Can phylogenetic signal, character displacement, or random phenotypic drift explain the morphological variation in the genus Geonoma (Arecales)?

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Plant clades may exhibit little or wide morphological variation as a result of (1) the retention of ancestral characteristics or phylogenetic signal, (2) character displacement, or (3) random phenotypic drift or convergence. Understanding the taxonomy and systematics of many plant lineages has been challenging due to continuous intraspecific morphological variation. To assess which evolutionary hypothesis could explain the morphological diversity in the genus Geonoma (Arecales), we performed a Mantel test between phylogenetic and morphological distances of 54 taxa, and tested for phylogenetic signal using Blomberg's K-statistic on continuous variables, and a randomization of character states. To obtain a phylogenetic (patristic) distance matrix for Geonoma, we constructed a molecular phylogeny of tribe Geonomateae using three nuclear DNA regions. A positive relationship between the patristic and a 26-discrete-character distance matrix ($R^2 = 0.55, P < 0.001$) supported the phylogenetic signal hypothesis. The randomization test showed that signal was present in 16 characters. No relationship was evident using a 17-quantitative-variable distance matrix ($R^2 = 0.07, P = 0.13$), supporting the random drift hypothesis or convergence, and all 17 K-values were close to 0, suggesting less phylogenetic signal than under the Brownian model. If most morphological variables traditionally used to classify Geonoma evolved randomly or convergently, it might explain Geonoma’s challenging taxonomy. © 2012 The Linnean Society of London, Biological Journal of the Linnean Society, 2012, 106, 528–539.


INTRODUCTION

Plant size and shape interact with the environment and determine the success of a species. Certain plant traits are known to possess an adaptive value. For example, it is well known that leaf size, branching patterns, and phyllotaxis change as a function of light availability (Poorter, Bongers & Bongers, 2006; Burns et al., 2008). However, not all plant traits may have a functional role because many present extensive plasticity within species, and thus could be regarded as evolutionarily labile. This is the case, for instance, for flower colour (McEwen & Vamosi, 2010). Understanding the taxonomy and systematics of plant families such as Commelinaceae (Evans et al., 2003) and Crassulaceae (Gontcharova & Gontcharov, 2009) has been challenging because of a documented morphological homoplasy or presumed plasticity. An improved understanding of the evolutionary behaviour of specific morphological variables should provide insight into their selective value and use in plant systematics.

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Based on a growing literature on the evolution of traits and niches (e.g. Blomberg, Garland & Ives, 2003; Ackerly, 2009; Maraun et al., 2009) we propose three hypotheses to explain evolutionary patterns of plant morphology (Fig. 1). (1) Closely related species tend to share the same morphology more than species drawn randomly from the tree, a pattern referred to as phylogenetic signal (Blomberg & Garland, 2002), whereas more distantly related species exhibit greater morphological variation. A plot of phylogenetic versus morphological distance will have a positive slope and be triangle-shaped under this hypothesis (Losos, 2008). (2) Recent species can be morphologically divergent or exhibit character displacement as a result of competitive exclusion (i.e. an adaptive radiation; Losos, 2000). Under this hypothesis, the relationship between phylogenetic and phenotypic distance will have a negative slope and also be triangular, with distant species keeping a divergent morphology or becoming more similar. (3) Morphological traits may have no selective value, or can be regarded as labile, corresponding to a random phenotypic drift hypothesis. A scatterplot with no relationship between phylogenetic history and morphology would result. This pattern would also arise under convergent evolution, in which different evolutionary trajectories result in similar solutions to the same ecological problem (Wake, 1991; Maraun et al., 2009).

Tribe Geonomatée (Arecales: Arecoideae) is a group of subcanopy and understorey palms with 103 recognized species in six genera (Dransfield et al., 2008; Henderson, 2011), which diversified during the Oligocene, approximately 31 Mya (Roncal et al., 2010). Geonoma Willd., the largest genus in the tribe, is one of the three largest palm genera in tropical America, with some species providing non-timber forest products (Svenning & Macia, 2002; Rodríguez-Buritica, Orjuela & Galeano, 2005). Species occur from southern Mexico over Central America to southeastern Brazil and also reach the West Indies (Dransfield et al., 2008). Areas with the highest Geonoma species diversity have annual precipitation regimes above 4000 mm, contain the oldest lineages, and are mostly in montane regions (Henderson, 2011; Roncal et al., 2011). Species delimitation and classification of Geonoma has been challenging because of the difficulty in finding morphological characters with phylogenetic value.

Morphological features such as habit, stem size, crown shape, leaf dissection, angle of primary veins with respect to the rachis, inflorescence and fruit colour, shape of flower-pit bracts, and flower-pit arrangement have been traditionally regarded as important for distinguishing Geonoma species (Spruce, 1869; Burret, 1930; Wessels Boer, 1968). However, a classification based on these characters or traits is difficult because of their homoplasious
nature, and within-species variation. Even in the last revision of the genus, 20% of the species were considered as complexes with no formal subspecific classification (Henderson, 2011). For example, a large variation in leaf shape that goes from the simple, narrow, wedge-shaped leaf to the regularly or irregularly pinnate leaf with sigmoid or straight pinnae can be observed within a species (Wessels Boer, 1968; Henderson, 2011). The same kind of variation can also be seen in other palm genera, such as *Bactris*, *Chamaedorea*, *Dypsis*, and *Pinanga* (Tomlinson, 1960; Dransfield, 1978; Hodel, 1992; Henderson, 2000). Wessels Boer (1968) hypothesized that the morphological variation observed in *Geonoma* results from a plastic response to environmental conditions or age, and therefore does not necessarily indicate a close relationship. Chazdon (1991) also noted that the solitary and clustered habit appeared to have originated several times within *Geonoma*, and thus suggested that convergence might be responsible for the similarities found among species.

We used *Geonoma* as a model group to test the phylogenetic signal, displacement, or random hypotheses on the evolution of morphological variation. We do this by presenting an improved molecular phylogeny of tribe Geonomatæ based on three low-copy nuclear DNA regions, one of which has only been used once in plant molecular systematics (Bacon, Baker & Simmons, 2012). We conduct a qualitative and quantitative analysis of the relationship between phylogenetic and morphological similarity among species, providing insight into the evolution of morphology and its implications for systematics.

**MATERIAL AND METHODS**

**MOLECULAR PHYLOGENY OF TRIBE GEONOMATÆ**

In this study we sampled four species (100%) of *Pholidostachys*, three (100%) *Calyptronoma*, the monotypic *Welfia*, ten (56%) *Calyptronyge*, two (40%) *Asterogyne*, 78 specimens of *Geonoma* representing 43 species (63%), and 19 species as outgroup (see Supporting Information, Table S1). For geographically widespread species or morphologically variable species complexes we sampled up to seven individuals. We used three nuclear loci: intron 4 of phosphoribulokinase (PRK; Lewis & Doyle, 2002), intron 23 of RNA polymerase II subunit 2 (RPB2; Roncal et al., 2005), and the region amplified by the conserved intron-scanning primer set #4 (CISP4; Bacon et al., 2008). We did not pursue the use of chloroplast genes because of lack of potential parsimony-informative characters during preliminary tests. The PRK and RPB2 datasets were largely taken from Roncal et al. (2005, 2010, 2011) and extended to include species from under-represented geographical areas, while the CISP4 dataset was newly generated for this study. Amplification, sequencing, cloning, and alignment followed the protocols described in Roncal et al. (2005, 2010) and Bacon et al. (2008). In total, 26% of the PRK, 39% of the RPB2, and 19% of the CISP4 sequences were cloned. When clones were monophyletic or unresolved in the individual gene tree analyses, we selected the one with the shortest branch length following the assumption that it most likely resembles the ancestor (Beilstein et al., 2008). There were five, two, and six taxa whose clones were polyphyletic or paraphyletic within the PRK, RPB2, and CISP4 tree, respectively. In these cases two clones appearing in different positions were selected for the combined analysis. Thus, for taxa such as *Geonoma cuneata* subsp. *linearis* with two PRK and two CISP4 clones, four entries were considered in the concatenated dataset.

We conducted maximum parsimony analysis in PAUP* 4.0b10 (Swofford, 2001) using the same indel coding, tree search strategy, and statistical support as in Roncal et al. (2010). The relative contribution of each dataset to the overall support of each node in the combined analysis was quantified using the Partition Bremer Support (PBS) as implemented in TreeRot v.2.0 (Sorenson, 1999). PBS was calculated using a maximum parsimony heuristic search with 1000 replications, TBR swapping, random stepwise addition, and saving a maximum of five trees in each replication. A positive PBS value indicates that a given partition supports a specific node in the combined tree over the most parsimonious tree lacking that node, while a negative PBS indicates that the partition supports a tree without that node over the combined tree. The absolute value of PBS reflects the amount of support or disagreement to a specific node by a certain partition (Lambkin et al., 2002). We also performed a Bayesian phylogenetic inference in MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003) using the same strategy as in Roncal et al. (2010), except that each Markov chain Monte Carlo run consisted of 10 million generations with a sampling frequency of one every 1000th generation, and we discarded the first 1 million generations as burn-in samples. Matrices and trees are available in TreeBase study number S11950.

**MORPHOLOGICAL VARIATION IN GEONOMA**

A taxonomic sampling of 54 *Geonoma* specimens in 38 species was used to collect information on 17 quantitative variables and score 26 characters (supporting Table S2). We excluded taxa that showed conflictive positions within the molecular phylogeny of the tribe (see Results). Quantitative variables and characters...
Evolution of morphology in Geonoma

TESTING THE THREE EVOLUTIONARY HYPOTHESES

We used a Mantel test of matrix correspondence (Nicholson, Harmon & Losos, 2007; Warren, Glor & Turelli, 2008; Pillar & Duarte, 2010) between a patrictic distance matrix and (1) a quantitative variable after log-transformation, using one randomly chosen tree from the 25 000 most parsimonious trees recovered from a combined maximum parsimony analysis of the 54 Geonoma specimens and Asterogyne martiana (outgroup). We tested correlations on independent contrasts fixing lines through the origin (Garland, Harvey & Ives, 1992) as implemented in the function ‘gls’ of the nlme R package v.2.14.0 (R Development Core Team, 2008).

RESULTS

Molecular phylogeny of tribe Geonomateae

Characteristics of the individual and combined data matrices, as well as tree statistics, are given in supporting Table S3. Within Geonoma, the PBS test showed four incompatibilities among gene partitions, which reflected the different clade positions of G. cuenata subspp. irena, G. interrupta, and G. pohliana within single trees. Despite some incongruencies among gene partitions, we used a concatenation approach because this is expected to allow shared phylogenetic signal to overcome non-phylogenetic noise that results from incomplete lineage sorting and introgression (de Queiroz & Gatesy, 2007). Parsimony and Bayesian analyses of the combined dataset produced consistent results. Geonoma was monophyletic and species were split into two main clades (Fig. 2): clade 1 contained 32 species and clade 2 had 11. Two clades supported by parsimony and Bayesian analyses were resolved within clade 1. Species growing at high elevation in the Andes (1000–3000 m) formed one of these clades, and the second included species from the Brazilian Cerrado and coastal Atlantic forest. Five taxa showed different positions within...
Figure 2. Bayesian 50% majority rule consensus topology for tribe Geonomatæae from combined PRK, RPB2 and CISP4 nuclear regions. Bootstrap and posterior probability values (BS/PP) are given above branches and partition Bremer support for each of the three gene partitions (PRK/RPB2/CISP4) below branches. Dashed lines represent clades that do not appear in the maximum parsimony strict consensus tree. C, clone number in which the first, second and third digits correspond to the PRK, RPB2 and CISP4 clone sequences, respectively, allowing us to distinguish the gene partition with polyphyletic clones.

Table 1. Seventeen quantitative morphological variables and their K-statistic (Blomberg et al., 2003) used to determine the amount of phylogenetic signal in the evolution of phenotypic variation in Geonoma

<table>
<thead>
<tr>
<th>Variable</th>
<th>K mean</th>
<th>K min</th>
<th>K max</th>
<th>P min</th>
<th>P max</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Plant height</td>
<td>0.064</td>
<td>0.052</td>
<td>0.079</td>
<td>0.397</td>
<td>0.712</td>
</tr>
<tr>
<td>2. Stem height</td>
<td>0.085</td>
<td>0.073</td>
<td>0.102</td>
<td>0.148</td>
<td>0.396</td>
</tr>
<tr>
<td>3. Leaf sheath length</td>
<td>0.105</td>
<td>0.076</td>
<td>0.154</td>
<td>0.044</td>
<td>0.240</td>
</tr>
<tr>
<td>4. Rachis length</td>
<td>0.064</td>
<td>0.051</td>
<td>0.079</td>
<td>0.381</td>
<td>0.627</td>
</tr>
<tr>
<td>5. Rachis diameter</td>
<td>0.087</td>
<td>0.066</td>
<td>0.109</td>
<td>0.194</td>
<td>0.535</td>
</tr>
<tr>
<td>6. Number of pinnae</td>
<td>0.146</td>
<td>0.104</td>
<td>0.207</td>
<td>0.046</td>
<td>0.212</td>
</tr>
<tr>
<td>7. Basal angle of pinnae</td>
<td>0.071</td>
<td>0.052</td>
<td>0.105</td>
<td>0.123</td>
<td>0.569</td>
</tr>
<tr>
<td>8. Apical pinnae length*</td>
<td>0.252</td>
<td>0.166</td>
<td>0.436</td>
<td>0.001</td>
<td>0.013</td>
</tr>
<tr>
<td>9. Apical angle of pinnae</td>
<td>0.111</td>
<td>0.093</td>
<td>0.136</td>
<td>0.056</td>
<td>0.202</td>
</tr>
<tr>
<td>10. Orders of inflorescence</td>
<td>0.101</td>
<td>0.091</td>
<td>0.112</td>
<td>0.071</td>
<td>0.277</td>
</tr>
<tr>
<td>11. Prophyll length*</td>
<td>0.283</td>
<td>0.229</td>
<td>0.371</td>
<td>0.001</td>
<td>0.006</td>
</tr>
<tr>
<td>12. Peduncular bract length*</td>
<td>0.272</td>
<td>0.205</td>
<td>0.392</td>
<td>0.001</td>
<td>0.009</td>
</tr>
<tr>
<td>13. Peduncle length*</td>
<td>0.253</td>
<td>0.216</td>
<td>0.305</td>
<td>0.001</td>
<td>0.005</td>
</tr>
<tr>
<td>14. Peduncle diameter</td>
<td>0.115</td>
<td>0.088</td>
<td>0.149</td>
<td>0.116</td>
<td>0.455</td>
</tr>
<tr>
<td>15. Number of rachillae</td>
<td>0.090</td>
<td>0.082</td>
<td>0.105</td>
<td>0.474</td>
<td>0.666</td>
</tr>
<tr>
<td>16. Rachillae length</td>
<td>0.043</td>
<td>0.036</td>
<td>0.053</td>
<td>0.668</td>
<td>0.897</td>
</tr>
<tr>
<td>17. Rachillae diameter</td>
<td>0.064</td>
<td>0.057</td>
<td>0.074</td>
<td>0.309</td>
<td>0.620</td>
</tr>
</tbody>
</table>

K was computed and averaged across 100 most parsimonious trees. See supporting Table S2 for description of variables. Variables with an asterisk had significant K-values less than one in all 100 trees indicating a lack of phylogenetic signal.

The combined phylogenetic tree: G. simplicifrons, G. undata subsp. skovii, G. leptospadix, G. sp., and Calyptrogyne fortunensis. Species complexes such as G. pohliana, G. longivaginata, G. interrupta, and G. undata were not monophyletic, while G. schottiana was monophyletic. A lack of resolution or low posterior probability in the combined analysis rendered an uncertain monophyly for the G. cuneata, G. macrostachys, and G. stricta complexes.

Morphological variation in Geonoma

The 17 quantitative components, which explained 82.3% of the morphological variation. Measurements of size such as rachis length, rachis diameter, leaf sheath length, orders of inflorescence branching, peduncle length, and stem height received the heaviest loadings in the first two components (supporting Table S4). Evolutionary correlations were found among most quantitative variables (supporting Table S5). Significant R coefficients were obtained in 59% of the correlations (80 out of 136) among vegetative and reproductive variables. For example, the number of rachillae is strongly positively correlated with the orders of inflorescence, stem height, and peduncle diameter, but negatively correlated with prophyll and peduncle lengths, and rachilla diameter. Only the basal angle of pinnae did not show a strong correlated evolution with any other variable (supporting Table S5).

Testing the three evolutionary hypotheses

Because the Mantel test indicated the absence of an association between quantitative variable and patristic distance ($R^2 = 0.077, P = 0.13$, Fig. 3A), we rejected the phylogenetic signal and displacement hypotheses. The scatter plot of this relationship was concordant with a random phenotypic drift scenario. Quantification of the amount of phylogenetic signal for the 17 quantitative variables using the K statistic corroborated results of the Mantel test. Mean K values ranged from 0.043 to 0.283 (Table 1). Only four quantitative variables had significant K values (apical pinnae length, prophyll length, peduncular bract...
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length, and peduncle length) but these were all less than 1 (mean $K$ values ranged from 0.252 to 0.283, Table 1). Thus, the $K$ analysis indicated that most quantitative variables are not influenced by the phylogeny, and only four variables have lower phylogenetic signal than expected under Brownian motion.

On the other hand, the Mantel test showed a positive overall relationship between morphological character and patristic distance ($R^2 = 0.548$, $P < 0.0001$, Fig. 3B), indicating that at least some characters present phylogenetic signal. The randomization analysis showed that 16 out of 26 characters presented phylogenetic signal (Table 2) because the empirical number of parsimony steps necessary to reconstruct these characters fell below the lower 99% confidence interval of the null distribution of step values. These characters are reproductive and refer to the shape of prophylls and peduncular bracts, the inflorescence branches or rachillae, the lips of flower pits, stamens, and fruits.

Our test of the three evolutionary hypotheses was based on a taxonomic sampling of 63% for Geonoma. Fifteen out of the 25 missing species (60%) in our analyses have narrow distributions and were recognized based on fewer than five herbarium specimens whose status as species is tentative pending the examination of additional material (Henderson, 2011). Our results would have to be confirmed under a better-sampled and more robust phylogeny, especially for variables for which no relationship with the phylogeny was found.

**DISCUSSION**

**PHYLOGENETIC SIGNAL HYPOTHESIS**

Phylogenetic signal has been defined as the tendency for closely related species to resemble each other more than they resemble species drawn at random from the phylogenetic tree (Blomberg & Garland, 2002) and may result from a Brownian motion-like evolution in which characters change in a small and random direction, or from stabilizing selection (Losos, 2008; Revell, Harmon & Collar, 2008). In Geonoma 16 characters showed phylogenetic signal as revealed by the randomization of tips test (Table 2). Interestingly, six of the 16 characters (ridged prophyll surfaces, fruit ovoid, staminodial tubes, proximal lips of flower pits, rachillae surfaces, and anthers) had non-homoplasious states that characterized six Geonoma clades in the morphological phylogenetic analysis of Henderson (2011). The staminodial tube’s shape was important enough for Spruce (1869) and Burret (1930) to divide Geonoma species into a different section or subgenus. Anther shape was regarded as an example of parallel specialization in Wessels Boer’s treatment because it suggested intergeneric relationships in disagreement with other morphological features. Our different evolutionary interpretation of this character (as evolutionarily conserved) might be due to Henderson’s (2011) different definition of the character states and the taxonomic level at work. Taxonomic scale should also be taken into account when detecting phylogenetic signal. For example, congeners can have similar leaf morphology but among...
genera leaf morphology could be evolutionarily labile (Givnish, 1987). Furthermore, the relatively low consistency index (CI) of 0.53 in the molecular phylogenetic tree indicated a high level of homoplasy in the nuclear DNA regions. The same was found in the morphological phylogenetic tree (CI of 0.42; Henderson, 2011), illustrating the difficulty in finding molecular and morphological characters with phylogenetic signal within Geonoma.

The four quantitative variables that had significantly less phylogenetic signal than expected based on the $K$ statistic were the length of prophyll, peduncular bract, peduncle and apical pinnae (Table 1), and we interpret this result as evidence of random or a convergent pattern of evolution in these variables. Silberbauer-Gottsberger (1990) suggested that in palms the inflorescence bracts can function as protective or visually attractive organs, as insect breeding sites, as pollination chambers, or in the aerodynamics of pollen capture. However, the specific evolutionary significance of the inflorescence bracts, peduncle, and apical pinnae has not been tested in Geonoma. The absence of a positive association between the quantitative variable and patristic distance matrices (Fig. 3A), and $K$-values less than one (Table 1), support the argument against the use of continuous variables in cladistics because they lack phylogenetic signal. However, there is evidence that continuous variables can contain phylogenetic signal (i.e. Thiele, 1993; Garcia-Cruz & Sosa, 2006; Goloboff, Mattoni & Quiteros, 2006), and proof of conservatism in the evolution of flower size (calyx and corolla) was found in Bignonieae using $K$-statistics (Alcantara & Lohmann, 2011). Therefore, the application of continuous variables in systematics should be assessed with caution in each case study.

Table 2. Test of phylogenetic signal in 26 morphological characters by comparing the observed number of parsimony steps required to reconstruct each character on 1000 most parsimonious trees with the 99% confidence interval step values obtained from a null distribution of 1000 simulated trees

<table>
<thead>
<tr>
<th>Character</th>
<th>Observed no. of parsimony steps</th>
<th>Upper 99% confidence interval</th>
<th>Lower 99% confidence interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Internode color</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>2. Leaf blade base</td>
<td>3</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>3. Bracts*</td>
<td>9 &amp; 10</td>
<td>13</td>
<td>20</td>
</tr>
<tr>
<td>4. Prophyll</td>
<td>6 &amp; 7</td>
<td>5</td>
<td>7</td>
</tr>
<tr>
<td>5. Ridged prophyll surfaces*</td>
<td>4 &amp; 5</td>
<td>7</td>
<td>9</td>
</tr>
<tr>
<td>6. Peduncular bracts*</td>
<td>4</td>
<td>5</td>
<td>7</td>
</tr>
<tr>
<td>7. Rachillae surfaces*</td>
<td>1</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>8. Rachillae drying</td>
<td>11 &amp; 12</td>
<td>9</td>
<td>13</td>
</tr>
<tr>
<td>9. Flower pit arrangement</td>
<td>4 &amp; 5</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td>10. Flower pits inside</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>11. Proximal lips of flower pits*</td>
<td>8 &amp; 9</td>
<td>14</td>
<td>22</td>
</tr>
<tr>
<td>12. Proximal lips recurved*</td>
<td>2 &amp; 3</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>13. Proximal lips hood-shaped*</td>
<td>5 &amp; 6</td>
<td>6</td>
<td>9</td>
</tr>
<tr>
<td>14. Proximal and distal lips</td>
<td>2</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>15. Distal lips of flower pits*</td>
<td>3 &amp; 4</td>
<td>5</td>
<td>6</td>
</tr>
<tr>
<td>16. Stamen number</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>17. Connective*</td>
<td>7 &amp; 8</td>
<td>10</td>
<td>12</td>
</tr>
<tr>
<td>18. Anthers*</td>
<td>5</td>
<td>9</td>
<td>11</td>
</tr>
<tr>
<td>19. Staminodial tubes*</td>
<td>8</td>
<td>13</td>
<td>17</td>
</tr>
<tr>
<td>20. Staminodial tubes of non-fertilized pistillate flowers</td>
<td>2</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>21. Fruit bases*</td>
<td>4</td>
<td>9</td>
<td>13</td>
</tr>
<tr>
<td>22. Fruit ovoid*</td>
<td>1</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>23. Fruit surfaces fibres</td>
<td>2</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>24. Fruit surfaces apices*</td>
<td>11–13</td>
<td>21</td>
<td>30</td>
</tr>
<tr>
<td>25. Operculum*</td>
<td>1</td>
<td>10</td>
<td>14</td>
</tr>
<tr>
<td>26. Fruit locular epidermis*</td>
<td>1 &amp; 2</td>
<td>4</td>
<td>6</td>
</tr>
</tbody>
</table>

See Table S2 for character descriptions. Characters with an asterisk had observed parsimony steps below the 99% confidence interval of the simulated trees, indicating the presence of phylogenetic signal.
Character displacement among closely related species is caused by competition for a limited resource and therefore is related to ecology by definition. The presence of a character displacement pattern of evolution would point to a predominant role of ecology over chance and shared ancestry in the evolution of morphology, as in the influence of habitat differentiation on plant speciation (e.g. Guzman, Lledo & Vargas, 2009; Givnish, 2010). This is of importance because it may shed light on the relationship between morphological variation and ecological niche at different spatial scales as discussed below. Our results showed an absence of a negative association between the morphological and patristic distance matrices, rejecting the character displacement hypothesis for both quantitative variables and characters (Fig. 3).

Diversification in certain palm genera was hypothesized to be related to an evolutionary divergence in size. For example, the formerly recognized genera Gulubia and Hydriastele are both protogynous with similar bract, flower, and seed characters, and were separated on the basis of size (Loo et al., 2006). Similarly, most of the interspecific and intraspecific variation in Geonoma lies in overall plant size (Chazdon, 1991; Borchsenius, 1999). Plant size at reproductive maturity is important because it can determine the degree of shade that Geonoma can tolerate. Using three Geonomeateae species, Chazdon (1985, 1986a, b) showed that relative shade tolerance was greatest in plants that maximized total leaf area, while minimizing biomass cost of leaf support. Chazdon’s studies hypothesized that the phylogenetic changes in plant size and shape may have facilitated the adaptive radiation of Geonoma. Her studies may thus lead to the hypothesis of character displacement caused by competition for abiotic factors, notably light, contradicting our results, or alternatively to a convergent pattern of evolution, which is more concordant with our findings. The adaptive advantage of most of the morphological variables we analysed is unknown (except for plant height). A thorough correlation analysis between plant size or shape and different habitats, microhabitats, or pollinators, at a smaller spatial and taxonomic scale, awaits further investigation and could reveal if ecology influences morphological variation of Geonoma at a local scale.

At a larger spatial and temporal scale that includes the whole evolutionary history of the genus, a geographical structure in the phylogeny was revealed in which clades with higher species richness (the Amazon and Andes) diversified first (Roncal et al., 2011). Interestingly, three of the four geographical clades are distinguished by character states that showed phylogenetic signal but whose ecological role is unclear. Species in the Amazon clade present staminodial tubes with spreading and acuminate lobes (Geonoma macrostachys clade of Henderson, 2011). Species in the Brazilian Cerrado and Mata Atlantica clade have ovoid fruits (G. schottiana clade), and species distributed in the Andean and Central American mountains have apiculate and lobed proximal lips of flower pits (G. undata clade). It has been proposed that adaptive traits, especially those related to thermal tolerance, resource use, phenology, and dispersal, contribute to the distribution of species richness through their influence on demographic and diversification processes (reviewed by Carnicer et al., 2011). However, until the adaptive role of the morphological variables we analysed here is known we cannot hypothesize how they might have shaped the demographic dynamics and distribution limits of Geonoma.

Random phenotypic drift hypothesis

The lack of any significant correlation between the quantitative variable and patristic distance matrices was concordant with the random phenotypic drift hypothesis (Fig. 3A). The application of the $K$-statistic, although not quantitatively comparable to the Mantel test, rejected the phylogenetic signal hypothesis for quantitative variables but could not support either of the remaining two hypotheses. This is because different evolutionary processes have been shown to produce a similar phylogenetic signal (Ackerly, 2009), and thus a weak phylogenetic signal ($K < 1$) like the one we report here (Table 1) may result from a random, convergent or segregating pattern of evolution (e.g. Eterovick et al., 2010).

Blomberg et al. (2003) conducted a meta-analysis of the presence of phylogenetic signal across 121 morphological, life-history, physiological, ecological, and behavioral traits from a wide spectrum of organisms including plants, mammals, birds, lizards, salamanders, and fish. Using their $K$-statistic, they found that most traits had less signal than expected under the Brownian motion along the tree ($K < 1$). Our results are consistent with this analysis but some of our $K$ values were even smaller than those reported by Blomberg et al. (2003). Low $K$ values may be an artefact caused by the short branch lengths resulting from the little molecular variation within Geonoma. We also acknowledge that errors in the estimation of species means will downwardly bias the estimation of $K$ (Blomberg & Garland, 2002; Blomberg et al., 2003; Ives, Midford & Garland, 2007).

A study of 24 tropical forest species showed that ‘the variety of shoot morphologies capable of efficiently capturing light in tropical forest understories is greater than initially thought, extending over
species with very different phyllotactic patterns, crown architectures, leaf sizes and morphologies’ (Valladares, Skillman & Pearcy, 2002: 1275). These divergent morphologies were functionally equivalent in terms of light capture. The morphological disparity in Geonoma can follow this model, with all labile traits producing different morphologies to similar environmental conditions. As Stebbins (1974) proposed, the evolutionary rates of these morphological traits could be faster than the rate of speciation causing homoplasy and high levels of morphological differentiation among populations. Alternatively, co-evolution or pleiotropic and developmental effects might cause the correlated evolutionary change we observed in most quantitative morphological variables. Thus, within clades morphological evolution might have occurred in different directions, resulting in the absence of an overall phylogenetic signal we observed.

CONCLUSION

Our results based on the current taxonomic sampling would indicate that the phenotypic disparity in Geonoma cannot be explained solely by phylogenetic relatedness, but mostly by random drift or convergence, which might explain why elucidating the taxonomy of Geonoma has been so challenging. Among-species variation of 16 morphological characters reflects common ancestry and proved useful for a morphological phylogenetic reconstruction (Henderson, 2011), while the quantitative morphological variables (mostly related to size) seem to evolve randomly or convergently, and are thus of limited phylogenetic use (but see Revell et al., 2008). A phylogeographical or population genetic approach may elucidate the evolution of diversity in clades with different stages of diversification among species, as in Geonoma. Our study is of relevance to other plant lineages with challenging taxonomies because it provides a testing framework for the evolution of morphological characteristics traditionally used in systematics, and a reflection on their selective value.

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SUPPORTING INFORMATION

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

Table S1. Taxon list for all samples used in the current study. Species are presented alphabetically. Missing GenBank sequences are noted with a dash. Format: Species; voucher specimen (herbarium acronym); locality–country (for ingroup species only); GenBank PRK; GenBank RPB2; GenBank CISP 4. Clone number follows GenBank accession numbers when appropriate.

Table S2. Description of the quantitative variables and characters used to determine the pattern of morphological evolution in Geonoma. Variables were taken from Henderson (2011).

Table S3. Characteristics and tree statistics of each nuclear DNA region used in the phylogenetic reconstruction of tribe Geonomateae and for the combined dataset. The total aligned characters in the individual matrices do not sum to the total aligned characters of the combined matrix due to the exclusion of two taxa and several clones in the combined analysis.

Table S4. The 17 quantitative variables and their loadings, eigenvalues, and cumulative percentage variation received in the four principal components of the PCA. Values in bold indicate the heaviest loadings for each axis.

Table S5. Correlations among phylogenetically independent contrasts of 17 log-transformed Geonoma qualitative morphological variables. *P < 0.05, **P < 0.01, otherwise non-significant correlation.

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