries. According to our analyses, leaf characters including type of trichomes and area covered by trichomes are significant for discrimination of groups in this complex. Unlike vegetative traits, most floral characters were insufficient for delimitation of the species. As an exception, glandular trichomes on phyllaries were important for grouping specimens, although they are lacking in *K. saltensis*. In this framework, in particular the glabrous leaves of *K. saltensis* are set apart from those of the other species of the complex, potentially explaining its clear distinction in the preliminary analyses.

Discrimination of the other five species of the complex was less conclusive. The DA results more clearly distinguished the groups than the PCA results. Together, the two analyses allowed the discrimination of *K. lasiophthalma* and, to a lesser extent, *K. rufescens*. The identification of the other three species of the complex (*K. arbuscularis*, *K. longipetiolata* and *K. uber*) was not supported. Previous authors (Robinson & Holmes, 2008) noted the similarity of these three species and sank two under *K. longipetiolata*.

SPECIES DISTRIBUTION AND CLIMATE NICHE OF THE ANDEAN COMPLEX OF *KAUNIA*

The distribution of K. longipetiolata *in Ecuador*

According to our results, the climatic variables that most influenced the distributions of the *Kaunia* spp. were annual mean temperature together with minimum temperature of coldest month and precipitation of warmest quarter (Fig. 3, Supporting Information, Appendix S2, Fig. S1). Specifically for *K. longipetiolata*, minimum temperature of coldest month was the most important climatic variable. Low temperatures at high elevations are known to affect tree distribution and diversity towards the tree line (Stevens & Fox, 1991; Blundo *et al.*, 2012). Low temperatures have been also indicated as a limiting factor for mountain forest, preventing recruitment outside of closed canopy forest for some tree species (Rehm & Feeley, 2015) or affecting tree cover (Greenberg *et al.*, 2015). In certain areas of Bolivia, *K. longipetiolata* dominates a community marginal to alder (*Alnus acuminata* Kunth) forests (Seibert, 1993), 2700–3000 (3400) m a.s.l. The importance of minimum temperature of coldest month in *K. longipetiolata* could be explained as a climatic control in the distribution related to elevation. Indeed, the low temperatures in the coldest month appear to have a high impact in *K. longipetiolata*, which is the only species of the genus with deciduous leaves during the coldest season.

The modelled potential distribution of *K. longipetiolata* extends its current distribution (from Argentina to Peru) northwards, suggesting suitable habitats in Ecuador. These results and those of our multivariate


Figure 1. Scattergrams for the principal coordinate (PCA) and discriminant (DA) analyses carried out on Andean *Kaunia* spp. A, first two components of the PCA (PC1 vs. PC2); B, first and third components of the PCA (PC1 vs. PC3); C, first and second canonical axis, from DA. In the four cases, the eigenvalues of each axis are provided in parentheses. Symbols: ♦, *K. arbuscularis* (orange); ▼, *K. lasiophthalma* (green); ■, *K. longipetiolata* (red); ●, *K. rufescens* (blue); ▲, *K. uber* (light blue).
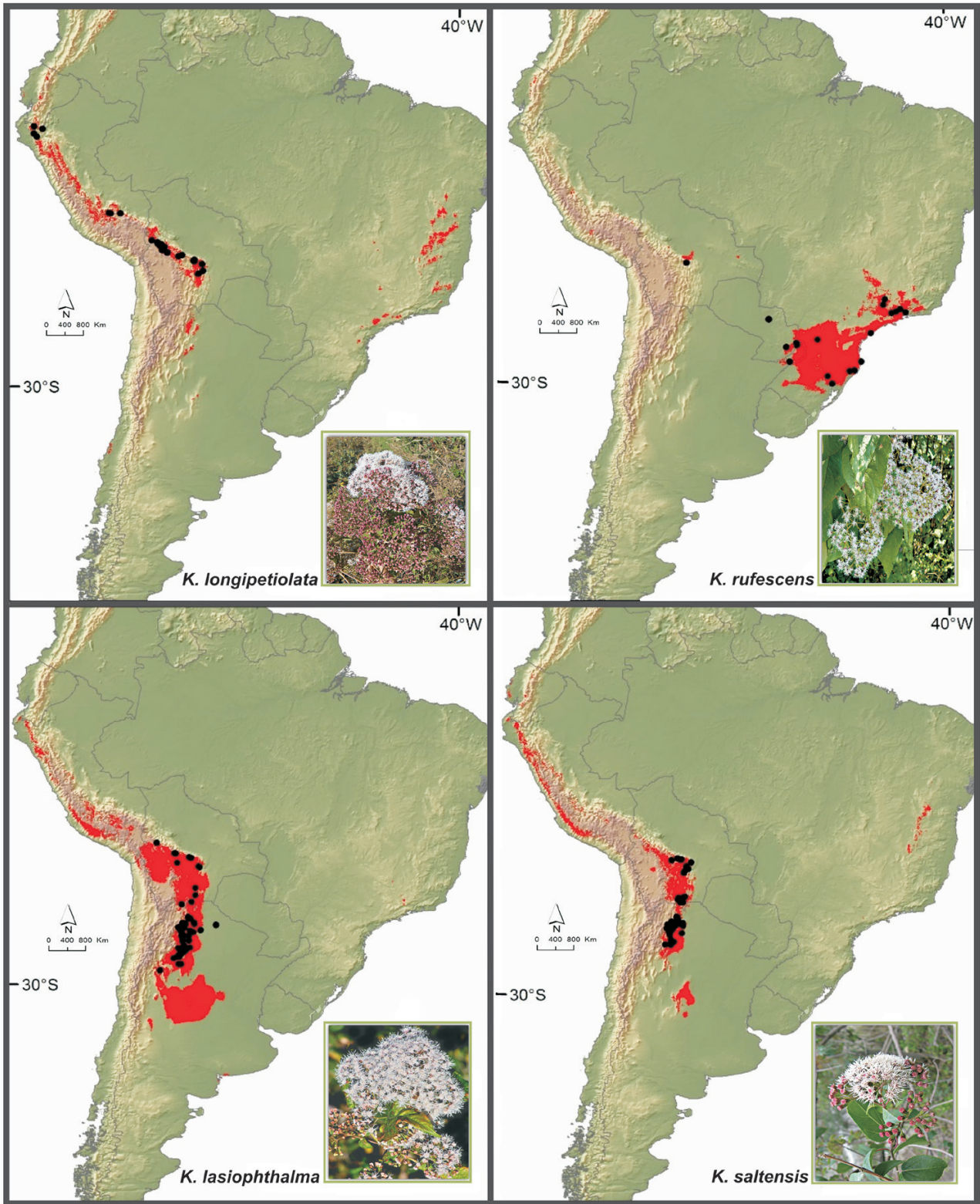
Figure 2. Potential distribution models for the four analysed Andean *Kaunia* spp. Red areas show the final binary model obtained from the ensemble of techniques in BIOMOD2. Black dots represent the records used for modelling.
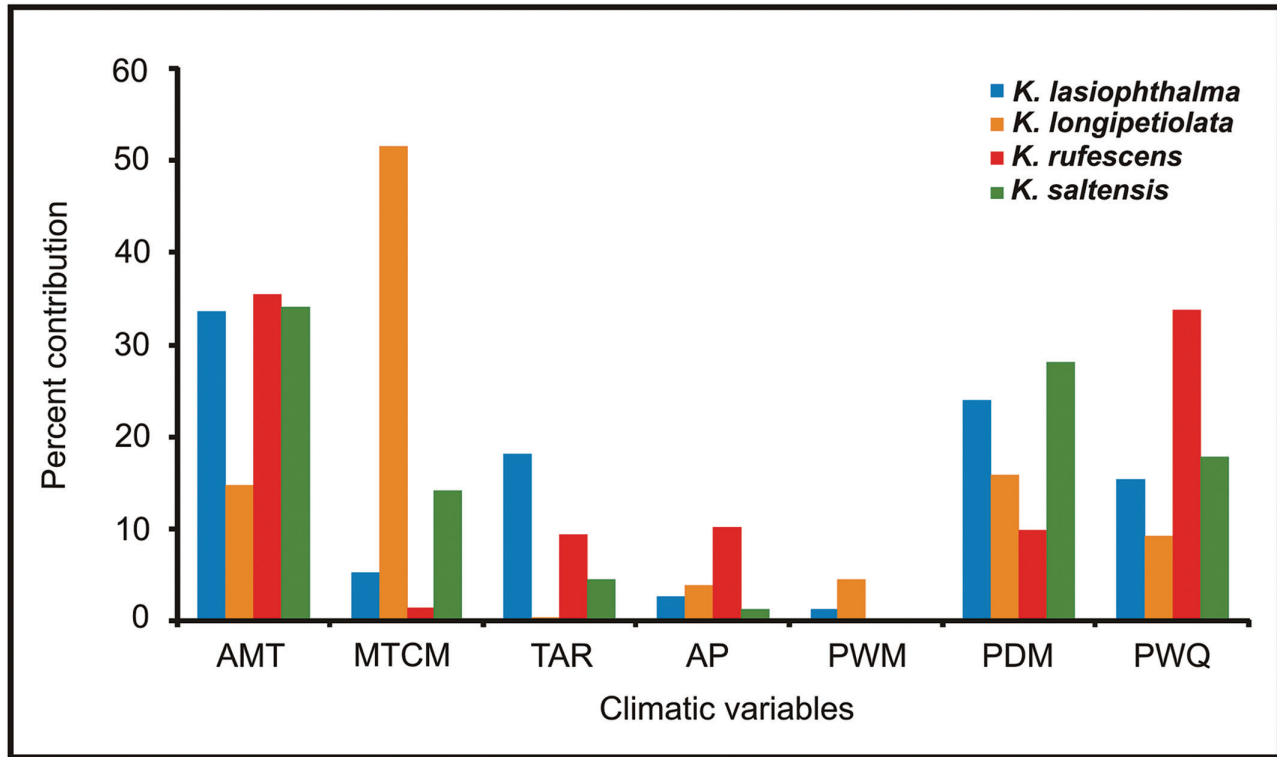
Figure 3. Importance of climatic variables used for the definition of potential distribution models of the analysed *Kaunia* spp. AMT, annual mean temperature; AP, annual precipitation; MTCM, minimum temperature of the coldest month; PDM, precipitation of driest month; PWM, precipitation of wettest month; PWQ, precipitation of warmest quarter; TAR, temperature annual range.

analyses provide additional evidence for combining this species with *K. uber* (from Peru) and *K. arbuscularis* (endemic to Ecuador and northern Peru) as proposed by Robinson & Holmes (2008). These results shed light on the uncertainty on the variable accounts of diversity of *Kaunia* in Ecuador (e.g. Jørgensen & León-Yáñez, 1999; Robinson & Holmes, 2008; Jørgensen *et al.*, 2010), restricting it to only *K. longipetiolata* and *K. pachanoi* (B.L.Rob.) R.M.King & H.Rob., the latter a species outside the complex of morphologically similar species.

As shown in our SDM, Andean forests from Bolivia to Ecuador provide suitable habitats for *K. longipetiolata*. Along this distribution, the Amotape–Huancabamba zone, in northern Peru and southern Ecuador, is an area where physical and environmental conditions of the Andes change dramatically (Weigend, 2002). The Amotape–Huancabamba zone has often been indicated as a dividing line between the floras of the northern and central Andes (Vuilleumier, 1968; Prance, 1989) or, in other cases, as a broad overlap zone especially for low- and mid-elevation taxa (Weigend, 2002; Struwe *et al.*, 2009). In this area, *K. longipetiolata* inhabits secondary forest on the east side of the Andes at 1900–2200 m a.s.l. Based on our model, the Amotape–Huancabamba

zone, instead of acting as a barrier, apparently allowed migration of *K. longipetiolata*.

In a historical biogeographical context, the diversification of Andean flora has been driven by a variety of processes (Luebert & Weigend, 2014). It could be that mountains played the role of a corridor for migration of some species (e.g. *K. longipetiolata*) along a latitudinal gradient, most probably after the last Andean uplift, when many other Asteraceae underwent high diversification (Luebert & Weigend, 2014).

The distribution of K. rufescens *in Brazil*

Apart from *K. longipetiolata*, annual mean temperature emerged as the most important variable to define the climatic niches of the modelled species. For *K. rufescens*, which occurs in the Andes and south-eastern Brazil, besides annual mean temperature, precipitation of the warmest quarter emerges as a relevant climatic variable, differentiating this species from the other three modelled here. The distinctiveness of *K. rufescens* observed when climatic spaces of the modelled species are compared might be due to the capacity of this species to live in environments different from those of the Andes.
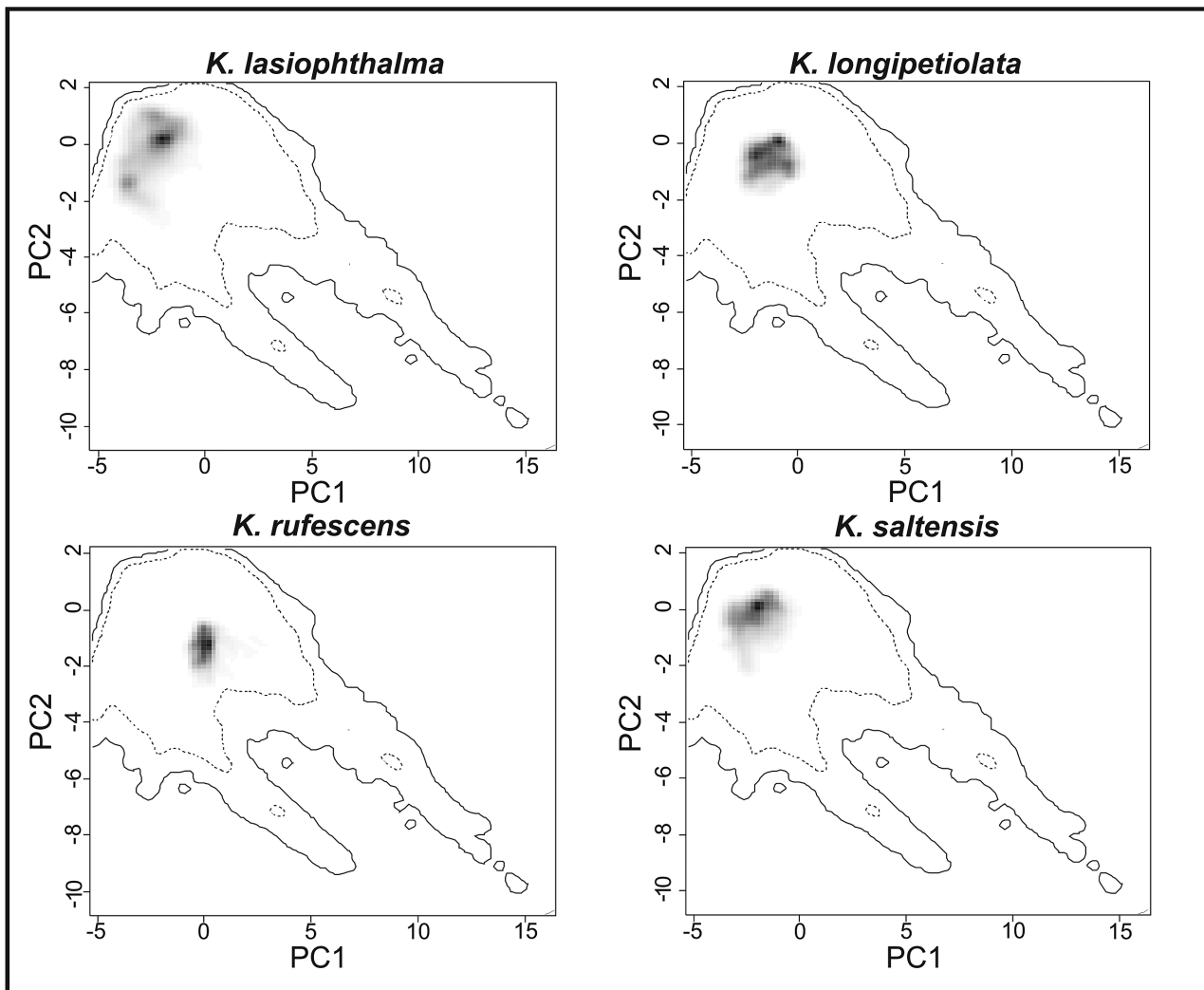
Figure 4. Climatic spaces of the four analysed Andean *Kaunia* spp. Grey scale shows the density of occupied area in climatic space. Dotted and solid lines depict 50 and 75% of the climatic space, respectively, used by the species.

Table 3. Pairwise comparisons results for Schoener's overlap index (*D*) and identity index (*I*) for *Kaunia* species

	K. lasiophthalma	*K. longipetiolata*	*K. rufescens*	*K. saltensis*
D				
K. lasiophthalma				
K. longipetiolata	0.2247115			
K. rufescens	0.0063773	0.0529206		
K. saltensis	0.5708719	0.4403371	0.0065346	
I				
K. lasiophthalma				
K. longipetiolata	0.4814474			
K. rufescens	0.3016955	0.332981		
K. saltensis	0.6847886	0.627598	0.3016902	

Many disjunct distributions between the Andes and eastern Brazil have been explained by a reduction of unfavourable habitats or the interposition of new patches of montane forest that allowed migration during the Quaternary (Simpson Vuilleumier, 1971; Safford, 2007; Michelangeli *et al.*, 2013), and this could

be the case for *K. rufescens*. Instead, long-distance dispersal has been regarded as unlikely for this distributional pattern (Safford, 2007).

Distinctiveness of K. saltensis *in the context of its similar climatic space with* K. lasiophthalma

Two pair of species, *K. longipetiolata* and *K. saltensis* on the one hand, and *K. lasiophthalma* and *K. saltensis* on the other, were the pairs with the most similar climatic space according to our results. However, in nature, *K. longipetiolata* and *K. saltensis* do not have overlapping distributions and they do not substantially coincide in their SDMs. The situation with *K. lasiophthalma* and *K. saltensis* differs, as they coexist in part of their distributional range but show, at the same time, an elevational gradient. Indeed, in the Andean subtropical forest of north-western Argentina, the presence of *K. lasiophthalma* and *K. saltensis* is related to the elevational gradient (Blundo *et al.*, 2012). *Kaunia saltensis* is found in dry and cloud forest, across a wide elevational gradient (400–2300 m a.s.l.), although it is more abundant in the upper cloud montane forest (1600–2000 m a.s.l.). In contrast, *K. lasiophthalma* is found in the lower cloud montane forest (900–1600 m a.s.l.), where it is most abundant. *Kaunia saltensis* and *K. lasiophthalma* also coexist in some environments (Brown & Malizia, 2007). In terms of phenology, these species have different flowering periods, *K. lasiophthalma* blooming during late winter and *K. saltensis* blooming during summer.

According to Lomolino (2001), the extant patterns of diversity along elevational gradients may, to some degree, represent historical legacies of past climates, and therefore some consideration of the historical biogeographical context that could have affected the distribution of *K. saltensis* and *K. lasiophthalma* can be explored. *Kaunia* is probably a recently diversified genus as indeed are Eupatorieae (*c.* 12 Mya; Schmidt & Schilling, 2000; Tippery *et al.*, 2014; Schilling *et al.*, 2015). Moreover, other members of the family have shown high diversification in the Andes during the Quaternary or at the earliest in the early Pliocene (Luebert & Weigend, 2014, and references therein). For a variety of other plant families, in addition, many studies have highlighted the exceptional diversification rates in the Andes as a possible consequence of the last Andean uplift (Vargas, Ortiz & Simpson, 2017) about 3 Mya.

Although part of a monophyletic group with the other *Kaunia* spp. (Rivera *et al.*, 2016), *K. saltensis* has been shown here to be somewhat morphologically distinct. The different flowering period of *K. saltensis* with respect to *K. lasiophthalma* is also important. Such temporal differences could provide evidence of sufficient divergence time for the establishment of the species and suggest a scenario in which ecological isolation may have played a role at some point in species differentiation of *Kaunia*. The expansions and contractions of biota along an elevational gradient as a response to alternating colder and warmer periods that occurred, most probably, during the Quaternary or late Pliocene were regarded by Luebert & Weigend (2014, and references therein) as one of the processes influencing the diversification of Andean flora. The temporal specifics and implications of this climatic alternation and the consequent isolation of populations of the ancestors of *Kaunia* remain unknown. However, the imprint that these events may have had in this genus could be reflected today in two morphologically and phenologically distinct species such as *K. saltensis* and *K. lasiophthalma*, which, at the same time, share similar climatic spaces and partially overlapping distributions.

REFERENCES

Araújo MB, Ferri-Yáñez F, Bozinovic F, Marquet PA, Valladares F, Chown SL. 2013. Heat freezes niche evolution. *Ecology Letters* **16:** 1206–1219.

Ariza Espinar L. 1994. Familia Asteraceae: tribu Eupatorieae. *Pródromo de la flora fanerogámica de Argentina Central* **1:** 16–65.

Blundo C, Malizia LR, Blake JG, Brown AD. 2012. Tree species distribution in Andean forests: influence of regional and local factors. *Journal of Tropical Ecology* **28:** 83–95.

Brako L, Zarucchi JL. 1993. *Catalogue of the flowering plants and gymnosperms of Peru.* St. Louis: Missouri Botanical Garden.

Broennimann O, Fitzpatrick MC, Pearman PB, Petitpierre B, Pellissier L, Yoccoz NG, Thuiller W, Fortin MJ, Randin C, Zimmermann NE, Graham CH, Guisan A. 2012. Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecology and Biogeography* **21:** 481–497.

Brown A, Malizia L. 2007. Lista comentada de los árboles de las yungas de Argentina. In: Brown AD, Montan MG, Ventura BN, Hilgert NI, Malicia LR, eds. *Finca San Andrés. Un espacio de cambios ambientales y sociales en el Alto Bermejo.* Tucumán: Ediciones del Subtrópico, Fundación Pro Yungas, 51–99.

Brown JL. 2014. SDMtoolbox: a phyton-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *Models in Ecology and Evolution* **5:** 694–700.

Cabrera AL. 1978. *Eupatorium.* In: Cabrera AL, ed. *Flora de la Provincia de Jujuy. República Argentina. Compositae–Colección Científica del INTA, Tomo XIII, Parte X.* Buenos Aires: Colección Científica, Instituto Nacional de Tecnología Agropecuaria, 106–155.

Cabrera AL, Klein RM. 1989. Compostas. 4. Tribo: Eupatorieae. *Flora Ilustrada Catarinense* **1:** 413–760.

Cook RE, Semple JC, Baum BR. 2009. A multivariate morphometric analysis of *Solidago* subsect. *Glomeruliflorae* (Asteraceae: Astereae). *Botany* **87:** 97–111.

De Candolle AP. 1836. *Compositae, Part I. Prodromus Systematis Naturis Regni Vegetabilis*, **Vol. 5.** Paris: Treuttel & Würtz.

Elith J, Graham CH, Anderson RP, Dudik M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton JMcC, Peterson AT, Phillips SJ, Richardson KS, Scachetti-Pereira R, Schapire RE, Soberon J, Williams S, Wisz MS, Zimmermann NE. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29:** 129–151.

Greenberg JA, Santos MJ, Dobrowski SZ, Vanderbilt VC, Ustin SL. 2015. Quantifying environmental limiting factors on tree cover using geospatial data. *PLoS One* **10:** e0114648.

Grisebach A. 1874. Plantae Lorentzianae. *Abhandlungen der Königlichen Gesellschaft der Wissenschaften zu Göttingen (Physikalische Classe)* **19:** 49–279.

Guisan A, Thuiller W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* **8:** 993–1009.

Guisan A, Zimmermann NE. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* **135:** 147–186.

Hammer Ø, Harper DAT, Ryan PD. 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* **4:** 9. Available at: http://palaeo-electronica.org/2001_1/past/issue1_01.htm

Hernandez PA, Graham CH, Master LL, Albert DL. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* **29:** 773–785.

Hieronymus GHE. 1897. Erster Beitrag zur Kenntnis der Siphonogamenflora der Argentina und der angrenzenden Länder, besonders von Uruguay, Paraguay, Brasilien und Bolivien. Fam. Compositae. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* **22:** 673–798.

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25:** 1965–1978.

Hind DJN. 2011. *An annotated preliminary checklist of the Compositae of Bolivia (version 2).* Available at: http://kew.org/science/tropamerica/boliviacompositae.

Jørgensen PM, León-Yáñez S. 1999. *Catalogue of the vascular plants of Ecuador.* St Louis: Missouri Botanical Garden.

Jørgensen PM, Nee M, Beck SG. 2010. *Catálogo de las plantas vasculares de Bolivia.* Available at: http://www.tropicos.org/Project/BC.

King RM, Robinson H. 1980. Studies in the Eupatorieae (Asteraceae) CCII. A new genus *Kaunia.* *Phytologia* **47:** 257–260.

Kostikova A, Salamin N, Pearman PB. 2014. The role of climatic tolerances and seed traits in reduced extinction rates of temperate polygonaceae. *Evolution* **68:** 1856–1870.

Kozak KH, Wiens JJ. 2010. Accelerated rates of climatic-niche evolution underlie rapid species diversification. *Ecology Letters* **13:** 1378–1389.

Liberman Cruz M, Pedrotti F. 2006. Woody formations in a mesothermic valley of Tarija Province, Bolivia. In: Gafta D, Akeroyd J, eds. *Nature conservation. Concepts and practice.* Berlin: Springer, 75–86.

Liu X, Petitpierre B, Broennimann O, Li X, Guisan A, Li Y. 2017. Realized climatic niches are conserved along maximum temperatures among herpetofaunal invaders. *Journal of Biogeography* **44:** 111–121.

Lobo JM, Jiménez-Valverde A, Hortal J. 2010. The uncertain nature of absences and their importance in species distribution modelling. *Ecography* **33:** 103–114.

Lomolino MV. 2001. Elevation gradients of species-density: historical and prospective views. *Global Ecology & Biogeography* **10:** 3–13.

Luebert F, Weigend M. 2014. Phylogenetic insights into Andean plant diversification. *Frontiers in Ecology and Evolution* **27:** 1–17.

Malizia LR, Blundo C, Pacheco S. 2006. Diversidad, estructura y distribución de bosques con cedro (*Cedrela* sp, Meliaceae) en el noroeste de Argentina y sur de Bolivia. In: Pacheco S, Brown AD, eds. *Ecología y producción de cedros (género Cedrela) de las yungas australes.* Tucumán: Ediciones del Subtrópico, 83–104.

Malizia L, Pacheco S, Blundo C, Brown AD. 2012. Caracterización altitudinal, uso y conservación de las yungas subtropicales de Argentina. *Ecosistemas* **21:** 53–73.

Michelangeli FA, Guimaraes PJF, Penneys DS, Almeda F, Kriebel R. 2013. Phylogenetic relationships and distribution of New World Melastomeae (Melastomataceae). *Botanical Journal of the Linnean Society* **171:** 38–60.

Novara LJ. 2009. Tribu Eupatorieae. Flora del Valle de Lerma. (Provincia de Salta, República Argentina). *Aportes Botánicos de Salta – Serie Flora* **9:** 1–124.

Prance GT. 1989. American tropical forests. In: Godall DW, ed. *Ecosystems of the World 14b, Tropical rainforest ecosystems.* Amsterdam: Elsevier, 99–132.

R Core Team. 2017. *R: A language and environment for statistical computing, version 3.3.3.* Vienna: R Foundation for Statistical Computing. Available at: https://www.R-project.org.

Rehm EM, Feeley KJ. 2015. Freezing temperatures as a limit to forest recruitment above tropical Andean treelines. *Ecology* **96:** 1856–1865.

Ralston J, DeLuca WV, Feldman RE, King DI. 2017. Population trends influence species ability to track climate change. *Global Change Biology* **23:** 1390–1399.

Rivera VL, Panero JL, Schilling EE, Crozier BS, Moraes MD. 2016. Origins and recent radiation of Brazilian Eupatorieae (Asteraceae) in the eastern Cerrado and Atlantic Forest. *Molecular Phylogenetics and Evolution* **97:** 90–100.

Robinson BL. 1920. The eupatoriums of Bolivia. *Contributions from the Gray Herbarium of Harvard University* **60:** 30–80.

Robinson H, Holmes WC. 2008. Compositae-Eupatorieae 190 (3). In: Harling G, Andersson L, eds. *Flora of Ecuador,* **Vol. 83**. Stockholm: Department of Systematic Botany, University of Göteborg & Section for Botany, Riksmuseum, 1–347.

Rusby HH. 1893. An enumeration of the plants collected in Bolivia by Miguel Bang, with descriptions of new genera and species. *Memoirs of the Torrey Botanical Club* **3:** 1–67.

Safford HD. 2007. Brazilian paramos IV. Phytogeography of the campos de altitude. *Journal of Biogeography* **34:** 1701–1722.

Schilling EE, Panero JL, Crozier BS, Scott RW, Dávila P. 2015. Bricklebush (*Brickellia*) phylogeny reveals dimensions of the great Asteraceae radiation in Mexico. *Molecular Phylogenetics and Evolution* **85:** 161–170.

Schmidt GJ, Schilling EE. 2000. Phylogeny and biogeography of *Eupatorium* (Asteraceae: Eupatorieae) based on nuclear ITS sequence data. *American Journal of Botany* **87:** 716–726.

Schnitzler J, Graham CH, Dormann CF, Schiffers K, Linder HP. 2012. Climatic niche evolution and species diversification in the Cape flora, South Africa. *Journal of Biogeography* **39:** 2201–2211.

Simpson Vuilleumier B. 1971. Pleistocene changes in the fauna and flora of South America. *Science* **173:** 771–780.

Seibert P. 1993. La vegetación de la región de los Kallawaya y del altiplano de Ulla-Ulla en los Andes Bolivianos. *Ecología en Bolivia* **20:** 1–84.

Stevens GC, Fox FJ. 1991. The causes of treeline. *Annual Review of Ecology and Systematics* **22:** 177–191.

Struwe L, Haag S, Heiberg E, Grant JR. 2009. Andean speciation and vicariance in Neotropical *Macrocarpaea* (Gentianaceae-Helieae). *Annals of the Missouri Botanical Garden* **96:** 450–469.

Thiers B. 2013. *Index Herbariorum: a global directory of public herbaria and associated staff.* New York Botanical Garden's Virtual Herbarium. Available at: http://sweetgum.nybg.org/ih/

Thuiller W, Georges D, Engler R, Breiner F. 2016. *biomod2: ensemble platform for species distribution modeling. – R package ver. 3.3–7.* Available at: http://CRAN. Rproject.org/package=biomod2.

Tippery NP, Schilling EE, Panero JL, Les DH, Casey SW. 2014. Independent origins of aquatic Eupatorieae (Asteraceae). *Systematic Botany* **39:** 1217–1225.

Vargas OM, Ortiz EM, Simpson BB. 2017. Conflicting phylogenomic signals reveal a pattern of reticulate evolution in a recent high-Andean diversification (Asteraceae: Astereae: *Diplostephium*). *New Phytologist* **214:** 1736–1750.

Vega AJ, Dematteis M. 2008. *Eupatorium rufescens* y *Vernonia oligactoides* (Asteraceae) nuevas citas para la Flora Argentina. *Bonplandia* **17:** 83–89.

Vuilleumier F. 1968. Population structure of the *Asthenes flammulata* superspecies (Aves: Furnariidae). *Breviora* **297:** 1–32.

Weigend M. 2002. Observations on the Biogeography of the Amotape-Huancabamba Zone in northern Peru. *The Botanical Review* **68:** 38–54.

APPENDIX

Voucher information of the specimens used in the morphometric analyses

Kaunia arbuscularis (B.L.Rob.) R.M.King & H.Rob. ECUADOR. Argelia. 2300 m, *Espinosa 691* (NY). Loja. Along the road to Loja, *c.* 4 km N of Loja, 6400 ft, *King & Garvey 6905* (NY); road La Toma-Loja, km 12., 2000 m, *Madsen & Ellemann 75199* (NY); vicinity of Las Juntas, *Rose 23229* (NY); between El Tambo and La Toma, 1000–2200 m, *Hitchcock 21348* (NY); 13,6 km E of Sambi on rd to Chinchicas (2 km W of Chinchicas), 2200 m, *Stuessy 5883* (LP); Zaragura, *Rose 23144* (NY).

Kaunia lasiophthalma (Griseb.) R.M.King & H.Rob. ARGENTINA. Catamarca. Andalgalá, Río del Potrero, 1600 m, *Venturi 4989* (GH); Ambato, Las Juntas, *Ulibarri 608* (CORD). Jujuy. Capital, Los Blancos, *Cabrera 15855* (LP). La Rioja. Capital, El Cantadero: Quebrada de la Aguadita, *Cerana 975* (CORD). Salta. Rosario de la Frontera, 900 m, *Venturi 9329* (LP); Guachipas, Pampa Grande, 1600 m, *Hunziker 1802* (LP). Tucumán. Cerro San Javier, *Cabrera 13586* (LP); Capital, 450 m, *Lillo 12912* (GH); Cuesta del Siambón, *Lorentz 508* (CORD). BOLIVIA. Cochabamba. Cercado, Valle del Cercado de Cochabamba, 2570 m, *Steinbach 37* (GH), *E.W.D. 396* (GH). Potosí. Charcas, San Pedro de Buena Vista, 2800 m, *Torrico & Peca 169* (LP).

Kaunia longipetiolata (Sch.Bip. ex Rusby) R.M.King & H.Rob. BOLIVIA. Cochabamba. Carrasco, Chua Khocha, 2300 m, *Renjel 14* (NY). Chuquisaca. B.Boeto, 2440 m, *Nee & Churchill 52797* (F); 2360 m, *Nee 52778* (F); Villa Taquina, 2900 m, *Eyerdam 25224* (F). La Paz. Inquisivi, 3550–3850 m, *Müller & Heinrichs 6418* (MO); 3200 m, *Lewis 881065* (NY); Larecaja, Sorata, 2800 m, *Beck 8633* (LPB); 7500 ft, *Williams 2408* (NY); Songo, *Bang 867* (NY); *Buchtien 651* (LP). PERÚ. Cajamarca. Jaén, Sallique de Catala a Piquijaca, 1940–2195 m, *Campos & Díaz 5408* (F). Cuzco. Paucartambo, Pillahuata, 2500 m, *Marin 1683* (F). Huancabamba. 4200 ft, *Towsend A174* (F).

Kaunia rufescens (P.W.Lund ex DC.) R.M.King & H.Rob. ARGENTINA. Misiones. Iguazú, Parque Nacional Iguazú, *Vanni 2770* (CTES); *Vanni 3441* (CTES). BOLIVIA. Santa Cruz. Caballero, 2500 m, *Nee & Mendoza 52543* (NY). BRASIL. Bananal. Estrada pa Sertao do Rio Vermello, *Brade 15901* (LP). Novo Horizonte. Lauro Müller, Vargem Grande, 350 m, *Reitz & Klein 6729* (LP); Lauro Müller, *Reitz & Klein 8861* (LP). Minas Gerais. Caldas, *Edwall 16336* (GH). Paraná. Larenjeiras do Sul, *Hatschbach 49550* (NY). Rio Grande do Sul. Farroupilha, Caldas, *Wasum 7972* (LP). Santa Catarina. Gravatal, 500 m, *Matzenbacher 28* (F). Sao Paulo. Serra da Mantiqueira entre Itajubá e Guaratinguetá, *Castellanos 23381* (F); Taimberinho, 50 m, *Ruiz c1148* (LP); Serra do Rio Rastro, 700 m, *Reitz & Klein 18139* (LP); Vila Flores, 800 m, *Wasum 8637* (NY). PARAGUAY. Charará region Guairá, *Rojas 6104* (LP).

Kaunia saltensis (Hieron.) R.M.King & H.Rob. ARGENTINA. Jujuy. Capital, Termas de Reyes, *Cabrera 8143* (LP); *Delucchi 1468* (LP); *Fabris 8037* (LP); Santa Bárbara, Cerro Centinela, *Fabris 5154* (LP); *Cabrera 17370* (LP); Tumbaya, Volcán, 2100 m, *Fabris 6329* (LP); Valle Grande: Río Jordán, 1600 m, *Fabris 5334* (LP). Salta. Cafayate, Río Colorado, *Krapovickas & Cristóbal 20687* (LP); Caldera, *Cabrera & Schwabe 218* (LP); Capital, San Lorenzo, *Cabrera 2991* (LP); Rosario de Lerma, Potrero de Linares, *Cabrera 13136* (LP). BOLIVIA. Cochabamba. Pojo, 2400 m, *King & Solomon 9652* (LPB). Comarapa. *King & Bishop 7663A* (F); Santa Cruz: Valle Grande, Loma Larga, 1966 m, *Hurtado 506* (LPB). Tarija. Eustaquio Méndez, 5 km antes de Padcaya, 1900 m, *Ehrich 45* (LP).

Kaunia uber (B.L.Rob.) R.M.King & H.Rob. PERÚ. Amazonas. Luya, Valley of Rio Utcubamba Tingo and Ponaya, 1750–1850 m, *Wurdack 1787* (GH). Cajamarca. Chota, arriba de Cochabamba, 2300 m, *Mostacero 1580* (MO); Celendín, Llanguat, 2500 m, *Mostacero 948* (F); Colasay, *Woytkowski 6843* (F); 2700 m, *Woytkowsky 6913* (F). Santa Cruz. ENE Monteseco, 1700 m, *Santisteban & Guevara 159* (NY). Lima. Jesus María, Jardín Botanico de INMETRA, 100 m, *Schunke Vigo 14685* (NY); *Plowman 11001* (F). Cuzco. Calca, *Boecke & Boecke 3248* (NY); gravelly river-valley floor (a tree common from here to Casma), 3000 ft, *Macbride & Featherstone 2549* (F). Cajamarca. Contumazá, Rupe (Chilete-Contumazá), 1500 m, *Sagastegui 9799* (MO); Anchash: Huailas, debajo de Pampa Romás, 2100 m, *Weberbauer 3184* (MOL). Cajamarca. San Ignacio, San José de Lourdes, Santo Tomas, 1950 m, *Quipuscoa 408* (MO).

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Morphological analysis. Table S1: Mean ± SD and range (minimum – maximum) for the 27 characters studied from the 75 analysed specimens of *Kaunia*.

Appendix S2. Potential distribution modelling and climate space. Figure S1: Importance of climatic variables for each of the four modelling techniques runs under the *biomod2* approach. Figure S2: Climatic space overlap obtained from the final binary ensemble model and similarity simulations compared for the four species in pairs.