Historical biogeography and the evolution of environmental niche and fruit type in Datureae (Solanaceae)

by

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Historical biogeography and the evolution of environmental niche and fruit type in Datureae (Solanaceae)

Thesis directed by Dr. Stacey D. Smith

My dissertation examines how the interplay between historical biogeographic events and environmental factors shaped species distributions and traits in the tomato family (Solanaceae). Historical biogeographic analyses were undertaken at a broad evolutionary scale level, considering the entire Solanaceae family (Chapter 1). To address environmental factors and plant traits, I then focused my work on a smaller group within Solanaceae, the tribe Datureae. Within this clade, I estimated the evolutionary relationships between its 18 extant species (Chapter 2), assessed environmental niche evolution of the different genera (Chapter 3) and evaluated changes in the plants morphology, specifically fruit morphology, related to dry and mesic environments (Chapter 4). My work demonstrated that South America is the ancestral area for Solanaceae, and dispersal was the principal driver of range evolution in the family. Most dispersals involved range expansions from South America into North and Central America, a trend that is likely due to the early build-up of species richness in South America, resulting in large pool of potential migrants. For Datureae, phylogenetic and biogeographic analyses point to an origin in the Andes of South America, with subsequent expansion to North America and other regions in South America. I also found that the ancestral environmental niche in the tribe is dry and that there has been a significant shift in one South American lineage towards a more mesic environment. Finally, my work showed an accumulation of morphological changes in the North American lineage of Datureae. In particular, this lineage (the genus *Datura*) evolved dehiscent capsular fruits from the ancestral state (berries) through a complex series of anatomical changes. Placing this work in a comparative developmental context, this work revealed the effect of ancestry on the trajectory of fruit evolution.

Dedication

Aos meus pais, Marcelo e Lúcia, à minha irmã, Caroll, e ao meu amor, Simon.

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Contents

Chapter

Bibliography   **108**

Appendix

Tables

Table

Figures

Figure

Introduction

Understanding the distribution of species is a major goal in ecology and evolutionary biology. Investigations of species distribution patterns trace as far back as the works of Buffon [20] in 1749, von Humboldt [228] in 1805, and De Candolle [40] in 1820. For example, Buffon [20] and von Humboldt [228] considered how climate and geographical distance influence species assembly, and De Candolle [40] factored in geological history and age to explain the distribution of different species. Darwin [36]) and Wallace [230] built on these ideas, acknowledging the importance of centers of origin and dispersal (including long distance), and recognizing that geographical distance was related to chronology, i.e., that species found close together likely share a more recent common ancestor. In the first half of the 20th century, new biogeographic theories emerged, including continental drift (Wegener [231]), mechanisms of allopatric speciation (Mayr [137]), multidimensional niche concept (Hutchinson [94]), and island biogeography (MacArthur and Wilson [241]). Theoretical and applied work in biogeography demonstrate that the distribution and ecological niche of a given clade are the product of the interplay of factors such as climate, geology and time (e.g. Lemmon [113]; Antonelli [2]; Niemiller [153]).

In this dissertation, these concepts and theories are used to form hypotheses and assess the relative contribution of factors influencing species distribution. Several factors can help us understand why species are found where they are today (Wiens [239]). For example, the initial level of isolation of a clade depends highly on where (geographically) it has originated. This geographical starting point will determine the environment where species originated and are adapted to, which may lead to a lag in moving and adapting to new areas. These areas can be accessible or not

depending on how close they are, or how contrasting their climate and species composition are. Moreover, the amount of time available for a given species to disperse to new areas should also be considered. Ultimately, these processes are influenced by clade-specific factors, including phylogenetic history and trait lability (Losos [123]; Mulroy [145]). One cannot talk about, for instance, ancestral environmental niche (or ancestral and derived states in general) if the relationships within a given clade are not well resolved.

Here, I consider the effects of these factors on species distributions by using methods to estimate historical biogeography and environmental niche evolution. Approaches for reconstructing historical biogeographic events have expanded from parsimony-based methods (Ronquist [194]) to the maximum likelihood (Ree [190]) and more recently, Bayesian-based ones (Landis [110]; Matzke [134]; Matzke [135]). Coincidently, the available models have become more complex, and a wider range of processes and events (e.g. sympatric speciation, vicariance, range expansion, range contraction) are now included. With this suite of tools, it became a crucial step to clearly delimit the factors considered relevant and to use datasets that are powerful enough for the hypothesis being tested. For this work, I used model-based maximum likelihood and Bayesian approaches (Matzke [136]; Matzke [135]), and applied biogeographical stochastic mapping (BSM) to the first empirical dataset (Dupin [51]).

To complement the results on the frequency and asymmetric rates of dispersals, I added an analysis of niche evolution to assess the contributions of environmental variables. The rationale behind it is that the patterns seen at a historical biogeography level are the result of processes at an ecological scale. Hypothesis about the evolution of environmental niches have been addressed with the use of the continuous environmental variables (e.g. temperature, precipitation) as input for comparative methods that estimate ancestral states in a clade (Schluter [203]; Pagel [165]; Pagel [166]). These methods can be powerful to detect shifts in environmental preferences within a clade. The use of comparative methods complements other approaches that have shaped the study of environmental niches, namely species distribution modelling and the assessment of environmental suitability (reviewed in Peterson [177]).

Here, these methods for studying historical biogeography and environmental niche evolution were applied to determine the factors that influenced the distribution of two plant groups, the family Solanaceae and the tribe Datureae. These groups gave me a chance to work on two spatial scales, given that Solanaceae has a global distribution and Datureae is distributed exclusively in the Americas. Solanaceae, popularly known as the tomato or the nightshade family, occurs on most continents, with the exception of Antarctica. It has about 2,800 species, which makes it one of the largest plant families (Olmstead [161]; Särkinen [200]). This family is also known for its many economically important species, such as potatoes, tomatoes, and tobacco. Its age has been recently estimated as between 30 and 50 million years (My) and its diversification began in South America (Olmstead [160]; Särkinen [200]). The familys species richness, cosmopolitan distribution and well-resolved phylogeny makes Solanaceae a good candidate for understanding historical biogeographic patterns of South American plant clades. In contrast, Datureae is a small tribe of 18 species within Solanaceae, and these species are distributed in exclusively Andean areas, southeast Brazil, and Mexico and southwest USA (Lockwood [120]; Bye [23]). Some of the species are used as ornamentals (common names jimsonweeds and angel trumpets), but they are more famous for their hallucinogenic properties (Lockwood [120]; Schultes [205]). The disjunct aspects of Datureae's distribution, along with the variety of types of environments its species inhabit (cloud forests, tropical forests, deserts and dry forests), raises questions about historical biogeography but also about the influence of the evolution of environmental niche in the clades distribution.

With Solanaceae, I examined how biogeographical events (e.g., vicariance, founder events, and dispersals) in the context of time and space contributed to the widespread distribution of the family (Chapter1). I found that South America is Solanaceaes current center of diversity and its ancestral range. The main type of biogeographical event that drives the evolution of geographical ranges in Solanaceae is dispersal events between areas, and these were most common in range expansions from South America into North and Central America. Dispersals from South America to other areas, in general, were more common than in the opposite direction. This directionality is likely due to the early build-up of species number in South America, resulting in large number of

potential dispersals from that area.

Now with Datureae, given the smaller size of the group, I combined a similar analysis of historical biogeography with the study of its environmental niche. In order to undertake both the biogeographical and niche analyses, the well-resolved phylogeny was required. While the tree for the Solanaceae family used here came from Sarkinen [200] work, a fully resolved phylogeny that includes all species in Datureae was not available. So, as part of the work on Datureae, I generated a phylogeny for the group (Chapter 2). This study presents the first phylogeny of the tribe that includes all accepted species to date. This phylogeny was estimated using nuclear markers, which have been useful in increasing the resolution of other clades within Solanaceae. As part of this study, I also reconstructed the history of morphological characters used to delimit genera in the tribe, such as flower position and size, and fruit type. The patterns of character evolution were largely consistent with the phylogeny, meaning that only minimal taxonomic changes were needed. Specifically, I reassigned a species that was currently placed in a different tribe within Solanaceae to Datureae and elevated it to its own genus.

In my studies of Datureae, I integrated historical and environmental factors to create a more detailed picture of how this clade colonized different parts of the Americas (Chapter 3). My results suggest that Datureae originated in Andean regions and subsequently expanded its range to North America and non-Andean regions. Moreover, I estimated that the ancestral environmental niche in the tribe is dry and that there has been a significant shift along the *Brugmansia* branch towards a more mesic type of environment. The long-distance dispersal to North America represented a range expansion into a familiar type of environment, a dry one. Even though range expansions ultimately resulted in a significant niche shift, our niche overlap estimates showed moderate overlap remains between *Datura* and *Brugmansia* niche regions. This is likely a result of as yet incomplete niche specialization within *Brugmansia* and two *Datura* species.

The long distance dispersal from the Andes to North America in Datureae was associated with changes in a large number of life history and morphological features, perhaps most notably the type of fruit. Fruits in Datureae are very diverse, and their traits are likely a product of adaptation

to distinct environments. In Chapter 4, I explored the anatomical differences between fleshy and dry fruits in the group, with special attention to the transition to the family's ancestral fruit state observed in one of the genera in the tribe (*Datura*). In addition to comparing the anatomical features of fleshy and dry fruits in the tribe, I explored the characters that could explain the different dehiscence mechanisms within species in *Datura*, including biomechanical tests of regular and irregularly dehisced fruits. Lastly, I placed these results into phylogenetic context to determine if the transition between berries and regularly dehisced capsules was a stepwise process, given the number of traits likely required for a dry fruit (e.g., creating dehiscence zones, opening to release seeds). I found that, while capsules and berries in Datureae are functionally different, there are overlapping anatomical characters between the two types of fruit. I also found that the vascular tissue is likely a major player in the dehiscence mechanism in *Datura*, in contrast to the mechanism seen in other genera with capsules in Solanaceae. These results demonstrated then the relevance of phylogenetic context when discussing the evolution of characters, and indicated that multiple mechanisms for the development of capsules exist within Solanaceae.

Chapter 1

Bayesian estimation of the global biogeographical history of the Solanaceae

Additional Supporting Information may be found in the online version of this article and, when possible, in the appendix of this thesis

1.1 Introduction

The growing availability of large phylogenies together with developments in statistical methods provide researchers with new opportunities to explore the complex biogeographical history of large cosmopolitan clades (Matzke [134], Yu [245]). Worldwide distributions can be achieved either through dispersal events, vicariance, or a combination of the two (Yoder [244], Nauheimer [150]). For example, Gondwanan clades that arose and diversified before continental separation may become cosmopolitan largely through vicariance (Gamble [62], Rasmussen [188]). By contrast, groups that have evolved subsequent to continental separation can only achieve wide distributions through long-distance dispersal events (Givnish [71], Szovenyi [218]). The relative importance of these processes is expected to vary across groups of organisms given intrinsic differences in dispersal ability and level of ecological specialisation (Gillespie [67], Edwards [54]).

The interplay of vicariance and dispersal in shaping cosmopolitan distributions has been relatively well studied in plants. For many widely distributed plant families, dispersal appears to be

the principal driver of range evolution (Givnish [72], Christenhusz [28]), whether by water (Gallaher [61]), wind (Munoz [147]), or animals (Nogales [154]). By contrast, relatively few widespread families show strong signatures of vicariance in shaping their present day distributions (Barker [6], Mao [128]). This pattern may be attributable to the fact that long distance dispersal of seeds or other germplasm, while limited on ecological timescales (Cain [24]), appears to be relatively frequent on macroevolutionary timescales (Renner [191], Nathan [149]). Moreover, the establishment of distantly dispersed lineages may be favoured by the absence of their native competitors, pathogens and predators (Janzen [102], Howe [88]). One caveat, however, with respect to the apparent predominance of dispersal is that many of the studied lineages are relatively young (but see Beaulieu [10]). Also, vicariance becomes harder to identify in older clades as subsequent dispersal and population movement, along with local extinction, can obscure the original geographical signature (e.g., Clayton [30]).

Here we examine the biogeographical history of a relatively young plant family, the Solanaceae. This clade of about 2,800 species began to diversify roughly 50 to 65 million years ago (Ma) (Särkinen [200], Magallón [127]) and is presently distributed on all continents except Antarctica. The Solanaceae contains a large number of important crops such as potato (*Solanum tuberosum* L.), tomato (*Solanum lycopersicum* L.) and tobacco (*Nicotiana tabacum* L.), and has long been the focus of genetic, biochemical, and morphological studies (e.g., Pabón-Mora [164]; Sato [202], Itkin [97]). Solanaceae is one of the groups in the Asterids I (Lamiids) that is especially species rich in the Neotropics, along with the Verbenaceae and Bignoniaceae (Olmstead [160]), and the Acanthaceae (Tripp [223]). Its sister group is the large morning glory family, Convolvulaceae, which also has a worldwide distribution. Despite its economic importance, the biogeographical history of Solanaceae has received relatively little attention beyond taxonomic or floristic surveys (e.g., Gentry [65], Hepper [80]). In a recent review of Solanaceae biogeography in the context of its phylogenetic history, Olmstead [160] suggested that the family's cosmopolitan distribution is due to repeated dispersals from South America to both nearby and distant continents. However, identifying the timing, number, and direction of these events was limited by the level of taxon sampling (ca. 5%

of species of the family) and the lack of a time-calibrated phylogeny.

In this study, we combine a recent dated phylogeny that includes nearly 40% of the species in the family (Särkinen [200]) with newly developed biogeographical stochastic mapping (BSM; Matzke [135]) to estimate the biogeographical events that account for the global distribution of the Solanaceae. Stochastic mapping (Nielsen [152]; Huelsenbeck [90]) is a simulation approach that builds on likelihood models of trait evolution and, in addition to estimating ancestral states at nodes, provides possible histories of changes along branches. By summarizing across many of these possible histories, we can obtain estimates of the number and phylogenetic location of various types of events (e.g., vicariance, dispersal between areas) along with measures of uncertainty. This approach was originally developed for mapping mutations onto phylogenies (Nielsen [152]) and was later expanded to accommodate morphological characters (Huelsenbeck [90]). Just as the morphological stochastic mapping was built on Pagel's (1999) [165] likelihood models for trait evolution, the development of stochastic mapping for biogeographical patterns relies on existing likelihood models describing how geographical ranges evolve (Ree [190], [134]). In the context of Solanaceae biogeography, we apply likelihood methods and BSM to (1) infer the most likely ancestral range of the family and major groups within it, (2) assess the relative contribution of vicariance and dispersal events to the distribution of extant taxa, and (3) detect directionality in dispersal between areas. In addition to elucidating the biogeographical history of this economically and floristically important family, these results provide new insights into the relative importance of alternate dispersal routes in the spread of plant clades to new areas.

1.2   Materials and Methods

1.2.1   Solanaceae Phylogeny and Species Distribution

We used the time-calibrated maximum clade credibility (MCC) tree from Särkinen ([200]), which was estimated using two nuclear and six plastid loci from 1075 species. This taxon sampling includes all but three of the 98 Solanaceae genera [*Darcyanthus* Hunz., *Capsicophysalis* Averett &

M. Martnez and *Tubocapsicum* (Wettst.) Makino)] and nearly 40% of all species. For the present study, we pruned (1) taxa that are widely cultivated and whose native distributions have been obscured by extensive human transport, and (2) taxa that were duplicated in the phylogeny (Table S1.1 in Appendix A.1 in Supporting Information). The phylogeny was pruned using 'ape' package (Paradis [167]) in R (R Core Team [184]). We also updated species names according to the most recent literature (Table S1.1 in Appendix A.1). The final pruned phylogeny used for downstream analyses contained 1044 species.

The current distribution for each species in the phylogeny was determined using numerous literature sources (e.g., Bentez de Rojas [43], Garcia [63]; Dillon [45]), online databases (Solanaceae Source, `http://solanaceaesource.org/`, last accessed on Nov. 2015; TROPICOS, Missouri Botanical Garden, `http://www.tropicos.org`, last accessed on Nov. 2015; Global Biodiversity Information Facility, `http://www.gbif.org`, last accessed on Nov. 2015), and experts' input (Table S1.2 in Appendix A.1). Considering current distribution patterns within the family, we chose to recognize seven major areas: South America (SAm), Central America (CAm), Caribbean (Car), North America (NAm), Eurasia (EU), Africa (AF) and Australia (OZ; includes Australia, other islands of Oceania and the Hawaiian islands). The decision to focus on these seven areas reflects the need to balance model complexity (i.e., the number of dispersal rates, within-area extinction rates, etc.) with the ability to detect major biogeographical shifts within this widely-distributed family. The Caribbean and Central America were maintained as separate areas in order to examine the origins of the many solanaceous lineages endemic to those regions. We grouped the six species native to Hawaii (*Solanum incompletum* Dunal, *S. sandwicense* Hook. & Arn., *S. viridifolium* Dunal, *Nothocestrum latifolium* A. Gray, *N. longifolium* A. Gray, and *Lycium sandwicense* A. Gray) with the Australian taxa (Table S1.2 in Appendix A.1). While dispersal to Hawaii and remote Pacific islands represents a long distance dispersal from any potential source, three of them are nested within clades found in Australia and New Zealand (*S. incompletum, S. sandwicense* and *S. viridifolium*), whereas the others represent putative Eurasian or New World ancestry (Levin [117], Levin [118], Olmstead [161], Vorontsova [229]). Our divisions are similar to those used in other studies

of widespread clades (e.g., Buerki [19], Sessa [208]), and will allow us to detect intercontinental movements as well as shorter range dispersal events (e.g., South America to the Caribbean).

1.2.2   Ancestral Range Estimation

We used the R package "BioGeoBEARS" (Matzke [136]) to compare biogeographical models and estimate ancestral ranges in the Solanaceae. 'BioGeoBEARS' implements maximum likelihood (ML) methods that replicate the key assumptions of three most commonly used methods in historical biogeography, namely DEC (DispersalExtinctionCladogenesis; Ree [190]), DIVA (Dispersal-Vicariance Analysis; Ronquist [194]) and BayArea (Bayesian Inference of Historical Biogeography for Discrete Areas; Landis [110]). These three methods were originally developed in different frameworks (likelihood for DEC, parsimony for DIVA, and Bayesian for BayAREA), but are all represented as likelihood models in 'BioGeoBEARS' to allow for direct comparison. The latter two models are thus not identical to their original formulation, and are referred to as DIVALIKE and BAYAREALIKE within 'BioGeoBEARS' (Matzke [136]). Collectively, these models allow for a wide range of processes, including within-area speciation, vicariance, range expansion (dispersal to a new area), and range contraction (extinction in an area) (Fig. 1.1). We also tested models with and without founder-event speciation, which is incorporated with the j parameter. In such an event, range switching (e.g., South America to North America) occurs at a lineage-splitting event (a node in the phylogeny), leaving one daughter lineage in a new range and the other daughter lineage retaining the ancestral range. Such range switching events are restricted to nodes (instead of occurring along branches) as it is considered unlikely that an entire lineage would simultaneously disperse to a new area and go extinct in its ancestral area (Matzke [134]).

We also incorporated time-stratified dispersal multiplier matrices in the model-fitting to account for the changing distances between the regions over geological time. We divided the history of Solanaceae into three strata: 50 to 24 Ma, 24 to 10 Ma, and 10 Ma to present. We began the strata at 50 Ma given the estimated depth of the Solanaceae phylogeny (ca. 49 Ma for the stem group age; Särkinen [200]). The breaks at 24 Ma and 10 Ma reflect recent studies showing

significant shifts in plant dispersal between South and North America at these time points (Bacon [4]). Also, the 10 Ma threshold approximates a new estimated age of the closure of the Panama isthmus during the mid-Miocene (Montes [142]; Bacon [3], but see O'Dea [156]). The dispersal multiplier matrices for each of these strata give the relative probability of dispersal between areas and are roughly scaled to represent the relative distance between the areas during each time slice (Appendix A.1). We examined models using these multiplier matrices directly and also with the matrices modified by the w parameter, also estimated with ML (Appendix A.1).

In total, we tested a set of 18 models (Table S1.3 in Appendix A.1) that varied in the number and types of free parameters included and in the type of dispersal multiplier matrices used. The free parameters were w, d (the base rate of range expansion), j (the per-event weight of founder-event speciation at cladogenesis; Matzke [134]) and e (the rate of range contraction). For models without the dispersal multiplier matrices, the probabilities of all dispersal events are equal (set to 1). Because not all of the models are nested, we used the Akaike information criterion (AIC) (Burnham [22]) to select among the 18 models; the best fit model with the lowest AIC score was used to infer the relative probabilities of ancestral ranges within the phylogeny.

1.2.3 Estimation of number and type of biogeographical events

We estimated the number and type of biogeographical events using BSM implemented in 'BioGeoBEARS' (Matzke [135]). Previous implementations of stochastic mapping used transition rate models (Pagel [165]) to simulate the histories of mutations or trait changes (Huelsenbeck [90]). Whereas the transition rate models involve only trait gain and loss, the biogeographical models used in BSM will include a range of anagenetic and cladogenetic events (Fig. 1.1). After providing a biogeographical model with specified parameters, BSM generates simulated histories ('realisations'), including the times and locations of all events along the branches in that simulation. These realisations of possible histories are constrained to produce the observed data given the phylogeny, and averaging over many realisations will result in the same ancestral state probabilities as those calculated analytically under the ML model (see Appendix A.1 for description and

BSM algorithm validation). Biogeographical events possible under the models include within-area speciation, vicariance, and dispersal events (range expansions and founder events; Fig. 1.1). For cases where a dispersal event occurs from a widespread ancestor occupying two or more areas, the exact source area was simulated using the dispersal probability multipliers matrix as modified by w. We conducted BSM on the Särkinen ([200]) MCC tree using a time-stratified four-parameter model (DEC+$j + w$) that produced a significantly better fit to the data compared to other tested models (see Results). Event frequencies were estimated by taking the mean and standard deviation of event counts from 100 BSMs. All stochastic maps and derived statistical estimates are conditioned on not just the phylogeny, the observed range data, and the model, but the inferred model parameters and the implicit Yule process (no lineage extinction) assumption shared by DEC and all other biogeographical models considered here.

1.3   Result

1.3.1   Ancestral Range Estimation and Time-stratified Analyses

The AIC model selection strongly supported the DEC+$j + w$ model including the dispersal multiplier matrices as the best fit. This is among the more complex models fitted (with four free parameters), and it was 47 AIC units lower than the second best model (DEC+j) (Table S1.3 in Appendix A.1). Across all the models, the inclusion of the j parameter (or the possibility of a founder event speciation where one of the lineages occupies an area not present in the ancestral range) consistently improved model fit, suggesting that range expansions alone are not sufficient to account for movements to new areas. Such an increase in the likelihood in models with j has been observed in other studies where, as in our case, the areas under consideration are continents or other large regions and thus, many lineages are single area endemics (Litsios [119], Voelker [227], Thacker [219]). It is also notable that the best model employed the user-specified dispersal matrices with the w modifier parameter. This result indicates that scaling the dispersal probabilities to the relative distance of the areas results in higher model likelihood. The w parameter, acting as an

exponent on the dispersal matrices, improves fit to our data (Table S1.3 in Appendix A.1, $+j$ models versus $+j+w$ models).

Ancestral range estimations under this best fitting model (DEC+$j+w$) showed that the most probable ancestral area for extant species of Solanaceae is South America (probability = 0.8, with 0.14 for South America + Australia, and 0.06 for other state combinations) (Fig. 1.2 & Appendix A.2). Other deep nodes in the family also have South America as the estimated range, supporting the idea that this area is the centre of origin of the family and major clades within it (Fig. 1.2). The first two clades in the family confidently inferred as having an ancestral range outside of the New World are the Hyoscyameae (ca. 12 Ma), nested within Atropina, which has Eurasia as the most probable ancestral state (0.95) and the clade Anthocercidae (ca. 9 Ma), nested within Nicotianoideae, which has Australia as the most probable ancestral range (0.98) (Appendix A.2).

1.3.2   Estimation of number, type, and directionality of biogeographical events

A summary of our BSMs revealed that most biogeographical events comprise within-area speciation (76%) and dispersals (20%), with only a few vicariant events (3%) (Table 1; see Appendix A.3 for an example of a BSM). The high number of within-area speciation events was expected given the large size of our regions (e.g., North America, Eurasia). The number of these events within each area was closely related to species richness, where, for example, 60% of the within-area speciation events occurred within South America, which is home to about 64% of the taxa (Table S1.4 in Appendix A.1). Among the dispersal events, range expansions were much more common than founder events (mean of 218 versus 38; Table 1) and were clustered towards the present (Fig. 1.3). The relative rarity of vicariance (mean = 42 events; Table 1) may reflect the fact that the diversification of Solanaceae postdates the Gondwanan break-up (180 Ma, early Jurassic – 94 Ma, mid-Cretaceous; McLoughlin [138]). Most of the estimated vicariance events involved adjacent areas (e.g., South America and North America) (Table S1.5 in Appendix A.1) and occurred following a range expansion. For example, the ancestor of the genus Jaltomata was estimated to have expanded its range from South America to South and North America, and this

expansion was followed by a division into subclades most diverse in South and North America (Appendix A.2; see also Mione [141]).

Focusing on dispersal events, we found that movement patterns varied tremendously across areas. The highest number of dispersals involved movements from South America to Central America (ca. 49 of 256 total estimated events), closely followed by movements from South America to North America (ca. 42 of 256) (Fig. 1.4(a)). Overall, South America was the source for 47% of the estimated dispersal events. North America was the next most common source (20%), and most of these dispersals were toward Central America (Fig. 1.4(a), Fig. 1.5). In total, dispersals among the four New World areas accounted for 81% of the events, while dispersal among the three Old World regions or between the Old World and New World were less common (10% and 9%, respectively). Among the Old World areas, Australia and the nearby islands of Oceania were the least common source and sink for dispersal events, and three of the estimated 11 dispersals into the area comprise the Hawaiian taxa previously shown to have originated from Eurasia and the New World (Levin [117], Levin [118], Olmstead [161], Vorontsova [229]). The relative importance of different regions as sources and sinks for dispersal differed to some degree depending on the type of dispersal event (range expansions versus founder events). Since the vast majority of dispersal events were range expansions, the pattern of those movements (Fig. 1.4(b)) largely mirrors the overall pattern (Fig. 1.4(a)), where South America is the most common source and Central America is the most common sink. By contrast, the most frequent founder event type involved dispersal from South America to North America (Fig. 1.4(c)), with the other transitions (e.g., to Central America, to Africa) occurring with roughly equal frequency. Thus, whereas the range expansions commonly occur between adjacent areas, the founder events more often involve distantly related regions. Indeed, movements between the Old World and New World accounted for just 6% of estimated range expansions, but 24% of the estimated founder events.

Regardless of the type of dispersal event, we inferred strong asymmetry in the movements between areas. For example, dispersal events from Central America to the Caribbean were more than twice as common as those in the opposite direction (10.12±1.41 versus 4.20±1.14; Fig. 1.4(a)).

Such directionality was observed for nearly all pairs of areas (compare upper diagonals and lower diagonals in Fig. 1.4) and was most marked for events involving South America (see also Fig. 1.5). The most prominent exceptions to this overall trend are dispersals between Africa and Eurasia, which have occurred in approximately equal numbers in both directions (Figs. 1.4, 1.5). The general asymmetry of transitions was consistent across all of the individual BSM realisations (chi-square contingency analysis, $p < 10^{-45}$ for each of the 100 realisations).

1.4   Discussion

Our analyses of the historical biogeography of Solanaceae confirm that the early evolution of the family took place in South America. Moreover, major clades in the family, such as the large '$x = 12$' clade (genera with a base chromosome number of 12) and the Solaneae ($Solanum+Jaltomata$), are also estimated to have originated in South America (Fig. 1.2), despite the fact that these groups today are very diverse in the Old World. Our best model, which included time-stratified matrices representing the continental area distances over time, presented a significantly better fit than those that did not incorporate palaeogeographical information. This suggests that distance is an important factor when estimating dispersal events between areas in Solanaceae. Finally, Solanaceae presents a marked directionality of dispersals over its history, with range expansions and founder events being significantly more common from South America to other areas than in the opposite direction.

1.4.1   The ancestral range of Solanaceae

Our estimation of biogeographical history shows that, for Solanaceae, South America is not only the family's distributional centre but also its ancestral range (Fig. 1.2). The radiation of the family appears to have continued in South America up to ca. 15 Ma, before the first lineages established on other continents (Fig. 1.2, Appendix A.2). Such a clustering of long distance dispersal events in the last 20 million years (Myr) was also observed in the Acanthaceae, a similarly species rich and largely Neotropical family (Tripp [223]). Across the history of the Solanaceae, we estimate

about 120 dispersals from South America to new areas, mostly to adjacent regions within the New World (Figs. 1.4, 1.5). This tendency for geographical movements to involve proximate areas is reflected in the fact that models that incorporated distance between areas through dispersal matrices were consistently a better fit for the data (Table S1.3 in Appendix A.1), as has been observed in studies of other taxa (e.g., Matos-Maravi [133]).

Although short range movements account for most of the spread of Solanaceae from South America, our results provide evidence of multiple long distance dispersals to Africa, Australia, and Eurasia. These dispersals to the Old World occur long after the separation of Gondwana (ca. 94 Ma), and therefore were likely to involve transoceanic movements. The Solanaceae have fruit types ranging from dry to fleshy and a variety of dispersal agents, including wind, water, and many animals such as birds, bats, small rodents, and ants (Knapp [106]). Thus, fruits could be blown in wind currents, float across the ocean, or be carried to new regions by migrating or rafting animals. Our results show that dry fruited and, more commonly, fleshy fruited lineages have experienced range expansions, including transoceanic movements (Table S1.7 in Appendix 1), consistent with previous studies in the family (Olmstead [160]). Transoceanic dispersal has been hypothesized to explain the spread of other New World families to the Old World (Perret [175], Tripp [223]). Still, we cannot exclude the possibility that these South American taxa reached the Old World through a series of shorter dispersal events (e.g., via a northern route through Beringia) followed by subsequent extinction in the intervening areas (Davis [39]).

Our estimate of the number of dispersal events from the New World to the Old World is strikingly similar to previous studies, despite the use of different methods. In surveying the biogeography of Solanaceae, Olmstead [160] suggested that a total of 15 to 17 long distance dispersal events from South America would be needed to account for the present distribution, assuming a most parsimonious reconstruction. Our model-based stochastic mapping estimates 20 ± 2.04 such events (summing all New World to Old World transitions, Fig. 1.3, Table S1.6 in Appendix A.1). Both of these totals are minimum estimates of the actual number of long distance dispersals in the history of extant Solanaceae because only ca. 40% of all species were sampled. For exam-

ple, the unsampled taxa include the monotypic genus *Tubocapsicum*, which is endemic to eastern temperate Asia and could represent an independent colonization from the New World. However, previous studies and overall morphology suggest that *Tubocapsicum* is closely related to the Hawaiian *Nothocestrum* and the African *Discopodium*, a placement that would favour an Old World origin as opposed to long distance dispersal from the New World (Olmstead [161]). By assigning Hawaiian native species to Australia in our analysis, we were able to include the one inferred dispersal to Hawaii from the New World (*Lycium*) in our estimates. We recognize that all dispersals to Hawaii, however, represent long-distance dispersals regardless of source area. Although a complete family-level phylogeny would be needed to arrive at a final estimate of the total number of New World to Old World dispersals, we expect the present study captures the vast majority of these events.

1.4.2   Patterns of speciation, vicariance and dispersal in Solanaceae history

Our simulations of biogeographical history using BSM identified within-area speciation as the most frequent type of event across the phylogeny (Table 1). This result is likely to reflect the scale of this analysis (global) and the size of the regions under consideration. The preponderance of within-area speciation events is consistent with the large clades of Solanaceae that are endemic to single areas as defined by our study. For example, the 31 species of Anthocercideae are restricted to Australia and New Caledonia and are inferred to have diversified entirely within Australia (Appendix A.2). Our study shows the importance of events at a global scale, but we acknowledge the need for future studies with a finer division of the regions, especially of South America, given its importance in the Solanaceae history. Such a division would likely reveal that many of these speciation events are actually associated with shifts in geographical range not revealed in our continental-scale analysis (see also Sanmartin [198]).

Among the remaining types of events, we found that dispersal was the principal driver of range evolution, occurring about six times more often than vicariance. While vicariant events appear to have been important for range evolution in many animal groups (e.g., Giribet [68]), dispersal seems to be the most common factor shaping the distribution of plant clades, even those whose origins

date to Pangaea or Gondwana (Sanmartin [198]). In the case of the Solanaceae, the crown age for the family is roughly 60 Myr after the separation of South America and Africa, making Gondwanan vicariance a less likely explanation for the family's pantropical distribution. Indeed, we inferred multiple dispersal events between South America and the Old World (Fig. 1.4, 1.5), and these are confined to the last 15 Myr of the Solanaceae evolution (Fig. 1.3).

Dispersal events between both proximate and distant regions appear to have been frequent in the history of the Solanaceae and they may have been facilitated by colonization of similar niches. For example, the genus *Lycium*, distributed across all of the recognized regions except for Central America (Appendix A.2, Table S1.2 in Appendix A.1), is restricted to dry habitats (Levin [117]). Moreover, all of the species inferred to show recent range expansions along their terminal branch (Fig. 1.3) are found in a single type of terrestrial ecoregion (e.g., dry, tropical, or temperate), with the vast majority (80%) from wet tropical areas (Table S1.7 in Appendix A.1). This pattern of niche conservatism has been documented in many plant groups (e.g., Francisco-Ortega [59], Martinez-Meyer [129]), leading to the idea that, at least in some clades, it is easier to move than to evolve (Edwards [54]). In Solanaceae, additional studies will be needed to assess the extent of niche conservatism and to test the specific factors, biotic or abiotic, that affect colonization of new areas. Certainly, despite the tendency for clades of Solanaceae to be restricted to particular environments (Olmstead [160]), the family as a whole is found in a wide range of habitats, from the driest deserts to wet forests in both tropical and temperate zones, indicating that major niche shifts must have occurred during its history.

1.4.3 Directionality of dispersal events

One of the most striking patterns to emerge from our statistically robust estimation of biogeographical history was the strong asymmetry of dispersals. For every pair of areas considered, transitions were consistently higher in one of the two directions. The directionality was most notable for range expansion events, where for example, dispersals from South America to North America were over four times more common than dispersals in the opposite direction. Similar

patterns of dispersal asymmetry have been observed in other studies at deep as well as recent time scales (Sanmartin [197]; Sanmartin [199]). For example, Bacon [4] found the overall migration rates for animals and plants from South to North America during the last 6 to 7 million years was ca. 30% higher than in the reverse direction.

In the case of Solanaceae, the strong directionality in transitions from South America to other regions may be attributable to the age of the South American lineages and their species richness. As our ancestral range estimations show, the origin and early diversification of the family took place in South America, making this region the principal source for migrants for most of the past 50 Myr (Fig. 1.2, Appendix A.2). In our dataset, South American species comprise roughly half of the taxa (Table S1.4), and also account for roughly half of the dispersal events (Fig. 1.4(a)). We observed a similarly close relationship between the species richness of an area and the number of dispersals out of that area for the all of remaining regions, with the exception of Australia (home to 13% of taxa but only the source for 1% of dispersals, Table S1.4). Although more extensive analyses would be required to formally test the relationship between species richness and dispersal, this congruence suggests that extrinsic explanations, such as directional wind or water currents or migratory paths of dispersers (Renner [191], Sanmartin [199], Gillespie [67]), may not be needed to explain the apparent biases in inter-area movements.

1.4.4   BSM as an approach to estimate biogeographical history of clades

As demonstrated by this study, the application of stochastic mapping to the estimation of biogeographical history gives researchers new power to address questions about patterns of range evolution. Whereas parsimony and likelihood reconstruction provide estimates of ancestral ranges at nodes, stochastic mapping also gives possible histories along branches and at nodes, including any of the events incorporated in the model. By summarizing over many histories, we can extract distributions for the numbers of the events and determine the relative importance of each type of event (e.g., range expansions, vicariance) in shaping present day distributions. Inferring the numbers and types of biogeographical events can also be achieved in a parsimony framework (e.g.,

Sanmartin [198]); however, this approach requires user-defined costs for different events and an inferred area cladogram. Recently developed Bayesian MCMC approaches (Hohna [83], Hohna [84]) could also be used for estimating distributions of event counts and timing of events, and have the benefit of directly incorporating uncertainty in the rate parameters. While implemented models are currently limited to DEC, additional models and tools are likely to be added in the near future (Matzke, pers. comm.).

Although our study used BSM primarily to examine the frequency and directionality of events, this approach could be used to explore other questions, such as how the prevalence of different events (e.g., range expansions or vicariance) varies across clades. Moreoever, subsequent studies targeting particular clades could employ a more fine-scale division of geographical areas, revealing dynamics that may not be apparent in this broad family-level analysis. We also envision that future work in biogeography will lead to the extension of the models with additional types of events, and as long as the models are developed in a probabilistic framework, the frequency of these events can be estimated with BSM. Applying these new methods to other plant families of New World origin would provide a powerful test of the generality of the patterns of speciation, dispersal and vicariance that we have inferred for the Solanaceae.

1.5   Acknowledgments

1.6   Tables and figures

Table 1.1. Summary of biogeographical stochastic mapping counts for the Solanaceae using the DEC+j+w model. Mean numbers of the different types of events estimated are shown here along with standard deviations. No range contractions were estimated because the relevant model parameter (e) was not required in the best fitting model (Table S1.3 in Appendix A.1).

Figure 1.1. Diagrams of different types of biogeographical events allowed in the models tested in this study (adapted from Matzke [135]). Cladogenetic events include within-area speciation, vicariance, and founder events. Anagenetic events include range expansion and range contraction.

Figure 1.2. Maximum likelihood ancestral range estimation in Solanaceae, using the best model DEC+j+w (model 16 in Table S1.3 in Appendix A.1). This tree is a simplified version of our 1044-tip tree (Fig 1.3, Appendix A.2 & Appendix A.3), and it includes 19 monophyletic groups within Solanaceae, representing either genera (italicized) or higher order taxa (not italicized). The pie diagrams at nodes show the relative probability of the possible states (areas or combinations of areas). The boxes on the right show the native ranges of taxa within these clades, including South America (SAm), Central America (CAm), the Caribbean (Car), North America (NAm), Africa (AF), Eurasia (EU), and Australia (OZ). The asterisk marks the ancestor for the x=12 clade, a group that shares the base number of 12 chromosomes and comprises roughly 85% of species in the family (Olmstead [159]). Outgroups are not shown.

Figure 1.3. Representation of timing of dispersal events in the Solanaceae chronogram. Range expansions = thick branches, founder-events = full circles. Transoceanic dispersals are represented in orange and non-transoceanic dispersals in black. Thicker branches and nodes with circles represented here were found in at least 95% of BSM realisations. Clade names follow Fig. 1.2.

Figure 1.4. Number of dispersal events estimated in the history of Solanaceae with biogeographical stochastic mapping. Counts of dispersal events were averaged across the 100 BSMs and are presented here with standard deviations in parentheses. Total event counts are given in (a)

and divided among the two types of dispersals in (b) and (c) (see Fig. 1.1 for depictions of range expansions and founder events). Colour temperature indicates the frequency of events; the warmer the colour, the more common the event. Note that given the standard deviations, values in green are often not different from zero. The ancestral states (where the lineage dispersed from) are given in the row, and the descendant states (where the lineage dispersed to) are given in the column. The sum and correspondent percentages of events involving each area, either as a source for dispersal (the rows) or as a sink (the columns) are given on the margins. Area names in rows and columns are: South America (SAm), Central America (CAm), the Caribbean (Car), North America (NAm), Africa (AF), Eurasia (EU), and Australia (OZ).

Figure1.5. Summary of dispersal events estimated with biogeographical stochastic mapping in the history of Solanaceae. Each of the seven areas in the analysis is shaded by its species richness (Table S1.4 in Appendix A.1), with darker areas being more species rich. Some species are native to more than one area thus contribute to species richness for more than one area. The arrows between areas represent direction and frequency of dispersal events. Only event counts that presented a mean of 0.95 or higher (Fig. 1.4 (a)) are depicted as arrows here; arrow line thickness corresponds to natural log of the events counts.

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Mode	Type	Means (StDevs)	%
Within-area speciation	Speciation	883.38 (6.99)	70.11
	Speciation - Subset	79.28 (7.77)	6.29
Dispersal	Founder events	38.26 (4.25)	3.03
	Range expansions	217.55 (4.23)	17.26
	Range contractions	0	0
Vicariance	Vicariance	41.53 (4.18)	3.29
Total		1,260.00 (4.23)	100

Figure 1.1: Diagrams of different types of biogeographical events allowed in the models tested in this study (adapted from Matzke [135]). Cladogenetic events include within-area speciation, vicariance, and founder events. Anagenetic events include range expansion and range contraction.

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(a) Summary of dispersal events counts (and standard deviations)

	SAm	CAm	Car	NAm	AF	EU	OZ	
SAm	-	48.6 (2.63)	15.13 (1.62)	41.65 (2.83)	5.67 (0.89)	5.03 (1.14)	3.58 (0.77)	119.66 47%
CAm	11.35 (2.32)	-	10.12 (1.41)	23.26 (4.21)	0.22 (0.19)	0.35 (0.34)	0.32 (0.31)	45.62 18%
Car	1.21 (0.94)	4.20 (1.14)	-	3.09 (1.02)	0.22 (0.27)	0.11 (0.17)	0.14 (0.08)	8.97 4%
NAm	9.12 (1.51)	32.44 (4.01)	7.39 (1.20)	-	0.59 (0.29)	2.33 (0.78)	1.34 (0.52)	53.21 20%
AF	0.03 (0.21)	0.04 (0.22)	0.07 (0.33)	0.13 (0.31)	-	10.15 (1.39)	3.89 (0.83)	14.31 6%
EU	0.09 (0.22)	0.08 (0.32)	0.11 (0.21)	1.17 (0.32)	8.28 (1.32)	-	1.78 (0.37)	11.51 4%
OZ	0.06 (0.12)	0.04 (0.21)	0.04 (0.11)	0.12 (0.34)	1.39 (0.71)	0.88 (0.27)	-	2.53 1%
	21.86 9%	85.4 33%	32.86 13%	69.42 27%	16.37 6%	18.85 8%	11.05 4%	255.81 100%

(b) Range expansion event counts (and standard deviations)

	SAm	CAm	Car	NAm	AF	EU	OZ	
SAm	-	45.79 (3.51)	12.52 (1.9)	30.01 (3.24)	3.16 (1.42)	2.2 (1.29)	2.61 (1.03)	96.29 44%
CAm	10.7 (2.58)	-	9.11 (2.09)	22.23 (4.41)	0.17 (0.44)	0.28 (0.53)	0.3 (0.48)	42.79 20%
Car	1.15 (1.03)	3.78 (1.65)	-	2.94 (1.51)	0.22 (0.46)	0.09 (0.32)	0.14 (0.4)	8.32 4%
NAm	7.88 (2.01)	31.81 (4.25)	6.53 (1.7)	-	0.32 (0.55)	1.16 (0.91)	0.71 (0.77)	48.41 22%
AF	0.02 (0.14)	0.04 (0.2)	0.06 (0.24)	0.12 (0.33)	-	8.24 (1.88)	1.31 (1.13)	9.79 4%
EU	0.07 (0.26)	0.07 (0.26)	0.11 (0.31)	0.74 (0.71)	8.02 (1.52)	-	1.2 (0.88)	10.21 5%
OZ	0.05 (0.22)	0.04 (0.2)	0.04 (0.2)	0.12 (0.33)	0.93 (0.88)	0.56 (0.72)	-	1.74 1%
	19.87 9%	81.53 37%	28.37 13%	56.16 26%	12.82 6%	12.53 6%	6.27 3%	217.55 100%

(c) Founder event counts (and standard deviations)

	SAm	CAm	Car	NAm	AF	EU	OZ	
SAm	-	2.81 (1.71)	2.61 (1.26)	11.64 (2.51)	2.51 (1.25)	2.83 (1.12)	0.97 (0.74)	23.37 61%
CAm	0.65 (0.78)	-	1.01 (1.24)	1.03 (0.92)	0.05 (0.22)	0.07 (0.26)	0.02 (0.14)	2.83 7%
Car	0.06 (0.24)	0.42 (0.59)	-	0.15 (0.36)	0 (0)	0.02 (0.14)	0 (0)	0.65 2%
NAm	1.24 (1.07)	0.63 (0.84)	0.86 (0.51)	-	0.27 (0.47)	1.17 (0.79)	0.63 (0.54)	4.8 13%
AF	0.01 (0.12)	0 (0)	0.01 (0.13)	0.01 (0.11)	-	1.91 (0.89)	2.58 (0.91)	4.52 12%
EU	0.02 (0.14)	0.01 (0.12)	0 (0)	0.43 (0.54)	0.26 (0.65)	-	0.58 (0.54)	1.3 3%
OZ	0.01 (0.12)	0 (0)	0 (0)	0 (0)	0.46 (0.56)	0.32 (0.47)	-	0.79 2%
	1.99 5%	3.87 10%	4.49 12%	13.26 35%	3.55 9%	6.32 17%	4.78 12%	35.26 100%

Figure 1.4: Number of dispersal events estimated in the history of Solanaceae with biogeographical stochastic mapping. Counts of dispersal events were averaged across the 100 BSMs and are presented here with standard deviations in parentheses. Total event counts are given in (a) and divided among the two types of dispersals in (b) and (c) (see Fig. 1.1 for depictions of range expansions and founder events). Colour temperature indicates the frequency of events; the warmer the colour, the more common the event. Note that given the standard deviations, values in green are often not different from zero. The ancestral states (where the lineage dispersed from) are given in the row, and the descendant states (where the lineage dispersed to) are given in the column. The sum and correspondent percentages of events involving each area, either as a source for dispersal (the rows) or as a sink (the columns) are given on the margins. Area names in rows and columns are: South America (SAm), Central America (CAm), the Caribbean (Car), North America (NAm), Africa (AF), Eurasia (EU), and Australia (OZ).

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Chapter 2

Phylogenetics of Datureae (Solanaceae), including Description of the New Genus *Trompettia* and Re-circumscription of the Tribe

[Manuscript to be submitted to the Taxon journal]

2.1   Introduction

Building on decades of molecular systematics research in Solanaceae, recent family-level phylogenies include over 40% of the roughly 2800 species and representatives of nearly all of the recognized genera (Olmstead [161]; Särkinen [200]; Ng [151]). Many of the major clades within the family, like the fleshy-fruited solanoids, have been supported as monophyletic since the earliest phylogenetic analyses (Olmstead [162]; Olmstead [159]) and are characterized by key differences in chromosome number, embryo shape, and fruit type. These diagnostic features had been previously used in family-level taxonomy (D'Arcy [35]; Hunziker [93]), facilitating revision of the traditional classification to create a new, phylogenetically structured classification (Olmstead [163], [161]). Given this well-supported phylogenetic classification, recent systematic studies have focused on tackling resolution of smaller clades through more comprehensive species sampling and increased numbers of loci (e.g., Peralta [174]; Levin [117]; Smith [211]).

The present study focuses on Datureae G. Don, a clade of 18 species sensu (Olmstead [162]). Species of Daureae, commonly known as jimsonweeds and angel trumpets, are easily recognizable due to their showy flowers, which are some of the largest in Solanaceae (Fig. 2.1). Their large flowers have made Datureae popular with horticulturists and gardeners, and indeed, humans have

been interested in this clade for hundreds of years (Schultes [205]). Some species are used by several Native American groups due to their hallucinogenic properties (Lockwood [120]; Schultes [205]), a phytochemical signature shared with many other species in the Solanaceae ([34]). Datureae is also known for its wide geographical distribution. Species comprising this clade range from the Mojave Desert in the southwestern USA to the Andes to southern portions of the Atlantic forest in Brazil. The tribe has two main centers of diversity: the northwestern Andes and Mexico. However, introductions by humans have expanded the native range of several species to other areas in North, Central, and South America, where several species are now commonly seen in disturbed areas.

In addition to being a well-supported clade in phylogenetic studies, Datureae and genera within the tribe can be easily distinguished through a suite of morpohological features. Hunziker [93] delimited the tribe Datureae by its unusual contorted-conduplicate corolla aestivation, where the lobes are folded lengthwise and twisted to overlap in bud. Within the tribe, two genera - *Datura* and *Brugmansia* - are defined by fruit type (dry vs. fleshy), fruit shape (fusiform vs. spherical or ovoid), and seed shape (reniform vs. not reniform) (Lockwood [120]; Hunziker [93]). Additionally, characters such as seed margin and presence of elaiosomes help define subclades within *Datura* (Bye [23]). Recent phylogenetic studies (Smith [211]; Olmstead [161]) have concluded that Datureae also includes one species previously described in *Iochroma*, but which possesses the contorted-conduplicate corolla aestivation diagnostic of Datureae. Here, we place this species in a new monotypic genus, *Trompettia cardenasiana*, and revise the characters that delimit the tribe and its three included genera.

While the monophyly of Datureae is not contested, additional work is needed to clarify relationships within and among genera. For example, *Brugmansia* has not been the focus of prior phylogenetic analysis even though a taxonomic treatment is available for the genus (Lockwood [120]). Additionally, placement of *Trompettia cardenasiana* within the tribe remains ambiguous: whereas some authors have placed it as sister to *Brugmansia* (Särkinen [200]), others have resolved it as sister to *Datura* + *Brugmansia* (Ng [151]). Finally, the sister group to Datureae remains unclear. Whereas some previous studies suggested that Datureae may be sister to the Solanoideae

clade containing Solaneae, Capsiceae, and Physaleae; Olmstead [161]; [151]) others have suggested Datureae is sister to the small South American genus *Nicandra* Adans. (Särkinen [200]).

In this study, we infer phylogeny and reconstruct evolution of morphological characters in Datureae (Solanaceae) in order to revise genus-level taxonomy and identify diagnostic characters. We use three nuclear markers to test the placement of *Trompettia cardenasiana* and incorporate fossil information to estimate divergence times in the tribe. We then reconstruct evolutionary history of characters used previously in taxonomic investigation of Datureae. Finally, we combine phylogeny and morphological reconstructions to identify characters diagnostic of clades and present a new classification for the tribe. This phylogenetic framework, which is based on complete sampling of species in Datureae, will facilitate future studies of biogeography, genetics, and biochemistry of this economically important group of plants.

2.2   Materials and Methods

2.2.1   Taxon sampling

In this study, we sampled a total of 26 species: 18 belong to the ingroup and seven representing outgroups (Table 2.1). The ingroup included all 18 species of Datureae: five *Brugmansia*, twelve *Datura*, and one *Trompettia*. Species sampling in *Datura* was based on Bye [23] (note that *D. ferox* was not included here because it was considered as a synonym of *D. quercifolia* as in Symon [217]), and in *Brugmansia* on Lockwood [120], who recognized five species. The outgroup sampling spanned species in six tribes within the subfamily Solanoideae (Capsiceae, Juanulloeae, Lycieae, Nicandreae, Physaleae, and Solaneae), which is the subfamily that includes Datureae, along with one species in the subfamily Nicotianoideae, the sister clade to Solanoideae. Of the total 26 species sampled, we included multiple accessions of 16 out of 18 ingroup species to assess reciprocal monophyly. Our total matrix consisted of 50 accessions (Appendix B.1).

2.2.2 Data Collection

We used several sources of leaf material: field collections, living collections from botanical gardens, specimens grown from donated seeds, and herbarium vouchers. We also obtained extracted DNA from collaborators and utilized Genbank sequences when available (Appendix B.1). For all leaf samples, we extracted total genomic DNA following a modified 2x CTAB protocol (Doyle [48]; Smith [211]).

For phylogenetic inference, we used three nuclear regions: the internal transcribed spacers 1 and 2 plus intervening *5.8S* (ITS; White [237]), the second to ninth exons, and introns, of the granule-bound starch synthase gene region (GBSSI or *waxy*; Peralta [174]), and the second and third exons, and second intron, of the LEAFY gene region (*lfy*; Schultz [206]). These regions have been useful for species level phylogenetics in other clades in the Solanaceae (e.g., Whitson [238]; Smith [211]; Tu [224]).

The ITS+*5.8S* region was amplified and sequenced using four different primers: ITS.leu1 (Andreasen [1]), ITS2 and ITS4 (White [237]), and ITS3B (Baum [8]). We used the following protocol for 25μL reactions: 2.5μL of 10x PCR Buffer (Qiagen, Valencia, California, USA), 2.5μL of 25 mM $MgCl_2$, 1.0μL of Bovine Serum Albumin (BSA), 1.0μL of 10mM dNTPs, 1.0μL of each primer (10μM dilutions), $0.125\ \mu$L of Taq polymerase (5 units/μL), and between 10-100ng of template DNA. We used the following PCR program: $95.0°$C for 4 min followed by 34 cycles of $95.0°$C for 2 min of denaturation, $48.0°$C for 1 min of annealing, and $72°$C for 1 min of elongation, and finally a final extension of $72°$C for 5 min.

The *waxy* region was amplified and sequenced using the primers *waxy*5', *waxy*3' and *waxy*B developed by Peralta [174] and Spooner (2001), and *waxy*F41, *waxy*F420 and *waxy*R991 developed by Smith [211]. The protocol for *waxy* is similar to that of ITS+*5.8S* except we used only 2.0μL of 25 mM $MgCl_2$ and added 1.0μL of Q solution (Qiagen). We used the following PCR program: $95.0°$C for 4 min, then 35 cycles of $95.0°$C for 45s of denaturation, $52.0°$C for 1 min of annealing, $72°$C for 2 min of elongation, and finally a final extension of $72°$C for 5 min.

The *lfy* region was amplified and sequenced using primers developed for this study (Appendix B.2). To accomplish this, we used transcriptome sequences for different *Datura* species as reference to design primers (transcriptome sequences available through the Medicinal Plants Transcriptome project, `http://apps.pharmacy.uic.edu/depts/pcrps/MedTranscriptomePlants`). The PCR protocol for *lfy* was the same as that for *waxy*, but we adjusted the annealing temperature depending on the primer pair used.

All PCR products were sequenced in both directions using ACGT Inc. sequencing services (Wheeling, Illinois, USA). The resulting sequences were manually edited in 4Peaks v1.7 and assembled into contigs using the MUSCLE online alignment tool (Edgar [53]) and secondarily edited in Mesquite v3.10 (Maddison [126]).

We used the g1 statistic (Hillis [82]) to assess phylogenetic signal in our datasets. This parsimony-based statistic measures the skew in the distribution of tree lengths for a set of random trees using the observed data; datasets with phylogenetic signal are expected to be left-skewed, with an excess of short (more-parsimonious) trees. For each of our datasets (ITS+*5.8S*, *lfy* and *waxy*), we estimated g1 using 10,000 randomly-drawn trees in PAUP* v4.0a150 (Swofford [216]) with significance levels based on Hillis ([82]).

2.2.3   Phylogenetic inference

We conducted three different phylogenetic analyses: analysis of the entire dataset using parsimony to yield initial phylogenetic hypotheses and to assess congruence between individual datasets conducted in PAUP* v4.0a150 (Swofford [216]); analysis of *Datura*-only sampling to assess gene tree-species tree conflict using starBEAST (Ogilvie [158]); and, Bayesian divergence time analyses on the combined dataset using two sets of fossils conducted in BEAST2 (Bouckaert [15]).

For the parsimony analysis, we built 50% majority rule consensus trees for each nuclear region separately using PAUP* v4.0a150 (Swofford [216]). Clade support was estimated through heuristic search with 1000 bootstrap replicates, each with 10 random sequence additions and tree-bisection-reconnection (TBR) branch swapping. For ITS+*5.8S* and *waxy*, the consensus tree included all

26 taxa. For *lfy*, it included 13 ingroup taxa. This latter reduction was due to a lack of complete *lfy* sequences for five species (*B. suaveolens*, *B. versicolor*, *D.lanosa*, *D. metel*, *D. reburra*) as well as difficulty aligning *lfy* sequences outside of Datureae given high variation in the intron. Next, we compared consensus trees for the three nuclear regions to identify cases of hard incongruence (conflicting clades with bootstrap support (BS) greater than or equal to 70%; Mason-Gamer[132]). This assessment was done in two steps: first, via a comparison between the consensus trees of ITS+*5.8S* and *waxy* that included all 26 taxa, and second via a comparison between all three region consensus trees but with a reduced dataset of 13 taxa to match all the species included in the *lfy* consensus tree.

Given minor instances of hard incongruence among gene trees for *Datura* (see results), we estimated the phylogeny of this genus only with the combined dataset of all three regions using methods that accommodate discordance. We implemented starBEAST2 (Ogilvie [158]), an extension of BEAST2 (Drummond [50]; Bouckaert [15]) that facilitates joint inference of a species tree topology and gene trees from multiple genes while allowing for potential conflicts in the estimated gene topologies. We included multiple samples for most species (with the exception of *D. arenicola* and *D. discolor* for which we had only one sample each) to assess reciprocal monophyly of species. Within starBEAST, we created 5 partitions: ITS+*5.8S*, *lfy*.exons, *lfy*.intron, *waxy*.exons and *waxy*.introns. For the *lfy* and *waxy* regions, we considered exons and introns as separate partitions to account for potential variation in rates and patterns of substitution among sites. The same was not done for ITS+*5.8S* given the small length of the *5.8S* coding region ($\approx$150bp). Although introns and exons were input separately, we linked the molecular clocks and estimated linked trees for exons and introns belonging to the same region, as they are expected to share the same history. The substitution models for each partition were determined using Likelihood Ratio Tests (LRTs), where the following models were considered: JC, K81, HKY85, HKY85 + Γ, HKY85 + Γ + I, GTR, GTR + Γ, and GTR + Γ + I. The best fitting likelihood models for each partition are presented in Table 2.2. starBEAST2 also requires priors for the individual gene trees, along with a prior for the species tree. For the gene trees, under "multispecies coalescent models", we chose the 'Linear with

constant root populations' option that allows population size changes over time through the act of smooth (i.e., not abrupt) changes. We used an uncorrelated lognormal clock model to describe the branch-specific substitution rates for all partitions (Drummond [49]). Finally, for our species tree, we specified a Birth-Death prior.

After assessing congruence and addressing the conflicts within *Datura*, we estimated the phylogeny of Datureae and divergence times within the lineage using a Bayesian approach implemented in BEAST2 (Bouckaert [15]). We incorporated the starBEAST2 results (see below) into this divergence time analysis by constraining two *Datura* clades with high posterior probability (>95%) to be monophyletic (1: *D. arenicola*, *D. discolor*, *D. quercifolia* and *D. stramonium*, and 2: *D. inoxia*, *D. kymatocarpa*, *D. metel*, *D. lanosa*, *D. leichhardtii* ssp. *pruinosa*, *D. reburra* and *D. wrightii*). Given reciprocal monophyly of species in the starBEAST2 results, we used a single individual to represent each taxon for the divergence time analysis. We input the individual alignments in the same fashion as for starBEAST2, including the same substitution models and linkage of molecular clock and trees for exons and introns belonging to the same region. We used an uncorrelated, lognormal relaxed clock model to describe the branch-specific substitution rates (Drummond [49]) and a Birth-Death tree prior. We carried out three MCMC runs for 35 million generations each, sampling every 1000 generations. Convergence and stationarity of the parameters were assessed using Tracer v1.6 (Rambaut [187]) and LogCombiner (part of the BEAST2 package), targeting minimum effective sample sizes (ESS) for all variables of at least 200. Finally, we used TreeAnnotator (part of the BEAST2 package), discarding a burn-in of the first 25% of trees, to construct a maximum clade credibility (MCC) tree that included the median value for node ages, 95% highest posterior density (HPD) of divergence times, and posterior probabilities (pp) for all nodes.

For fossil calibrations, we incorporated fossil ages as node priors with log-normal distributions. The first fossil we used is a macrofossil (seed) identified as *Datura* cf. *stramonium* by Velichkevich [225]. Based on its reniform shape, its thick testa of dark coloration with numerous, irregular, shallow pits, a small incision, and lack of a convex margin triple-ridge, Velichkevich [225] assigned this fossil to the crown clade formed by *D. stramonium* and *D. quercifolia*. Since the mentioned

study was published, a new species of *Datura* has been described, *D. arenicola* (Bye [23]), whose seeds also resemble the macrofossil in all morphological aspects listed above except that it has a larger incision. Because *Datura* arenicola does not form a clade with *D. stramonium* and/or *D. quercifolia*, we chose to use the fossil age, between 3.6 and 2.6 million years ago (Ma), as a minimum age reference for the crown age of the entire *Datura* genus. The second fossil calibration was a set of macrofossils recently described as a *Physalis* species (Wilf [240]). The macrofossils (fruits) have an estimated minimum age of 52.2 Ma. Even though the fossils are assigned to *Physalis*, we here used it as a prior to constrain the Solanoideae node for two reasons. First, *Physalis* is paraphyletic (Olmstead [161]; Särkinen [200]) and overall the phylogeny of Physaleae, which includes many other taxa with similarly inflated calyces, is poorly resolved (Whitson [238]; Ng [151]). Second, the primary character used to identify the fossils as *Physalis* - the presence of an inflated calyx- may be pleisiomorphic in Solanoideae. Indeed, this character occurs in multiple Solanoid lineages, including Hyoscyameae, Juanulloae, Nicandreae, Solaneae and Withaninae (He [77]; Hu [89]).

2.2.4   Character Evolution within Datureae

We estimated the history of character changes for seven traits: flower orientation (pendant vs. erect), flower pigmentation (presence of anthocyanins vs. absence), fruit type (fleshy vs. dry) and fruit shape (fusiform vs. round/ovoid), seed elaiosomes (presence vs. absence), seed margin type (single ridge vs. triple ridge margin, see diagram in Taxonomic key below), and life history (perennial vs. annual/bi-annual). We defined this set of characters based on significance to Solanaceae (Hunziker [93]) and Datureae (Lockwood [120]; Bye [23]) taxonomy. We scored character states based on species descriptions and observations of living and herbarium collections.

For ancestral state reconstructions, we used a pruned version of the MCC tree estimated here. This pruned tree included all Datureae species and the inferred sister group, *Nicandra*. We carried out these analyses using the R (R Core Team [184]) packages 'ape' v4.1 (Paradis[167]) and 'phytools' v0.5-64 (Revell [193]). For each character separately, we first compared models that assumed equal rates of transition between character states or different rates (using the function

ace in 'ape'). The likelihood of each model was estimated and compared using a likelihood ratio test. Once we identified the best model, we estimated the history of each character using the function make.simmap in 'phytools'. This function uses stochastic character mapping (Nielsen [152]; Huelsenbeck [90]) to sample states at ancestral nodes and build possible histories for a given character. For each of our characters, we simulated 100 histories and summarized the results at each node to give the relative posterior probability at each state.

2.3   Results

2.3.1   Assessment of congruence among datasets

Our results suggest little incongruence among the three nuclear regions. The individual consensus trees showed no conflict among the datasets regarding the position of *Trompettia carde-nasiana*, the monophyly of the two genera, or the sister group to Datureae. Nonetheless, there was variation in resolution and phylogenetic signal that the individual datasets provided (see Fig. 2.2 for individual consensus trees and Table 2.2 for summary statistics). The only instance of hard incongruence (BS > 70%) was between ITS+*5.8S* and *waxy*, which yielded conflicting information regarding the position of two clades: (1) *Datura stramonium* and *D. quercifolia* and (2) *D. ky-matocarpa* and *D. leichhardtii* ssp. *pruinosa*. In ITS+*5.8S* these four taxa form a clade while in *waxy* they do not (Fig. 2.2). Our combined starBEAST2 analysis, which estimated the species tree topology while allowing for gene tree conflict, supported the *waxy* topology where *D. stra-monium*, *D. quercifolia*, *D. kymatocarpa* and *D. leichhardtii* ssp. *pruinosa* do not form a clade (Appendix B.3).

2.3.2   Phylogenetic relationships and divergence times in Datureae

Our Bayesian analysis of the combined dataset yielded a MCC tree in which *Datura* and *Brugmansia* were resolved as monophyletic with strong support (posterior probability [pp] of 1.0), with *Trompettia cardenasiana* as sister to the two (Fig. 2.3). The combined dataset analysis is

mostly driven by the patterns seen in the *waxy* dataset. The sister group to the tribe was well supported as *Nicandra physalodes* (0.97 pp). Our analyses resolved two major clades within *Datura* (Fig. 2.3). The first clade comprised *D. wrightii*, *D. lanosa*, *D. metel*, *D. reburra*, *D. kymatocarpa*, *D. inoxia*, and *D. leichhardtii* ssp. *pruinosa* while the second clade was formed by *D. stramonium*, *D. quercifolia*, *D. discolor*, and *D. arenicola*. *Datura ceratocaula* was well supported as sister to all other *Datura* species. These relationships differ from those of Bye [23] except in the position of *D. ceratocaula* as sister to the rest. Only two nodes within *Datura* were marked by low pp values (0.5 and 0.52; Fig. 2.3). We attribute these to the lack of variation in ITS+*5.8S* and *waxy* sequences for many species in *Datura* along with the missing *lfy* sequences for three species in *Datura* (*D. lanosa*, *D. metel*, and *D. reburra*). Within *Brugmansia*, our analyses resolved two clades with strong support, the first comprising *B. arborea* and *B. sanguinea* and the other containing *B. suaveolens* and *B. versicolor* as sister species, with *B. aurea* sister to the pair (Fig. 2.3).

The divergence time estimates placed the origin of subfamily Solanoideae in the Eocene (ca. 54 Ma) and early stages of diversification of Datureae in the late Eocene to early Oligocene (Fig. 2.3; see Appendix B.4 for divergence dates with confidence intervals). The median age of the crown Datureae, and *Trompettia*, was estimated as 34.7 Ma (95% HPD interval: 23.8-46.8 Ma). The split between *Datura* and *Brugmansia* was estimated as 28.5 Ma (95% HPD interval: 18.7-39.2 Ma), during the middle Oligocene (Fig. 2.3). Major splits within these two genera were inferred to occur during the Miocene (between 10 and 18 Ma; Fig. 2.3).

2.3.3 Character evolution

Many of the characters analyzed in this study were diagnostic for clades or subclades of Datureae and thus may be useful for classification (Fig. 2.4). Flower orientation, fruit type and life history characters distinguish *Datura* from *Brugmansia* and *Trompettia*. These three traits show the same pattern where one transition between states is estimated along the *Datura* stem lineage (Fig. 2.4). The remaining four characters vary within the genera, and most are associated with particular subclades. For example, fusiform fruit shape is diagnostic for the *B. versicolor*

and *B. suaveolens* lineage, with one change inferred along their stem branch. Within *Datura*, seed margins with a triple ridge are present only in the clade containing *D. metel*, *D. wrightii*, *D. lanosa*, *D. reburra*, *D. kymatocarpa*, and *D. inoxia*, although this state has apparently been lost in *D. kymatocarpa*. In addition, the clade comprising *D. wrightii* and *D. lanosa* (Fig. 2.4) is the only lineage of *Datura* that lacks elaisosomes. Compared to these characters, flower pigmentation (presence of anthocyanins vs. absence) was highly homoplastic across the phylogeny, and thus is not likely to be of taxonomic utility (Fig. 2.4).

2.4 Discussion

Our molecular results show that Datureae is formed by three genera: *Datura* and *Brugmansia*, which are sister taxa, and the monotypic genus *Trompettia*, which is sister to both other genera. The placement of *Trompettia* is furthermore supported by our comparison of morphological features among the genera. Diversification analysis here demonstrate that Datureae started diversifying around 35 Ma, likely in dry areas in the central and southern Andes. Finally, our results show that evolution of numerous morphological characters (e.g., transition from fleshy to dry fruits and from pendant to erect flowers) within the tribe happened along the branch giving rise to *Datura*.

2.4.1 Phylogenetic Relationships

Our study supports the placement of Datureae within subfamily Solanoideae and recovered most of the major relationships among Solanoids identified in previous studies. As in Olmstead ([161]) and Särkinen ([200]), the lineage containing *Lycium* is sister to all other species in Solanoideae, and *Physalis* plus *Capsicum* form a monophyletic group (Fig. 2.3). The position of some of the outgroup taxa (*Mandragora*, *Juanulloa*) differ from previous studies, but it does not conflict prior results. Thus, our analyses do not present any instances of hard conflict in terms of the outgroup taxa compared with other recent phylogenies (Olmstead [161] and Särkinen [200]).

We also recovered *Nicandra* as the sister clade to the monophyletic Datureae, as in Särkinen ([200]). Like *Trompettia* and some species of *Brugmansia*, *Nicandra* has an Andean distribution,

with its three described species occuring from Peru to northern Argentina (Hunziker [93]; Leiva Gonzalez [111]; Leiva Gonzalez [112]). The genus has many unique features (a 3 to 5-carpellate gynoecium, auriculate calyx segments, imbricate-plicate corolla aestivation) and has thus has been placed in its own tribe, Nicandreae (Wettstein [235]). Beyond these characters, *Nicandra* shares many features in common with Datureae. Additional studies may seek to identify morphological synapomorphies that unite *Nicandra* with Datureae.

Within Datureae, our analysis confirms the monophyly of each genus and places *Trompettia* as sister to the remaining two. The monophyly of the genera in Datureae, once disputed based on morphological characters (Persoon [176]; Bernhardi [12]; Safford [196]; Barclay [5]), has been supported in multiple studies (Bye [23]; Särkinen [200]; Ng [151]) and is corroborated here with comprehensive species sampling. By contrast, the position of *Trompettia* has varied across analyses, sometimes appearing as sister to *Brugmansia* (Särkinen [200]). Our molecular phylogenetic analysis confidently places *Trompettia* within the tribe as sister to both *Datura* and *Brugmansia*, as demonstrated in Ng [151]. While the MCC combined analysis result is likely driven by the *waxy* dataset, the integration of the molecular analysis with the analysis of the several shared morphological features prompts our establishment of a new genus to accommodate this monotypic lineage (see Taxonomic Innovations).

While many of the clades that we inferred mirror those in prior studies, relationships within *Datura* differ markedly from those presented in previous analyses. Bye [23] also sampled all species of *Datura* and defined two major sections within *Datura*: *Dutra* and *Datura*. Our study failed to recover monophyly of species representing these two sections (Fig. 2.3). These different outcomes likely relate to the markers used (plastid DNA in Bye [23]; nuclear in the present study) and may reflect introgression or incomplete lineage sorting (Soltis [212]; Wendel [234]). Nonetheless, both our study and that of Bye [23] recovered *D. ceratocaula* as sister to all other species in the genus, suggesting concordance along some branches. Future phylogenetic work within the genus would benefit from the inclusion of more accessions of each species, a greater number of markers, and the application of methods that allow for a mix of both reticulate and divergent processes (e.g. Eaton

[52]).

Although this study represents the first comprehensive molecular phylogenetic analysis of *Brugmansia*, relationships within the genus recovered here were similar to those proposed by Lockwood [120] in his monographic treatment. Based on morphology, geographical distribution, and crossing experiments, Lockwood [120] divided the genus into two informal groups: *B. suaveolens* and *B. versicolor* from the Amazonian and Ecuadorian lowlands, and *B. arborea*, *B. sanguinea*, and *B. aurea* from high elevations in the northern and central Andes. The concordance of our phylogeny with the distribution of the taxa suggests that geographic isolation may have played a key role in the divergence of these lineages.

2.4.2   Dating the Diversification of Datureae

Divergence time estimates within Solanaceae have been challenging because of the scarcity of fossils that can be confidently assigned to the family or clades within it. Here, we incorporate recently described fruit macrofossils (Wild [240]) into divergence time analyses and recover dates that are older than those estimated in previous studies (Särkinen [200]; De-Silva [44]). Although we conservatively assigned these fruit fossils to the Solanoideae stem lineage, they are roughly twice as old as any of the fossils previously used to calibrate this node (52.2 Ma vs. 28 Ma, Särkinen [200]). With our two calibration points (the *Datura* seed fossil of 3.6 Ma and the fruit macrofossils of 52.2 Ma), we estimate a crown age for Datureae of 34.7 Ma (95% HPD interval: 23.8-46.8 Ma; Fig. 2.3). This compares to 8.5 Ma (95% HPD interval: 5.5-11.7 Ma) in Särkinen ([200]) and 11.5 Ma (95% HPD interval: 6.8-17.4 Ma) Ma in De-Silva [44] who used secondary calibrations from an angiosperm wide analysis (Magallón [127]).

Although divergence times in Solanaceae are likely to remain contentious until more fossils are described, the older dates we estimate for cladogenetic events in Datureae are well aligned with major changes in the global climate and geological events in the Americas. The Andean uplift began roughly 40 Ma (Sebrier [207]; Ege [55]; Graham [73]), with the diversification of Datureae starting soon thereafter, around 35 Ma. The rise of the Andes created new habitats and new

ecological opportunities that fostered speciation (Pennington [173]; Särkinen [200]). Moreover, around the same time, which corresponds to the late Eocene/early Oligocene boundary, there was a major shift from a global "greenhouse" climate to an "ice-house" climate (Prothero [183]). This decrease in mean temperatures and increase in seasonality (Zachos [246]; Zachos [247]) was already a trend in the glocal climate and the proportion of global areas with arid, cooler, open-habitat environments was closer to what we observe today (Prothero [183]; Stromberg [214]). The distribution of *Trompettia cardenasiana* in the dry, central Andes as well as *Nicandra physalodes* in similar dry areas in the central and southern Andes suggests that the ancestor of Datureae was adapted to dry environments. The expansion of seasonal areas that occurred during the Oligocene could have contributed to the expansion of ancestral populations into other areas of South America and North America, where the *Datura* species are most species-rich today.

2.4.3   Character Evolution

The evolution of Datureae is marked by major transitions in morphology and life history, which may be driven by differences in geographical distribution and habitat. The woody, perennial taxa (*Brugmansia* spp. and *Trompettia*) are native to tropical regions of the Americas, while the herbaceous, annual taxa (*Datura* spp.) are distributed in dry, seasonal areas of Mexico and the southwestern United States. Correlated shifts in life history and habitat seasonality have been observed in many other plants groups, such as Onagraceae and Asteraceae (Evans [58]; Cruz-Mazo [33]). Annual habit likely evolves as an adaptive response to seasonal or unpredictable environments, where the shift represents a defense against conditions that would adversely affect adult perennial plants (Friedman [60]).

In *Datura*, the transition to seasonal dry areas has also been accompanied by changes in reproductive traits. All species in the genus produce capsules, unlike the rest of Datureae, and many release seeds with elaiosomes. Within Solanaceae, the production of elaiosomes is exclusive to *Datura* and is associated with dispersal by ants (O'Dowd [157]; Marussich [130]). Elaiosomes have evolved at least 100 times in angiosperms, often in seasonal, northern hemisphere taxa like *Datura*

and several genera in the Asteraceae, Fabaceae and Malvaceae families, to cite a few examples (Lengyel [114]; Lengyel [115]). *Datura* also shows a shift toward erect flowers, with one exception, *D. ceratocaula*, whose flowers are oriented at roughly 90 degrees from the branch. Erect or semi-erect flowers in short shrubs are advantageous for pollination by moths, which are common floral visitors in open, dry areas, and indeed the principal pollinators of *Datura* are hawkmoths (Raguso [186]; Bronstein [18]). Although less is known about pollination of *Brugmansia* and *Trompettia*, the pendant flowers, which are fragrant in some species, are likely visited by moths, bats, and/or hummingbirds (Lockwood [120]; Knudsen [107]; Weiss [233]).

2.4.4 Taxonomic Implications

The separation of *Datura* and *Brugmansia* has long been a topic of debate in the taxonomic literature. *Datura* was described in 1753 by Linnaeus based on the type species, *D. stramonium*. Subsequently, Persoon [176] transferred *D. arborea* to a new genus, *Brugmansia*, based on its persistent calyx with a lateral split, and non-spiny, bilocular fruits. This separation was subsequently rejected by many others (e.g., Bernhardi [12]; Safford [196]; Barclay [5]) because some of the diagnostic characters could also be found in one *Datura* species, *D. ceratocaula*. Specifically, *D. ceratocaula* produces fruits with smooth surfaces that do not completely dry before dehiscing and a fugacious calyx once fruit development initiates. This combination of characters is intermediate between species of *Datura*, which have dry, spiny, dehiscent fruits without persistent calyces and species of *Brugmansia*, which for the most part have fleshy, smooth, indehiscent fruits with persistent calyces. Hence, *D. ceratocaula* was seen by Bernhardi [12], Safford [196], and Barclay [5] as an irrevocable link between *Datura* and *Brugmansia*, justifying the argument to maintain all the species as belonging to a single genus. Only with the work of Lockwood [120] did the recognition of the generic rank of *Brugmansia* become more popular. In addition to their many differences in habit, longevity, habitat, fruit type, flower position, and seed morphology (Table 2.3), species in the two genera have proved extremely difficult to cross artificially (Carson [25]; Joshi [103]). The position of *D. ceratocaula* as sister to all other *Datura* species (see Fig. 2.3; see also Bye [23])

reaffirms that this species should be treated in *Datura*. Its unique combination of characters may represent changes specific to its lineage and/or retention of ancestral or intermediate states (e.g., smooth fruits, incomplete dehiscence).

Given the distinctiveness of *Trompettia* we recognize it was a third lineage in Datureae, as a new genus. When first described (Hunziker [92]), *T. cardenasiana* was placed in *Iochroma* due to morphological similarities with other species in the Iochrominae such as size of the flower, its infundibuliform (trumpet-shaped) corolla, and its geographical distribution. However, the lack of flower buds, fruits, and seeds on the type specimen prevented comprehensive comparison of this species to other species in *Iochroma* and other genera. Even though *T. cardenasiana* has fruits that are small, round berries, which are common in Iochrominae and several other clades in Solanoideae, the seeds are tetrahedral and have a thin corky seed coat, very similar to those of *Brugmansia*. Also, the small trumpet-shaped flowers of *T. cardenasiana* have distinctly flared corolla lobes that are arranged in a contorted-conduplicate fashion in the bud, a character diagnostic of Datureae. These features support a close relationship of *Trompettia* to remaining Datureae, as further emphasized by our molecular data. *Trompettia* can, however, easily be distinguished from *Datura* and *Brugmansia* by several features, in particular the size of flowers and fruit and the distinct form of the fruiting calyx (Table 2.3). Additionally, *T. cardenasiana* has a very restricted distribution in the southern parts of Bolivia, which does not overlap with the native ranges of species of *Datura* or *Brugmansia* in the north and central Andes, Central America, and southern parts of North America.

Below, we describe *Trompettia* and make the new combination. We then formally re-circumscribe Datureae to include all through genera and their species. Finally, we provide a taxonomic key to identify species of Datureae worldwide.

2.5 Taxonomic Innovations

Trompettia J. Dupin, **gen. nov. ined.** (ICN Article 30.8, McNeill [139])

TYPE: *Trompettia cardenasiana* (basionym: *Iochroma cardenasiana* Hunz.)

Perennial shrubs with simple and alternate leaves. Flowers solitary in leaf axils, pedicellate, and pendant. Corollas infundibuliform. Stamens five, filaments adnate to basal portion of corolla tube, included entirely within the corolla. Anthers basifixed, dehiscence latrorse. Ovaries superior, bilocular, surrounded by a nectary at the base, the styles included within corollas. Fruits baccate. Seeds tetrahedral, embryos coiled.

Etymology: The generic name *Trompettia* from the French trompette, diminutive of trompe (horn), alludes to the type species' flowers that are shaped like small trumpets.

Trompettia cardenasiana (Hunz.) J. Dupin, **comb. nov. ined.** (ICN Article 30.8, McNeill [139]) ≡ *Iochroma cardenasiana* Hunz., Kurtziana 10: 21. 1977. TYPE: Bolivia, Dpto. Potosí: Cotagaita, 3000m alt., XII 1932, M. Cardenas 323, (holotype, US-00385907!). EPITYPE in support of the holotype, **designated here**: Bolivia, Dpto. Potosí: Nor Chichas, 3113m, Carretera Potosí-Orkhola-Tumusla, 5 km N of Orkhola, dry west-facing slope with cacti and Acacia, II 2004, S.D. Smith, S. Leiva & S.J. Hall 384 (epitype, MO-1393217!).

Woody shrubs to 2m tall. Stems erect but arching towards apices, many of these becoming spiny, older portions glabrous, becoming pubescent towards younger portions of stem, the internodes 4-35mm long. Leaves borne in clusters on very short shoots (these < 1 mm long), subtended by dense protrusions of trichomes (Fig. 2.5), on short petioles to 5mm long, these pubescent with short eglandular trichomes or glabrous, the blades simple, alternate, narrowly obelliptic to narrowly elliptic, 20-50 x 3-10mm, (2-)4.7 to 7.5 times longer than wide, the bases attenuate, the apices broadly acute to obtuse, the margins entire, both surfaces covered by glandular trichomes (these appearing as black spots on pressed specimens) with occasional sparse simple trichomes along midrib of abaxial surface. Flowers solitary in leaf axils, on pedicels to 6mm long, pubescent with eglandular trichomes, pendant. Calyces 9 to 12mm long at anthesis, the tubes 5-6 x 4-5mm, light green, the

lobes subulate, 5-6mm long, pubescent adaxially, slightly accrescent during fruit maturation and eventually splitting along longitudinal axis to expose mature fruit. Corollas infundibuliform (these more tubular just before anthesis), 30-35mm long including lobes and 12-17mm wide at the mouth, yellow (paler at base, becoming more vibrant towards apex), the lobes 2-4 x 7-10mm, primary lobe veins extending into acuminate tip, external surfaces pubescent with uniformly distributed short, eglandular trichomes. Stamens 5, the filaments 22-25mm, adnate to the basal 5-8mm of the corolla tube, free portions 17-19mm, included within corolla, pubescent only along the adnate portion. Anthers 3-4 x 2-2.5mm, basifixed, dehiscence latrorse, glabrous. Ovary superior, bilocular, surrounded by dark red nectary at base, glabrous, the styles 27-29mm, included within the corolla. Fruits baccate, round, 5-10mm wide, immature fruits green turning dark brown in pressed specimens. Seeds tetrahedral, 3-4mm, brown to dark brown, ca. 10-20 per fruit, embryo coiled. Scientific illustration of *Trompettia cardenasiana* in Fig. 2.6.

Notes: Above, we designate an epitype in support of the holotype given that the former contains reproductive structures not present in the holotype and has a greater abundance of vegetative tissue (ICN Article 9.8, McNeill [139]). To reflect a more complete understanding of this species in light of additional material collected since the holotype, we have provided a fuller, revised species description that expands upon the original description presented by Hunziker [92].

At present, there exist only five collections of this *Trompettia cardenasiana*, all deriving from a small region in southern Bolivia in the department of Potosí. This record suggests that the species is rare (albeit still extant) in its native environment. However, we caution that Bolivia remains underexplored botanically such that future fieldwork in the area and surrounding countries may yield discovery of new, additional populations.

2.6 Taxonomic Treatment

Datureae G. Don. 1838. Gen. Hist.: 4, 472.

Brugmansia

Datura

Trompettia

Brugmansia Pers.

Brugmansia arborea (L.) Lagerh.

Brugmansia aurea Lagerh.

Brugmansia sanguinea (Ruiz & Pav.) D. Don

Brugmansia suaveolens (Humb. & Bonpl. ex Willd.) Sweet

Brugmansia versicolor Lagerh.

Datura L.

Datura arenicola Gentry ex Bye & Luna-Cavazos

Datura ceratocaula Ortega

Datura discolor Bernh.

Datura inoxia Mill.

Datura kymatocarpa A.S. Barclay

Datura lanosa Barclay ex Bye

Datura leichhardtii ssp. *pruinosa* (Greenm.) A.S. Barclay ex K. Hammer

Datura metel L.

Datura quercifolia Kunth

Datura reburra A.S. Barclay

Datura stramonium L.

Datura wrightii Regel

Trompettia J. Dupin

Trompettia cardenasiana (Hunz.) J. Dupin

2.7 Taxonomic Key of Worldwide Diversity in Datureae

1.   Flower pendant, fruit baccate 2
1'.   Flower never pendant, fruit a capsule 7
2.   Flower 2.5 to 3.5cm long, corolla always yellow .... *T. cardenasiana*
2'.   Flower > 3.5cm, corolla never yellow 3
3.   Flowering calyx tubular, with apex 2-5 toothed 4
3'.   Flowering calyx spathe-like, clearly splitting along one side and tapering to a long point 5
4.   Flower more than 25cm long, corolla tube constricted beyond calyx, fruit oblong .... *B. versicolor*
4'.   Flower 15 to 20cm, corolla tube not constricted beyond calyx, fruit ovoid .... *B. arborea*
5.   Corolla tubular, base yellow and apex red .... *B. sanguinea*
5'.   Corolla not tubular, base not yellow 6
6.   Flowering calyx glabrous, corolla tube constricted beyond calyx apex (Fig. 2.7), anthers connivent to free .... *B. suaveolens*
6'.   Flowering calyx slightly pubescent, corolla tube not constricted beyond calyx apex, anthers free
B. aurea
7.   Fruit surface spiny 8
7'.   Fruit surface not spiny, surface smooth .... *D. ceratocaula*
8.   Fruit erect, seed without elaiosome 9
8'.   Fruit never erect, seed with elaiosome 10
9.   Fruit spines numerous, of similar length, evenly distributed .... *D. stramonium*
9'.   Fruit spines of unequal length, with long apex spines, distribution uneven .... *D. quercifolia*
10.   Seed convex margin of triple-ridge (Fig. 2.7) 11
10'.   Seed convex margin without triple ridge 15
11.   Seed testa dark brown with smooth, shiny depressed central area .... *D. reburra*
11'.   Seed testa black, rey, or light brown without distinctive central area as above 12
12.   Leaf glabrous, fruit spines short, blunt, sometimes reduced to bumps, corolla commonly with two verticils and purple outer surface .... *D. metel*
12'.   Left pubescent, fruit spines not reduced, sharp to the touch, corolla with single vertical and not purple on the outside 13
13.   Corolla outer surface glabrous .... *D. inoxia*
13'.   Corolla outer surface pubescent 14
14.   Leaf surface densely covered with short trichomes giving it a gray aspect; leaf has peanut butter smell when rubbed .... *D. wrightii*
14'.   Leaf surface covered with fine, long trichomes giving it a white and lanate aspect; leaf has no peanut butter smell .... *D. lanosa*
15.   Seed coat verrucose (Fig. 2.3) .... *D. kymatocarpa*
15'.   Seed coat not verrucose 16
16.   Circumscissile fruiting calyx deflexed .... *D. leichhardtii ssp. pruinosa*
16'.   Circumscissile fruiting calyx reflexed 17
17.   Corolla longer than 8cm, with purple throat .... *D. discolor*
17'.   Corolla no longer than 4cm, without purple throat .... *D. arenicola*

2.8   Tables and figures

Table 2.1. Taxon list. All species in the ingroup are within Solanoideae. Subfamily and tribe are specified for each outgroup species.

Table 2.2. Properties of the nuclear regions used to estimate phylogenies for Datureae. * indicates the following: for our analysis of the combined dataset, we used partial sequences of *lfy* exons 2 and 3 for six outgroup species: *J. speciosa*, *N. physalodes*, *N. tabacum*, *P. peruviana*, *S. demissum*.

(a) denotes significant phylogenetic signal ($P < 0.001$) according to the $g1$ statistic critical values (see Hillis [82])

Table 2.3. Comparison of morphological characters between *Datura*, *Brugmansia* and *Trompettia cardenasiana* (see Lockwood [120]).

Figure 2.1. Flowers of different species of Datureae. On the left, *Datura stramonium* (top), *D. wrightii* (middle) and *Trompettia cardenasiana* (bottom; formerly *Iochroma cardenasiana*). On the right, *Brugmansia sanguinea* (top), *B. suaveolens* (middle) and *B. aurea* (bottom). *Datura* flowers vary in length from 5 to 18cm, *Brugmansia* flowers vary between 20 and 35cm, and *Trompettia cardenasiana* flowers vary between 2.5 and 3.5cm. Photos by J. Dupin.

Figure 2.2. 50% majority rule consensus trees from parsimony bootstrap analysis on individual regions. Numbers on nodes indicate bootstrap support values. Outgroup species names were abbreviated to genus only (see Table 2.1 for full names).

Figure 2.3. Bayesian Maximum Clade Credibility phylogeny and divergence time estimation of Datureae and outgroups, as result from combined dataset analysis. Numbers on nodes represent posterior probabilities (*pp*); nodes with an asterisk have a *pp* of 1.0. Blue node bars represent the 95% highest posterior density (HPD) of divergence times. Most recent common ancestor of Solanoideae pointed with arrow. Outgroup species names were abbreviated to genus only (see Table 2.1 for full names). Timescale represent main periods and epochs.

Figure 2.4. Ancestral state reconstruction of the following characters using stochastic map-

ping: flower orientation, fruit type, life history, seed margin, elaiosomes, fruit shape, and flower color. Below each reconstruction we indicate the mean number of transitions (changes) between the states given the indicated transition directionality.

Figure 2.5. Short branches in *Trompettia cardenasiana*

Figure 2.6. Scientific illustration of *Trompettia cardenasiana*. a, *Trompettia* branch showing leaves, flower, fruit and flower bud. b, longitudinal section of flower. c, seed longitudinal section. d, gynoecium. e, fruit with fruiting calyx. f, fruit cross section. g, anther. Illustration by J. Dupin.

Figure 2.7. Diagrams illustrating corolla constriction and seed margins. a, corolla tube constricted beyond calyx. b, seed margin of triple-ridge. c, seed coat verrucose. Illustration by J. Dupin.

Table 2.1: Taxon list. All species in the ingroup are within Solanoideae. Subfamily and tribe are specified for each outgroup species.

Ingroup	*Trompettia cardenasiana* (Hunz.) J. Dupin
	Brugmansia arborea (L.) Lagerh.
	Brugmansia aurea Lagerh.
	Brugmansia sanguinea (Ruiz & Pav.) D. Don
	Brugmansia suaveolens (Humb. & Bonpl. ex Willd.) Sweet
	Brugmansia versicolor Lagerh.
	Datura arenicola Gentry ex Bye & Luna-Cavazos
	Datura ceratocaula Ortega
	Datura discolor Bernh.
	Datura inoxia Mill.
	Datura kymatocarpa A.S. Barclay
	Datura lanosa Barclay ex Bye
	Datura leichhardtii ssp. *pruinosa* (Greenm.) A.S. Barclay ex K. Hammer
	Datura metel L.
	Datura quercifolia Kunth
	Datura reburra A.S. Barclay
	Datura stramonium L.
	Datura wrightii Regel
Outgroups	Solanoideae, Capsiceae - *Capsicum lycianthoides* Bitter
	Solanoideae, Juanulloeae - *Juanulloa speciosa* Dunal
	Solanoideae, *Mandragora chinghaiensis* Kuang & A.M. Lu
	Solanoideae, Lycieae - *Lycium tenue* Willd.
	Solanoideae, Nicandreae - *Nicandra phyalodes* (L.) Gaertn.
	Solanoideae, Physaleae - *Physalis peruviana* L.
	Solanoideae, Solaneae - *Solanum demissum* Lindl.
	Nicotianoideae - *Nicotiana tabacum* L.

Table 2.2: Properties of the nuclear regions used to estimate phylogenies for Datureae
* indicates the following: for our analysis of the combined dataset, we used partial sequences of *lfy* exons 2 and 3 for six outgroup species: *J. speciosa*, *N. physalodes*, *N. tabacum*, *P. peruviana*, *S. demissum*.
(a) denotes significant phylogenetic signal ($P < 0.001$) according to the $g1$ statistic critical values (see Hillis [82])

Region	Coverage (No. taxa sequenced)		No. characters	No. variable characters	No. parsimony informative characters	g1 statistic	Best fitting likelihood model
	Ingroup	Outgroup					
ITS	18	9	813	273	141	-0.48 (a)	GTR+ Γ
lfy	13	*	1669	277	113	-1.26 (a)	exons: JC69 / intron: GTR+ Γ
waxy	18	9	1451	477	161	-0.49 (a)	exons: HKY85 / intron: HKY85

Table 2.3: Comparison of morphological characters between *Datura*, *Brugmansia* and *Trompettia*

Datura	*Brugmansia*	*Trompettia*
Habit and Life history		
Shrubs with large leaves	Woody, arborescent shrubs or small trees with large leaves	Shrub with very small leaves and old branches becoming spines
Annual (or bi-annual)	Perennial	Perennial
Flower		
Flower 5 to 18cm	Flower 20 to 35cm	Flower 2.5 to 3.5 cm
Position erect or semi erect	Position pendant	Position pendant
Anthesis one or two days	Anthesis several days	Anthesis several days
Flowering calyx not spathe-like (except in *D. ceratocaula*), calyx teeth usually separating more or less equally	Flowering calyx frequently spathe-like or split along more than one side, calyx teeth not separating or splitting into two groups	Flowering calyx campanulate, with teeth separating equally
Fruiting calyx circumscissile near the base and falls away with the corolla (except in *D. ceratocaula* where it falls away completely), the persistent base forming a disk, cup or reflexed frill subtending the mature fruit.	Fruiting calyx not circumscissile, either falling away entirely or forming a persistent husk-like structure around the mature fruit	Fruiting calyx not circumscissile, slightly accrescent during fruit maturation and eventually splitting along a longitudinal axis to expose mature fruit
Fruit		
Fruit a capsule, round to ovoid, borne on short pedicels in an erect, sub-erect or nodding position.	Fruit a large, ovoid to elongated, pendant berry borne on much elongated pedicel	Fruit a small, round, pendant berry
Bicarpellate and tetralocular due to presence of false septa.	Bicarpellate and bilocular	Bicarpellate and bilocular
Fruit regularly or irregularly dehiscent	Fruit indehiscent	Fruit indehiscent
Pericarp usually spinose (except in *D. ceratocaula* where it is smooth)	Pericarp smooth and unarmed	Pericarp smooth and unarmed
Seeds		
Seeds relatively small, discoid, lacking a corky seed coat	Seeds large, slightly tetrahedral, with a thick, corky seed coat	Seeds relatively small, tetrahedral, with a thin, corky seed coat
Elaiosomes present in most species	Elaiosomes not present	Elaiosomes not present

Figure 2.1: Flowers of different species of Datureae. On the left, *Datura stramonium* (top), *D. wrightii* (middle) and *Trompettia cardenasiana* (bottom; formerly *Iochroma cardenasiana*). On the right, *Brugmansia sanguinea* (top), *B. suaveolens* (middle) and *B. aurea* (bottom). *Datura* flowers vary in length from 5 to 18cm, *Brugmansia* flowers vary between 20 and 35cm, and *Trompettia cardenasiana* flowers vary between 2.5 and 3.5cm. Photos by J. Dupin.

ITS +5.8S

Nicotiana
Nicandra
Mandragora
Lycium
Juanulloa
T. cardenasiana
100
88 Capsicum
Solanum
77 Physalis
71 B. sanguinea
B. arborea
75 B. aurea
100 B. versicolor
51 B. suaveolens
D. ceratocaula
92 D. stramonium
D. quercifolia
99 89 D. leichhardtii
D. kymatocarpa
69 71 D. discolor
D. arenicola
54 D. reburra
D. metel
71 D. inoxia
D. wrightii
100 D. lanosa

waxy

Nicotiana
Solanum
Nicandra
Mandragora
Lycium
100 Juanulloa
Capsicum
Physalis
T. cardenasiana
65 B. sanguinea
B. arborea
100 B. aurea
99 90 B. versicolor
99 97 B. suaveolens
D. ceratocaula
D. leichhardtii
89 D. kymatocarpa
100 D. stramonium
70 99 D. quercifolia
D. reburra
77 D. metel
63 D. inoxia
D. wrightii
97 D. lanosa
D. discolor
63 D. arenicola

lfy

T. cardenasiana
B. aurea
100 B. sanguinea
98 B. arborea
D. quercifolia
D. ceratocaula
D. stramonium
100 54 D. leichhardtii
D. kymatocarpa
52 D. wrightii
97 D. inoxia
65 D. discolor
78 D. arenicola

Figure 2.2: 50% majority rule consensus trees from parsimony bootstrap analysis on individual regions. Numbers on nodes indicate bootstrap support values. Outgroup species names were abbreviated to genus only (see Table 2.1 for full names).

Figure 2.3: Bayesian Maximum Clade Credibility phylogeny and divergence time estimation of Datureae and outgroups, as result from combined dataset analysis. Numbers on nodes represent posterior probabilities (*pp*); nodes with an asterisk have a *pp* of 1.0. Blue node bars represent the 95% highest posterior density (HPD) of divergence times. Most recent common ancestor of Solanoideae pointed with arrow. Outgroup species names were abbreviated to genus only (see Table 2.1 for full names). Timescale represent main periods and epochs.

Figure 2.4: Ancestral state reconstruction of the following characters using stochastic mapping: flower orientation, fruit type, life history, seed margin, elaiosomes, fruit shape, and flower color. Below each reconstruction we indicate the mean number of transitions (changes) between the states given the indicated transition directionality.

Figure 2.5: Short branches in *Trompettia cardenasiana*

Figure 2.6: Scientific illustration of *Trompettia cardenasiana*. a, *Trompettia* branch showing leaves, flower, fruit and flower bud. b, longitudinal section of flower. c, seed longitudinal section. d, gynoecium. e, fruit with fruiting calyx. f, fruit cross section. g, anther. Illustration by J. Dupin.

Figure 2.7: Diagrams illustrating corolla constriction and seed margins. a, corolla tube constricted beyond calyx. b, seed margin of triple-ridge. c, seed coat verrucose. Illustration by J. Dupin.

Chapter 3

Integrating historical biogeography and environmental niche evolution to understand the geographical distribution of Datureae (Solanaceae)

[Manuscript to be submitted to the American Journal of Botany]

3.1   Introduction

A main goal in biogeography is to understand patterns of clade distribution, that is, why different lineages have dispersed and established populations in some areas and not in others. Distribution patterns are shaped by abiotic factors such as climate and edaphic aspects, biotic factors such as competition or mutualism, and historical aspects such as dispersal limitation. For example, abiotic variables like temperature and precipitation are key in predicting the success of range expansion in invasive plants (e.g. Beerling [11]; Petitpierre [178]), while the addition of biotic factors, such as positive interactions between species, help explain the distribution of sympatric species in marine systems (e.g. Pigot [180]); Crotty [32]). Further, the geographical starting point of a clade along with limitations to its dispersal imposed by geographical barriers over time can be a major player in shaping the distribution of clades, as observed in birds and marsupials (e.g. White [236]; Giarla [66]).

These diverse abiotic, biotic and historical factors shaping distributions may act at different scales. For instance, while the climatic variables such as annual temperature and precipitation seasonality on a species' niche influence species distributions at continental scales, biotic interactions are more predictive of local and regional patterns of occurrence at a regional, local scale (Elith [56]).

Historical factors can act at multiple scales (Wiens [239]) as the amount of time available for a clade to expand its range can determine if there was opportunity for dispersal. As an example, a clade's center of origin determines its ancestral environment and, indirectly, contributes to defining a clade's dispersal limitations, such as physical barriers and type of surrounding environment.

In the present study, we estimate historical events and aspects of the environmental niche evolution in Datureae to explain the current geographical distribution of this clade. Here we use niche to refer to a clades environmental space, which includes climate and soil factors. Datureae is a tribe in the Solanaceae family, with an estimated age of ca. 35 million years (My; Chapter 2 of this dissertation) and it is composed of 18 species divided into three genera, *Brugmansia* Pers., *Datura* L. and *Trompettia* J. Dupin. These species are distributed in contrasting types of environments. *Brugmansia* species occupy areas in North and Central Andes at varying elevations, and one of its five species is native to southern portions of the Brazilian Atlantic forest. Most *Datura* species are native to tropical dry forests in Mexico and arid lands in northern Mexico and southwest USA (Luna-Cavazos [124]). *Trompettia*, a monotypic genus, is only found in dry high elevation areas in southern portions of the Bolivian Andes.

This investigation of the historical biogeography of Datureae presents an opportunity to assess how movements between areas separated since the Oligocene influenced the niche evolution in this clade of South American origin. Under a niche evolution scenario, the dispersal events during Datureae's history may have directly contributed to shifts in environmental niche. Studies have shown that range expansions are associated with environmental niche shifts in many widely distributed clades such as *Microseris* (Asteraceae) (Vijverberg [226]), *Clarkia* (Onagraceae) (Raven [189]) and *Gilia* (Polemoniaceae) (Morrell [144]). Niche evolution may be likely in the case of Datureae given that long distance dispersal events have the potential to introduce species to areas that are environmentally distinct from the ancestral area. Alternately, range evolution in Datureae may follow a pattern of niche conservatism, where species disperse between similar habitats (Donoghue [47]; Edwards [54]). In order to test these contrasting hypotheses, we estimated the historical biogeography of Datureae to determine where the group originated and the directionality of its range

expansions over time. We then characterized the realized niche of the genera of Datureae (portion of the fundamental niche that the species occupy as a result of limiting factors; Hutchinson [94]) and tested shifts in environmental niche across the phylogeny. Lastly, we quantified niche breadth for each genus and estimate the degree of overlap between them. Combining these results we consider how range evolution in Datureae has influenced niche diversity and breadth. More broadly, our results will contribute to a better understanding the relative importance of movements between South and North America and niche shifts in shaping the distribution of clades and the formation of floras in both portions of the American continent.

3.2 Methods

3.2.1 Historical biogeography of Datureae

3.2.1.1 Datureae phylogeny

For our historical biogeography analysis and the study of environmental niche evolution in Datureae, we used the time-calibrated maximum clade credibility (MCC) tree from Chapter 2 of this dissertation. This phylogeny was estimated using three nuclear loci, ITS+*5.8S* (White [237]), *waxy* (Peralta [174]) and *lfy* (Schultz [206]). The original tree included all 18 recognized species in Datureae and seven outgroups. For our purposes, we pruned the tree using the 'ape' package v4.1 (Paradis[167]) in R (R Core Team [184]) to retain all species in Datureae and a representative of its sister clade, the small Andean genus *Nicandra* Adans. (Fig. 3.1).

Geographic ranges of Datureae - To determine species distribution ranges, we compiled a database with location points for all 18 species in Datureae species based on voucher information from several herbaria (ARIZ, BHCB, COLO, DES, GH, MEXU, QCA, QCNE, RSA) along with online databases (TROPICOS, Missouri Botanical Garden, `http://www.tropicos.org`, last accessed on Nov. 2016; Global Biodiversity Information Facility (GBIF), `http://www.gbif.org`, last accessed on Nov. 2016). To determine species native ranges, we cross-checked collection points with numerous literature sources, including taxonomic research papers, species descriptions and

floras (e.g., [120]; [124]; [23]).

3.2.1.2   Historical biogeography estimation

We used the R package 'BioGeoBEARS' v0.2.1 (Matzke [136]) to compare biogeographical models and estimate ancestral ranges and events in Datureae. 'BioGeoBEARS' implements maximum likelihood (ML) methods that replicate the key assumptions of two of the most used types of models in historical biogeography, DEC (Dispersal-Extinction-Cladogenesis; Ree [190]) and DIVA (Dispersal-Vicariance Analysis; Ronquist [194]). Both DEC and DIVA allow for a wide range of processes, including within-area speciation, vicariance, range expansion (dispersal to a new area), range contraction (extinction in an area) and founder-event speciation. A founder-event is characterized by range switching (e.g., Andes to North America) that occurs at a lineage-splitting event (a node in the phylogeny), leaving one daughter lineage in a new range and the other daughter lineage retaining the ancestral range (Matzke [134]).

For this set of analyses, we classified native species distributions into three main areas, Andean (AA), Non-Andean regions of South America (AN) and North America (NO), and combinations of the three. We limited the number of single areas to these three given the small number of species in Datureae and the current distribution patterns within the tribe. Moreover, we chose not to code Central America as a separate area in the analysis given that this area forms the southern part of the native range for only two otherwise North American species (*Datura metel* L. and *Datura inoxia* Mill.), which are nested within the North American clade. Thus, dispersal into Central America would be estimated as independent range expansion events with no significant influence on node state estimations.

We also incorporated time-stratified dispersal multiplier matrices in the model-fitting to account for the changing distances between the regions over geological time. The continental distribution of Datureae in areas of North and South America required that we incorporate the potential influence of the closure of the Panama isthmus in our analysis. Therefore, to accommodate the recent discussion about the closure of the isthmus sensu stricto, we set up three sets of analyses:

one that include the date suggested by O'Dea ([156]) of ca. 3.5 million years ago (Ma), a second one to address the estimates made by Montes ([142]) of a closure between 16 and 7 Ma, and a third set of models with matrices with a date of ca. 20 Ma as the results from Bacon ([4]) indicated. The dispersal multiplier matrices for each of these strata give the relative probability of dispersal between areas and are roughly scaled to represent the relative distance between the areas during each time slice. All models included the matrices modified by the w parameter (matrix exponent), also estimated with ML.

In total, we tested 12 models (Appendix C.1) that varied in the number of free parameters included and in the time periods used for the dispersal multiplier matrices. The free parameters were w (matrix exponent), d (the base rate of range expansion), j (the per-event weight of founder-event speciation at cladogenesis; Matzke [134]) and e (the rate of range contraction). Because not all models are nested, we used the Akaike information criterion (AIC, Burnham [22]) to select among the 12 models; the best fit model with the lowest AIC score was used to infer the relative probabilities of ancestral ranges within the phylogeny.

3.2.2 Analyses of niche evolution

3.2.2.1 Environmental data

We retrieved environmental data for all species using the locations database described under "Geographical data" and summarized it as mean values. We initially considered 34 environmental layers at 30 arc-seconds resolution (listed in Appendix C.2): 19 bioclimatic layers of temperature and precipitation (Hijmans [81]) and 15 soil layers (Hengl [79]; Hengl [78]). The bioclimatic variables represented annual trends (e.g., mean annual temperature, annual precipitation), seasonality (e.g., annual range in temperature and precipitation) and extreme factors (e.g., temperature of the coldest and warmest month). These variables are the translation of monthly temperature and rainfall values into variables that are meaningful from a biological point of view because they represent annual trends (Hijmans [81]). The soil layers included variables that characterize physical soil properties,

such as percentage of sand, silt and clay fractions, soil bulk density (kg/m^3) and percentage of coarse fragments. All of these factors influence the water-storage capacity of the soil, which in turn, influences the levels of soil moisture available for plant growth. Soil texture, then, becomes important in highly seasonal areas, such as dry areas in Mexico, especially when compared to mesic, tropical areas (Prentice [181]).

We reduced the complexity of these environmental data in two steps before carrying on the niche analysis. First, we performed a collinearity test on these layers using the function removeCollinearity from the R package 'virtualspecies' v1.4-1 (Leroy [116]). This function uses the Pearson's correlation coefficient to analyze correlation among variables with a given cut-off value. We chose the default value of 0.7, meaning variables that presented a correlation index above 0.7 would be grouped together. The results of this test reduced the number of environmental layers from 34 to 12 (these 12 are highlighted in Appendix C.2). Second, we used a phylogenetic PCA (pPCA) approach to estimate principal components while correcting for phylogenetic relatedness. We input the mean value for each of the 12 environmental variables for each species in the function phyl.pca from the R package 'phytools' v0.5-64 (Revell [193]) to estimate the principal components along with their loadings and scores. To determine which principal components significantly contribute to the variation seen in our dataset, we used the broken-stick test (Jackson [101]) through the function screeplot in the R package 'vegan' v2.4-2 (Oksanen [98]).

3.2.2.2 Shifts in optima in environmental niche

We tested for shifts in environmental niche in Datureae using the r package 'l1ou' v1.41 (Khabbazian [104]). We used the pPCA scores for phylogenetic principal component 1 ($pPC1$) to represent Datureaes environmental niche as a continuous variable, given that pPC1 explained 94% of the variance in the data. Even though the scores for pPC1 were generated under a method that corrects for phylogenetic relatedness, it is recommended to use those results in subsequent analyses that also take the phylogeny into consideration (Revell [192]). The 'l1ou' algorithm identifies changes in the expected mean trait values by using the OrnsteinUhlenbeck (OU) process and

assesses the likelihood of the data under different models of character evolution. Moreover, l1ou does not require that the regimes of tips and internal branches are identified a priori. The algorithm uses a phylogenetic Bayesian information criterion (pBIC) that accounts for the phylogenetic correlation between species. This criterion does not suer model overtting as it can occur to other information criteria (Khabbazian [104]). Finally, the 'l1ou' package also allows for evaluation of the uncertainty in the detected shifts by incorporating a bootstrap option. Here we estimated the supported for the identified shifts by running 500 bootstrap replicates.

3.2.2.3   Estimating niche region and testing for niche overlap between genera

We used the r package 'nicheROVER' v1.0 (Lysy [125]) to estimate the niche region for each genus in Datureae and quantify the pairwise niche overlap between the genera. Niche region here is equivalent to niche size or niche breadth. In this approach, the niche is constructed following Hutchinson's [94] definition of a niche as an n-dimensional hypervolume embedded in the n-dimensional space generated by the n environmental layers (with here $n = 2$, $pPC1$ and $pPC2$). The input data here was different from the one described for the test of optima shifts with surface. Instead of using pPC scores that resulted from a $pPCA$ of mean values for each species, we considered each collection location as an independent data point within each genera and obtained pPC scores for each individual point. For instance, *Brugmansia*, which has only five species, was represented here by more than 300 data points (collection localities). This approach makes the test more conservative with respect to the hypothesis of niche divergence. It increases the number of data points and so better represents the niche regions, making it possible to identify overlap that could go undetected when using a dataset reduced to species means. To construct the environmental niche of each genus, we then extracted the scores for $pPC1$ and $pPC2$ for all individuals of the genus and built a 2-dimensional niche ellipse in the $pPC1$-$pPC2$ space that represented a 95% probability region in multivariate space (Swanson [215]).

Once the niche region was estimated, we quantified the pairwise niche overlap between the genera. Overlap values range from 0 (no overlap) to 1 (complete overlap) with a cutoff of 0.05.

Overlap is calculated as the probability that an individual from a genus is found in the niche region of another. This pairwise comparison accounts for asymmetry, meaning the probability that an individual from this latter genus is found in the niche region of the former will be distinct. Finally this metric of niche overlap also incorporates uncertainty by adopting a Bayesian inference framework (Jackson [100]). Specifically, it assigns a prior distribution to the model parameters so these are sampled and used to estimate niche region ellipses and niche overlap values, and it assesses the variability in each of these measures (Swanson [215]).

3.3 Results

3.3.1 Historical biogeography

The ancestral state for Datureae is Andean (probability = 0.74) in accordance with previous work with a smaller sampling of taxa (Dupin [51] (Chapter 1 of this disssertation)) (Fig. 3.1). The colonization of North America is inferred to have occurred via a jump dispersal from Andean regions between 28 and 15 Ma. The range expansion into non-Andean areas of South America occurred ca. 6 Ma on the stem branch of the clade formed by *B. versicolor* and *B. suaveolens*.

Our model selection supported the use of models that included the founder-event parameter (range switching at a lineage-splitting event, j). These results also showed that the most likely biogeographical history for Datureae is independent of the dating of the closure of the Panama isthmus (Appendix C.1) because the estimates for the splits between the three genera in Datureae all pre-date even the oldest date for the closure of the Panama isthmus. Moreover, there was no significant difference between the histories estimated using DEC+j and DIVALIKE+j models, as all models recover the same highest probability state at every node. The inclusion of j, allowing for one of the daughter lineages to inhabit a new area not part of the ancestral range, was crucial to allow for events such as the one between the Andes and North America, as a priori an estimation of a widespread ancestor seemed as likely as a jump dispersal between North and South America. The alternative to a jump dispersal would be range expansion resulting in a widespread ancestor

(spanning North, Central and South America) followed by extinction in the latter two areas. This scenario would not have been possible as the split between the North and South American lineages occurred before the rise of the isthmus and the Central American connection. We present the results for the historical biogeography estimation of Datureae under DEC+j in Figure 3.1.

3.3.2 Phylogenetic principal component analysis of environmental variables

Our results show that $pPC1$ (out of 12 estimated $pPCs$) explains 94% of the variance in our dataset. Under $pPC1$, the variables are organized in two sets with distinct response profiles (Fig. 3.2). Four variables load strongly in the $pPC1$ axis, with Annual Precipitation and Precipitation of the Driest Quarter being positively correlated (loading values of 0.99 and 0.92) and Mean Diurnal Range and Soil being negatively correlated (loading values of -0.93 and -0.88) (see Table 3.1 for the full list of loading values). The estimated scores for the species in Datureae place them in different areas of the pPC biplot. *Brugmansia* species occupy the space where precipitation amounts are higher. *Datura* species and *Trompettia* cluster in regions of the plot where seasonality aspects are more significant (e.g. mean diurnal range and precipitation seasonality) and soil bulk and clay content are higher.

3.3.3 Shifts in optima in environmental niche space

Species in Datureae were inferred to track two significantly different environmental optima. We estimated that Datureae started diversifying under a dry environmental niche and this environmental state was retained by species in *Datura* and *Trompettia*. *Brugmansia*, on the other hand, presents a shift from the tribe's ancestral environmental niche. Its species tracked a significantly different optimum, under a more mesic environment. These results were reinforced by our bootstrap analysis, where the detected shift along the *Brugmansia* stem branch was recovered in 80% of the replicates, and other branches or tips, where no shifts were reported in our results, had bootstrap support of less than 0.8%. We incorporated the results of this optima analysis in Figure 3.1, where the branch width in the tree identifies the species under a same optimum (with the exception of

the tribe's sister group, *Nicandra*, which was not included in this set of analyses because of uncertainty about its native environmental niche). We report the estimated values, under l1ou, for the log-likelihood of the data, shift value, pBIC score, adaptation rate , variance 2, stationary variance , and pBIC score in Table 3.2.

3.3.4   Niche overlap between genera

Our estimates of generic niche overlap revealed that between *Datura* and *Brugmansia* there is moderate to low overlap in their environmental niche regions (Fig. 3.3(a)). The probability of finding a *Brugmansia* individual in the niche region of *Datura* is 49.3 (95% CI: 36.5 - 57.6, Fig. 3.3(b)). Conversely, the probability of finding a *Datura* individual in the niche region of *Brugmansia* is 9.6 (95% CI: 6.8 - 12.2, Fig. 3.3(b)).

We report the results involving *Trompettia* with caution given the low number of samples and the small niche region estimated for this species. The results show that the probability of finding a *Trompettia* individual in *Brugmansia* or *Datura* niche regions is very small (0.46 and 3.73, respectively). The reverse situation gave us probabilities of 1, when estimating the chances of finding a *Brugmansia* or *Datura* individual in the niche region of *Trompettia*. We show the estimated niche regions and the niche overlap results in Figure 3.3.

3.4   Discussion

Our analyses show that Datureae originated in Andean regions and subsequently expanded its range to North America and non-Andean regions. Moreover, we estimated that the ancestral environmental niche in the tribe is dry and that there has been a significant shift along the *Brugmansia* branch towards a more mesic type of environment. The long-distance dispersal to North America represented a range expansion into a familiar type of environment, a dry one. Over time, *Datura* and *Brugmansia* continued to expand their realized niche towards different areas of the niche space creating a niche shift, with *Brugmansia* occupying a significantly different niche region from the ancestor (Fig. 3.4). While such expansion generated the detected shift, it did not erase

the overlap in environmental preferences between the genera in Datureae.

3.4.1   Historical biogeography of Datureae – a clade of South American origin

An Andean orogenesis that starts ca. 40 Ma (Sebrier [207]; Ege [55]; Graham [73]) makes Datureae, stem age estimated as 35 Ma, as one of the clades whose diversification was possible due to the new habitats created by the uplift. Within the Andes, the ancestral range was likely centered in the mid-elevation areas (1,000-3,000 m) in the Central Andes where both *Trompettia* and *Nicandra* (the sister clade of Datureae) are distributed. Under this scenario, the more northern Andean distribution of *Brugmansia* would reflect a northward range expansion within South America as those sections of the Andes formed in the Oligocene, ca. 30 Ma (Parra [168]). Our results also revealed that Datureae further expanded north leading to the clade currently recognized as *Datura* (Fig. 3.1).

Considering the wide disjunction between *Datura* and the other members of Datureae, there are two possible explanations for its present-day distribution of *Datura*. One possibility is a series of shorter dispersal events followed by extinction in the intervening areas. The ancestors of *Datura* could have first colonized Central America before the closure of the isthmus via dispersal from South America. From Central America, the clade could have then expanded its range northward into drier portions of North America. The present-day disjunction could then be explained by subsequent extinction of the Central American populations. Alternately, the disjunction could have arisen from successful longer distance dispersal between Andes and North America, without the intermediate step of colonization of Central America. In the absence of an extensive fossil record, it is not possible to confidently reject one of the two explanations. However, it is notable that the latter scenario, involving dispersal from dry areas in South America to similarly dry areas in North America, fits the patterns reported by Donoghue ([47]) and Crisp ([31]) that transoceanic colonizations are often accompanied by niche conservatism.

In general, the directional expansion of Andean clades towards the north is an emerging theme in biogeographical analyses. For example, Gentry ([64]) described 61 families of plants centered in

the Andes but which subsequently dispersed to Central and North America, and other continents. Bacon ([3]) also report that migration rates between South and North America were asymmetric, with northward bound events around 30% higher than in southward ones. This pattern is found across Solanaceae at the family level, where Dupin ([51]) estimated that the number of dispersal events from South America to Central and North Americas is at least four times larger than in the opposite direction. Dupin ([51]) suggested this directionality was due to the early diversification of the family in South America, providing a large pool of migrants for dispersal. Similar analyses in other clades of inferred South American origin would be needed to test the generality of this explanation.

3.4.2   Datureae's environmental niche evolution

Datureae's likely center of origin in Central Andes places the clade's initial diversification in a dry environment, an inference that is supported by our analysis of optima in which the tribe's root is placed under the drier optimum (Figs. 3.1, 3.4). *Datura* species and *Trompettia* have retained the dry optimum while the second optimum, mesic, is occupied only by *Brugmansia* species. Lockwood's monograph [120] defines the Andes of southern Colombia and Ecuador (Northern Andes) as the native range for three of the five species of *Brugmansia*, *B. aurea*, *B. arborea*, and *B. sanguinea*, while *B. suaveolens* and *B. versicolor* are found in the low tropics of the southern Atlantic Brazil and the Guayaquil Basin of Ecuador, respectively; putting the evolution of all *Brugmansia* species under mesic areas in South America. Within the mesic regime, *Brugmansia* has expanded from high elevation Andean areas to lowland tropical forest. Additionally, the estimated crown age of the *B. suaveolens* and *B. versicolor* clade (ca. 6 My) is compatible with the availability of the Guayaquil Basin for colonization by *B. versicolor*, given that this basin formed around the middle Miocene (ca. 12 Ma).

These results contradict the hypothesis that dispersal events in Datureae's history corresponded to shifts in environmental niche and instead support a pattern of niche conservatism during dispersal. The two main dispersal events estimated, from Andean areas to North America and

to non-Andean areas do not correspond to environmental niche shifts. Instead, the detected shift happened within clades of Andean distribution. We estimated that the ancestral niche environment in Datureae was dry and that *Brugmansia* represented a significant shift from that ancestral state to a mesic one. Datureae started diversifying during the Eocene-Oligocene boundary, when major climatic changes were underway. The Eocene-Oligocene boundary marks the change from a dominance of tropical biomes to more arid, cooler, open-habitat environments worldwide (Prothero [183]; Stromberg [214]). This change is a consequence of a decrease of mean temperatures and increase in seasonality (Zachos [246]; Zachos [247]). These changes accentuated the differences between the drier Central and Southern Andes, and the more mesic Northern Andes.

The environmental shift we estimated in *Brugmansia* aligns with results from studies on other clades that originated in seasonally dry areas and present directional transitions into mesic environments. For example, Ireland ([96]) estimated that transitions from seasonally dry to ever wet vegetation in the genus *Ateleia* DC. (Fabaceae) were more frequent than in the opposite direction. Similarly, *Bursera* Jacq. ex L. (Burseraceae), which originated in dry areas in North America, has experience multiple shifts away from seasonally dry environments, including one to the tropical rain forest (De-Nova [42]). One explanation for this pattern is that fewer special adaptations are required to survive a wetter climate, favoring transitions from dry to wet instead of the reverse.

Successful dispersal events of ancestral populations from dry areas into mesic ones should be seen as likely given the patterns of invasiveness seen in *Datura* today. A quick analysis of floras of South American countries along with the distribution of collection points available in the GBIF database shows that *Datura* species have been introduced and have escaped garden's successfully in much of South America. This indicates that, without dispersal limitation, these could expand their ranges into more mesic areas, as the ancestral populations likely did. The opposite does not hold true however. While *Brugmansia* species have been brought into North America for horticultural uses, they are not seen thriving on roadsides or dry areas after having escaped from cultivation. This difference is also present in our results for the pairwise niche overlap between genera: the probability of finding a *Datura* species in the *Brugmansia* niche region is roughly 5 times greater

than the reverse situation (Fig. 3.2).

3.4.3   Contributions of historical events and niche dynamics over space and time to the distribution of Datureae species

Our results suggest that the current geographical distribution of Datureae results from three elements: an initial diversification in Central Andes under a dry environmental niche, a subsequent long distance dispersal to North American areas of similar environment and a crucial, and constant, exposure to mesic environments of the northern Andes and non-Andean areas of South America (Fig. 3.3). While there were certainly limitations to dispersal between these areas, the amount of time elapsed since the beginning of the tribe's diversification, at least 17 Ma, likely allowed for enough successful dispersal events and the evolution of the niche in Datureae to happen. The colonization of areas in North America represented a range expansion into a known type of environment, a dry one. On the other hand, the colonization of non-Andean areas of South America was likely a consequence of an initial range expansion that allowed for a continuous specialization into the mesic environment (Fig. 3.3). Even though range expansions into these two types of environments ultimately resulted in a significant niche shift, our niche overlap estimates showed that moderate overlap remains between *Datura* and *Brugmansia* niche regions. This is likely a result of as yet incomplete niche specialization within *Brugmansia* and two *Datura* species, *D. metel* and *D. inoxia*, that have native ranges that include areas in Central America representing then the expansion of the niche towards the wetter side of the spectrum.

These changes in geography and niche may be the main drivers of the morphological and life history differences among the genera. *Datura* is composed entirely of species with annual and bi-annual cycles, a life history that accords with the strong seasonality of these dry areas (Evans [58]; Cruz-Mazo [33]; Friedman [60]). Moreover, the large erect flowers of these short herbs (< 1m) are principally pollinated by hawkmoths, common floral visitors in open, dry areas (Raguso [186]; Bronstein [18]). By contrast, *Brugmansia* species are large perennial shrubs (two to three meters tall), with pendant flowers often pollinated by hummingbirds, moths and bats (Lockwood

[120]; Knudsen [107]; Weiss [233]). *Trompettia* is also a perennial species but of smaller size than *Brugmansia*. The smaller flowers and fruits of *Trompettia* may reflect of the cost of being a perennial shrub in a dry area. Nothing is known with respect to the pollination biology of this monotypic genus, but the lack of detectable scent and floral phenology suggests diurnal pollinators, like insects and hummingbirds.

3.4.4   Conclusions and future directions

The results seen here for Datureae of an initial diversification in dry habitats in South America align with patterns of the appearance and spread of seasonal areas in the continent. The transition between the Eocene and the Oligocene eras (ca. 40-35 Ma) is marked by a decrease of global temperatures, triggering the transition from areas heavily forested to a mix of open areas and forests (Stromberg [214]). Studies on the flora of Patagonia show that, with the change in global mean temperatures, at first, dry areas, here specifically grasslands, became a minor components in overall forested habitats (Barreda [7]; Stromberg [214]). The continuity of such low temperatures for the next several million years up to middle Miocene (ca. 12 Ma) led to a significant expansion of such grasslands in southern South America. It is possible that a similar pattern followed in central portions of South America, meaning that small pockets of arid areas appeared ca. 35 Ma and their abundance slowly increased towards the present. This pattern of isolation can, for instance, help us understand the level of endemism found in small, dry areas along the Andes (see Särkinen ([201], for an example in Fabaceae genera). Such an interpretation could explain why *Trompettia* is isolated in a small portion of southern Bolivia in dry intermountain valleys.

This study on the range and niche evolution of Datureae provides the foundation for future studies of distribution dynamics at regional and local scales. Such fine scale studies would benefit from incorporating biotic factors, which have been shown to be relevant when explaining distributions at smaller scales (e.g. Meier [140]; Boulangeat [16]; Wisz [242]). For example, *Datura* species' ranges may be shaped by the distributions of ants, which are thought to be their primary disperser (O'Dowd [157]; Marussich [130]). By coupling the results on abiotic preferences shown here (e.g.

drier environments for species in *Datura*) with regional biotic factors (e.g. specific dispersers and pollinators native to regions of North America) we can test the potential role of adaptation to distinct environments and ecological interactions in morphological divergence and speciation. Such an integration of factors can help us explain the differences in species richness among the genera in Datureae and between regions of South and North America.

3.5 Tables and figures

Table 3.1. Variable loadings for $pPC1$ as a result of the $pPCA$ analysis. Precipitation variables (Annual Precipitation, Precipitation Driest Quarter and Precipitation Warmest Quarter) along with soil bulk density and mean diurnal range are the variables that contribute more for the variation within $pPC1$. (1) Soil bulk refers to soil bulk density in kg/m^3, an indicator of soil compaction. (3) Soil fragment refers to the percentage of soil coarse fragments (mean estimates). (2), (4), (5) refer to the percentage of clay, sand and silt fractions, respectively (mean estimates).

Table 3.2. Results of the 'surface' simulation on the evolution of $pPC1$. An OU model with two optima best explains the environmental data in Datureae.

Figure 3.1. Historical biogeography of Datureae using MCC tree from Dupin ([51]). Node states and biogeographical events represented here were estimated using the DEC+j model (although there was no significant difference between the estimated history under any of DEC+j or DIVA+j models). The most likely ancestral state in Datureae is Andean. Branches represented by plain lines identify the two optima for the environmental niche in Datureae - dry (thin branches) and mesic (bold branches). The outgroup, *Nicandra*, was not included in the shift analysis, hence its dashed branch.

Figure 3.2. Biplot of $pPC1$ and $pPC2$. The first element of this plot is the set of vectors. Vectors represent how much each variable contributes to the pPC. The longer the vector the higher its contribution. The angle between vectors represents the amount of correlation between variables. The second element is the distribution of pPC scores in the $pPC1$-$pPC2$ space for all the data points, in our case, the species in Datureae. Here we only present variables with loading

values above 0.6 or below -0.6. Variable names have been abreviated, see Table 3.1 for full names. (Plot made with most recent version of the biplot.phyl.pca function (March 15th 2017))

Figure 3.3.Niche regions and niche overlap of the genera in Datureae. (a) Niche regions of *Brugmansia* (dark grey circles), *Datura* (light grey triangles) and *Trompettia* (black squares), given $pPC1$ and $pPC2$. Individual collection points for each genus were included to represent the distribution and placement of each niche region in trait space. (b) Pairwise niche overlap between genera, the first column on the left represents the probability that an individual of *Brugmansia* would be found living in the niche region (NR) of *Datura* (top graph) and NR of *Trompettia* (bottom graph). The same organization follows on the other two columns. The scale of the graphs aligned in columns is equivalent, but a zoomed in region is presented for the instances where the results are tightly clustered. Plain vertical black line marks the mean probability value; dashed vertical lines delimit the 95% region of the estimated overlap probabilities.

Figure 3.4. Dynamics over space and time of Datureae's environmental niche. This diagram (adapted from figure 1 in Pearman [170]) represents the evolution of Datureae's environmental niche. Curves with full colors represent realized niche regions while curves with equivalent but transparent colors represent the fundamental niche as a reference to the niche space that is not occupied by the species due to competion and other factors not measured in this study. The abscissa on the left represent the a scale for type of environment, were the extremes are a dry environment and a wet one.

Table 3.1: Variable loadings for $pPC1$ as a result of the $pPCA$ analysis. Precipitation variables (Annual Precipitation, Precipitation Driest Quarter and Precipitation Warmest Quarter) along with soil bulk density and mean diurnal range are the variables that contribute more for the variation within $pPC1$. (1) Soil bulk refers to soil bulk density in kg/m^3, an indicator of soil compaction. (3) Soil fragment refers to the percentage of soil coarse fragments (mean estimates). (2), (4), (5) refer to the percentage of clay, sand and silt fractions, respectively (mean estimates).

Variable	pPC1 Loading
Annual Mean Temperature	-0.234
Mean Temperature Warmest Quarter	-0.532
Annual Precipitation	0.997
Precipitation Seasonality	-0.669
Precipitation Driest Quarter	0.917
Precipitation Warmest Quarter	0.879
Mean Diurnal Range	-0.926
Soil bulk 0.3m (1)	-0.879
Soil clay 0.3m (2)	-0.591
Soil fragment 0.3m (3)	-0.334
Soil sand 0.3m (4)	0.49
Soil silt 0.3m (5)	0.63

Table 3.2: Results of the 'l1ou' simulation on the evolution of $pPC1$

Log-Likelihood	-28.59
Number of shifts	1
Shift value	-5.44
pBIC score	77.47
Adaptation rate α	11.79
Variance σ^2	33.19
Stationary variance γ	1.41

Figure 3.1: Historical biogeography of Datureae using MCC tree from Dupin ([51]). Node states and biogeographical events represented here were estimated using the DEC+j model (although there was no significant difference between the estimated history under any of DEC+j or DIVA+j models). The most likely ancestral state in Datureae is Andean. Branches represented by plain lines identify the two optima for the environmental niche in Datureae - dry (thin branches) and mesic (bold branches). The outgroup, *Nicandra*, was not included in the shift analysis, hence its dashed branch.

Figure 3.2: Biplot of $pPC1$ and $pPC2$. The first element of this plot is the set of vectors. Vectors represent how much each variable contributes to the pPC. The longer the vector the higher its contribution. The angle between vectors represents the amount of correlation between variables. The second element is the distribution of pPC scores in the $pPC1$-$pPC2$ space for all the data points, in our case, the species in Datureae. Here we only present variables with loading values above 0.6 or below -0.6. Variable names have been abreviated, see Table 3.1 for full names. (Plot made with most recent version of the biplot.phyl.pca function (March 15th 2017)

Figure 3.3: Niche regions and niche overlap of the genera in Datureae. (a) Niche regions of *Brugmansia* (dark grey circles), *Datura* (light grey triangles) and *Trompettia* (black squares), given *pPC*1 and *pPC*2. Individual collection points for each genus were included to represent the distribution and placement of each niche region in trait space. (b) Pairwise niche overlap between genera, the first column on the left represents the probability that an individual of *Brugmansia* would be found living in the niche region (NR) of *Datura* (top graph) and NR of *Trompettia* (bottom graph). The same organization follows on the other two columns. The scale of the graphs aligned in columns is equivalent, but a zoomed in region is presented for the instances where the results are tightly clustered. Plain vertical black line marks the mean probability value; dashed vertical lines delimit the 95% region of the estimated overlap probabilities.

Figure 3.4: Dynamics over space and time of Datureae's environmental niche. This diagram (adapted from figure 1 in Pearman [170]) represents the evolution of Datureae's environmental niche. Curves with full colors represent realized niche regions while curves with equivalent but transparent colors represent the fundamental niche as a reference to the niche space that is not occupied by the species due to competion and other factors not measured in this study. The abscissa on the left represent the a scale for type of environment, were the extremes are a dry environment and a wet one.

Chapter 4

Evolution of fruit type in Datureae (Solanaceae)

[Manuscript to be submitted to the International Journal of Plant Sciences]

4.1 Introduction

Angiosperms produce a wide diversity of fruit forms, ranging from berries to drupes to capsules. In addition, transitions among these forms are frequent on evolutionary timescales. For example, the high number of transitions between fleshy and dry fruits in families such as Melastomataceae (Clausing [29]) and Solanaceae (Knapp [106]) likely helped generate the diversity in fruit morphology that is seen today in both groups. Such diversity in fruits can be a product of factors as adaptations to new habitats, for example in monocots (Givnish [70]), or adaptations to dispersers, as seen in Rubiaceae (Bremer [17]). Variations in fruit type are then ultimately tied to plant dispersal success, and consequently to plant fitness (e.g. Smith [210]; Price [182]; Biffin [13]).

Phylogenetic studies show that transitions between dry and fleshy fruits can occur in both directions, but the degree of bias in these transitions varies across clades. For instance, studies on subclades in the Campanulaceae have showed that while there is a tendency toward transitions from fleshy to dry fruits, transitions on the opposite direction are also present, meaning it is not a unidirectional process (Givnish [69]; Lagomarsino [109]). In contrast, a study on the Campanulid clade of ca. 35,000 species estimated no reversals to the clade's capsular ancestral state following multiple transitions to berries and achenes, suggesting strong constraint on fruit evolution (Beaulieu [9]). Several factors that can give rise to directional trends in evolutionary transitions such as time,

trait lability, and fitness consequences. A longer period of time provides more opportunities for trait transitions, and these transitions depend on the lability of the underlying characters. Additionally, a specific fruit type can increase the fitness of species, which leads to transitions favoring that type of fruit (e.g. Beaulieu [9]).

The Solanaceae is a useful model system for studying the evolution of fruit morphology because it presents a high diversity of fruit forms and has a robust phylogeny. The types of fruits for all the genera and major clades within the family have been previously classified (Hunziker [93]) and they encompass berries and drupes (both fleshy fruits), as well as capsules, mericarps and non-capsular dehiscent fruit (all forms of dry fruit) (Knapp [106]). Even though the family is best known for its fleshy fruits, Knapp ([106]) inferred that ancestral state for Solanaceae fruit is dry (capsule). She also estimated a similar number of transitions between fleshy and dry fruits. Using the phylogenetic framework presented by Knapp ([106]), Pabon-Mora ([164]) compared the development of several dry and fleshy fruited members of the family and suggested that fleshy and dry fruits can be differentiated anatomically, although variations within each fruit type were also observed. Nonetheless, many of the focal taxa were distantly related, making it difficult to identify the specific changes required to transition from fleshy to dry fruits and vice versa. Studies at finer phylogenetic scales comparing sister taxa that differ in fruit type may offer a greater potential to determine the developmental steps required for fruit type transitions (e.g. Hall [76]; Chiarini [27]; Mummenhoff [146]).

In this study, we explore the transitions between fruit types in Datureae, a tribe in the Solanaceae that displays a range of fruit types and presents a rare case of reversal from fleshy berries to dry capsules. Datureae is a clade of 18 species that belongs in the otherwise fleshy-fruited subfamily Solanoideae. Among the species in its three genera, *Brugmansia* Pers., *Datura* L. and *Trompettia* J. Dupin, we observe both fleshy and dry fruits (berries and capsules, respectively, Fig. 4.1). Within each fruit type there is variation in morphology. For example, the large berries of *Brugmansia* differ in size, shape and fruit wall thickness from the small round berries of *Trompettia*. The capsules of *Datura* species also vary in shape and size, and particularly in the mechanism of

dehiscence. Two species, *D. stramonium* and *D. quercifolia*, produce regularly dehisced fruits, where the fruit opens along four valves that coincide with the septa. The remaining species produce irregularly dehisced capsules, where the fruit wall ruptures irregularly. Another peculiarity of *Datura* fruits is that they produce false septa that give the bottom half of the fruits four chambers instead of the regular two seen in other Solanaceae fruits (Fig. 4.2).

Here we sample all principal fruit types in the Datureae tribe to trace the anatomical and developmental changes associated with the transition from a fleshy berry to a dry capsule. By focusing on Datureae, we can build on the previous work by Pabon-Mora ([164]), which included the irregularly dehisced capsules of *Datura inoxia*. In addition to comparing the anatomical features of fleshy and dry fruits in the tribe, we explore the characters that could explain the different dehiscence mechanisms within species in *Datura*. Specifically, we test the hypothesis that regularly dehisced fruits are anatomically more organized, that is, that dehiscence zones are clearly marked, and pericarp cell organization is more uniform. Lastly, we place these results into phylogenetic context to determine if the transition between berries and regularly dehisced capsules was a stepwise process, given the number of traits likely required for a dry fruit (e.g., creating dehiscence zones, opening to release seeds).

4.2   Methods

4.2.1   Anatomy and Morphology

Our species sampling included examples from all the fruit types in Datureae. We collected fruits at different developmental stages from the following species: *Brugmansia versicolor* (berry) and *B. sanguinea* (berry), *Trompettia cardenasiana* (berry), *Datura* ceratocaula (non-spiny, irregular dehisced capsule), *D. discolor* (irregularly dehisced capsule), *D. lanosa* (irregular dehisced capsule), *D. wrightii* (irregular dehisced capsule), and *D. quercifolia* (regularly dehisced capsule) and *D. stramonium* (regularly dehisced capsule). Samples of fruits of *B. versicolor* and *B. sanguinea* came from specimens growing at living collections in botanic gardens (Huntington Botanical Gar-

dens, CA, and Mildred E. Mathias Botanical Garden, UCLA, respectively), making the observations for these taxa more limited, and harder to control for specific stages. Individuals of *Trompettia* and *Datura* were sampled from living greenhouse collections at the University of Colorado-Boulder. In order to compare similar stages (which were limited for *Brugmansia*), we focused on the late stage of fruit development (fruit fully developed, largest developmental size) to identify the main differences between fruit types (Table 4.1).

Fruit materials were either sampled fresh or fixed in a formalin acetic acid alcohol (FAA) solution for at least 24 hours. We sampled three fruits per individual, in at least two individuals per species. Fixed material was dehydrated through an alcohol-xylene series and embedded in Paraplast X-tra (Fisher Healthcare, Houston). We sectioned the samples at 10 mm with an AO Spencer 820 rotary microtome (GMI, Ramsey, MN), and stained them following a Sharman Stain Series (Sharman [209]) that uses 2% tannic acid and 1% iron alum solutions with safranin and orange G stains. These sections were digitally photographed using a compound microscope equipped with a Leica EC4 digital camera. We conducted most of the anatomy work at the facilities of Rancho Santa Ana Botanic Garden, California. Fresh samples were hand sectioned and stained with toluidine blue O. Images for these samples were taken using a dissecting scope.

To identify the anatomical differences between berries and capsules in Datureae, we first considered the characters described by Pabon-Mora ([164]). We followed their definition of the layers in the pericarp of Solanaceae fruits: endocarp is defined as the innermost layer of cells and all layers internal to the vascular tissue, mesocarp is the tissue found between the endocarp and the outer epidermis, and exocarp is the outer epidermis (outermost layer of cells) ((Fig. 4.3)). In their study, Pabon-Mora ([164]) listed the following features as characteristic of capsules: formation of a sclerified endocarp, dehiscence zones delineated by discontinuities of the sclerified endocarp, dehiscence upon drying of the fruit, and extensive intercellular spaces form in the pericarp and the placenta (these can be also common in berries, but not as numerous as in capsules) . For berries, the main characters were the presence of collenchyma in the mesocarp, expansion of the endocarp into the locules, forming fleshy protrusions, and expansion of the placenta into the locules, forming

fleshy outgrowths. For this study, we considered the presence and location of both collenchyma and sclerenchyma tissues in the fruits, along with the presence of any intercellular spaces (lacunae), and the presence and type of dehiscence. We also recorded the type and location of vascular bundles. In *Datura stramonium*, the vascular bundles have been reported to constitute the tissue of resistance, crucial for building the tension along the fruit wall that results in the fruit opening (Roth [195]).

Finally, to test the effects of dehiscence zones delimitation and the amount of tension required to open the capsule we complemented the study of differences in dehiscence types in *Datura* with a compression test. Fruits of *D. discolor* and *D. wrightii* (both irregularly dehisced), and *D. quercifolia* and *D. stramonium* (regular dehiscence) at late stages of development, but before starting to visibly dry out, were placed in an Instron 3345 Single Column System, where they were compressed with controlled pressure increments (in kilonewtons, kN, units) until a crack in the fruit wall occurred. We recorded the final compressive load before the crack and the compressive strain (how much, in mm, the fruit deformed), and compared the means of maximum load and strain under both types of dehiscence with a Students t test. With this test we identified if there was a significant difference on the load required for each fruit type to crack open (e.g. if regularly dehisce fruits required less force to crack), and where that crack happened (e.g. if regularly dehisced fruits tend to open along the septa).

4.2.2   Reconstruction of ancestral anatomical states

For our analysis of fruit type evolution in Datureae, we used the time-calibrated maximum clade credibility (MCC) tree from Dupin (see Chapter 2). The original tree included all 18 recognized species in Datureae and seven outgroups. For our purposes, we pruned the tree using the ape package (Paradis [167]) in R (R Core Team [184]) to retain only the representative species analyzed here: *Brugmansia versicolor*, *B. sanguinea*, *Trompettia cardenasiana*, *Datura ceratocaula*, *D. discolor*, *D. lanosa*, *D. quercifolia*, *D. stramonium*, and *D. wrightii*. We reconstructed the ancestral state of six characters: fruit type (berry, capsule), endocarp collenchyma (present, absent), intercellular spaces in the pericarp (present, absent), dehiscence type (none, regular, irregular), mesocarp

sclerenchyma (present, absent), and placement concentric vascular bundles (pericarp, septa, both). We conducted these reconstructions using the r packages 'ape' (Paradis [167]) and 'phytools' (Revell [193]). For each character separately, we first compared models that assumed equal rates of transition between character states or different rates (using the function ace in 'ape'). The likelihood of each model was estimated and compared using a likelihood ratio test. Once we identified the best model, we estimated the history of each character using the function make.simmap in 'phytools'. For each of our characters, we simulated 100 histories and summarized the results at each node to give the relative posterior probability at each state. The final reconstructions were analyzed to address our hypothesis of a stepwise transition between the two fruit types.

4.3   Results

4.3.1   Anatomical comparison between berries and capsules

Capsules and berries in Datureae present some of the expected characters of each fruit type, but we also see overlap in traits not previously reported. Intracellular spaces are common in both capsules and berries in Datureae, but capsules tended to have more of these, especially at a late developmental stage (qualitative observation only; intercellular spaces marked with blue circles in Fig. 4.4). In *Trompettia* berries, which do not have false septa, these spaces are restricted to the septa tissue, likely as a result of having very few pericarp cell layers. In all other fruits, they are found in the pericarp, the septa and the false septa. *Datura* fruits do not possess an endocarp, as is the case with other capsules in Solanaceae (Pabon-Mora [164]). *Datura* capsules do present a mesocarp with fibers, where the sclerenchyma fibers are associated with the formation of the spines (Fig. 4.4 f). These fibers are not seen in *D. ceratocaula* as it lacks spines. Berries present collenchyma tissues in both the meso and endocarp tissues (collenchyma layers showed with blue arrows in Fig. 4.4), as expected, but they lack any signs of expansion of the endocarp into the locules and the expansion of the placenta into the locules. Notably, the capsules studied here present collenchyma in the mesocarp, and the capsules in *D. discolor* show expansion of the endocarp into

the locules (Fig. 4.4 l), both characters described as common in berries of Solanaceae (Pabon-Mora [164]). Finally, berries in both *Brugmansia* and *Trompettia* present a distinct innermost layer of cells in the pericarp that is characterized by cells with thicker, secondary walls, a trait not seen in any of the capsules (marked with black triangles in Fig. 4.4 a, d, e).

Our results also show that the presence, placement, and elaboration of concentric vascular bundles varies between and within fruit types when comparing mature fruits. The berries of *Brugmansia versicolor* and *B. sanguinea*, and the capsules of *Datura quercifolia* and *D. stramonium* present thick, well developed concentric vascular bundles in the pericarp, and in the septa and false septa tissues (Fig. 4.4 a, c, g, i). These are classified as amphicribral bundles given that the xylem is internal to the phloem. *Trompettia* berries, as many other berries in Solanaceae, present only underdeveloped amphicribral bundles (Fig. 4.4 d, e), meaning the bundles are not fully circular and there are fewer layers of low lignified xylem and phloem cells. For the remaining samples, *D. discolor*, *D. lanosa*, *D. wrightii* and *D. ceratocaula*, there are fully developed amphicribral bundles in the septa and false septa tissue (Fig. 4.4 p) but only underdeveloped ones in the pericarp (Fig. 4.4 m, q).

4.3.2   Regular and irregular dehiscence mechanisms in *Datura*

Fruit opening in regularly dehisced capsules is always basipetal (Fig. 4.5 a, b), while in irregular dehisced capsules, the direction is variable but typically basipetal. We identify the well-developed amphicribral vascular bundles in the pericarp as one of the major determinants of the type of dehiscence in *Datura*. Regularly dehisced capsules have these bundles in their pericarp, and their distribution and function as the tissue of resistance when the fruit is drying out delimits the four valves in the fruit and the dehiscence zones (Fig. 4.5 c). These vascular bundles are not found in the pericarp of irregularly dehisced fruits so, once the drying process starts, the lack of an orientation defined by the large vascular bundles along the pericarp allows the fruit to rupture at any region or orientation.

Examining the anatomical changes in the dehiscence zones, we can identify the steps leading

to regular dehiscence. First (Fig. 4.5 a), the septa detach from the apex of the fruit creating a discontinuity on the innermost layer of cells. This detachment happens not only along the connection point of the septa and the fruit wall but also coincides with the position of the false septa, even though the latter does not touch the full extension of the fruit wall, only the bottom half. This detachment creates four weak lines that are translated towards the base of the fruit. This translation is maintained and promoted by the drying process that happens on the pericarp. With the loss of water, the cells shrink and increase the tension within the fruit wall. The dehiscence process starts on the innermost layer of cells and proceeds outward towards the exocarp (Fig. 4.5 b).

As predicted, the compression tests showed that regularly dehisced fruits require less compression load to crack open than the irregularly dehisced fruits (Fig. 4.6). Regularly dehisced fruits of *Datura quercifolia* and *D. stramonium* deformed less (mean of compressive strain = 3.5 mm) and took a lighter compressive load (mean = 0.05 kN) to open. In contrast, the mean number for both compressive strain and compressive load were significantly higher in the irregularly dehisced fruits of *D. discolor* and *D. wrightii*, 18.8 mm and 0.21 kN respectively. Additionally, regularly dehisced fruits always opened along the septa and false septa regions, while the irregular ones presented a variation in the position of the crack.

4.3.3   Evolution of anatomical characters

The history of the characters we reconstructed with a stochastic mapping approach points to a stepwise anatomical evolution in Datureae towards regularly dehisced capsules (Figs 4.7, 4.8). Our results show that the loss of endocarp collenchyma is likely coordinated with the gain of mesocarp sclerenchyma, and this step precedes the development of amphicribral bundles in the pericarp of regularly dehisced capsules (Fig. 4.7). Moreover, the results show that the evolution of fruit type, endocarp collenchyma, and intercellular spaces is consistent with the phylogenetic relationships in the tree, meaning the number of changes observed is the minimum possible to explain the data. Fruit type and endocarp collenchyma present a single change along the *Datura* stem branch, and

the placement of intercellular in the pericarp shows one change along the *Trompettia* branch. The remaining characters present multiple changes between states. In dehiscence type, with three possible states, we found a mean of 4.13 changes along the phylogeny; in mesocarp sclerenchyma, with two states, a mean of 3.5; and in amphicribral (concentric) vascular bundles, given its three states, a mean of 5.7 (Fig. 4.8).

4.4 Discussion

Our anatomical comparison of capsules and berries in Datureae and the analyses of character evolution show that the reversal seen in *Datura* fruits (from berry to capsule) results from a complex series of steps. The transition to a regularly dehisced capsule involves first the loss of endocarp collenchyma and gain of mesocarp sclerenchyma, followed by a change to having fully developed amphicribral bundles in the pericarp. The presence and distribution of amphicribral vascular bundles is homoplasious in Datureae, but even so, we conclude that the organization of bundles is an important factor in dehiscence mechanism in capsules of *Datura*, and in differentiating regular and irregular dehiscence. While capsules and berries in Datureae are functionally different, we found overlapping anatomical characters between the two types of fruit, such as the presence of collenchyma in the mesocarp.

4.4.1 Transition from berry to capsule in Solanaceae

The reversal in fruit type observed in Datureae is rare in Solanaceae. In fact, *Datura* is the only genus in a family of estimated size of 2800 species described as producing capsules that evolved from berries. There are several possible explanations for the rarity of reversals. On the one hand, transitions towards berries might prevent the re-evolution of capsules. A similar pattern of strong directionality was documented in the Campanulids, where capsules could not be re-evolved once any of the component characters (being dehiscent, dry, or containing multiple seeds) were lost (Beaulieu [10]), and in Rubiaceae, where transitions from capsules to berries are unlikely because of the evolutionary costs of de-specializing the highly sclerified endocarp tissue (Bremer [17]). On the

other hand, there is the possibility of non-equilibrium when it comes to fruit types in Solanaceae, if the overall transition rates between states is slow. In this case the rarity seen in Datureae could mean that there has not been enough time to observe multiple transitions, given low rates of capsule evolution. This implies that at equilibrium we might expect additional cases of reversal across the family.

The limited transitions between capsules and berries observed in Solanaceae and the Campanulids is not necessarily the rule. Clausing ([29]) showed that, in Melastomataceae, shifts between those fruit types are common in both directions, a pattern which may be attributed to their fruit anatomy between Melastomataceae. In Melastomataceae, fruits can be originated from the development of the hypanthium (expanded flower receptacle), the ovary or a combination of both, which allows for multiple opportunities for tissue differentiation resulting in a great diversity in fruit morphology (Clausing [29]). This lability is not observed at the anatomical level in Solanaceae, given that its fruits are a product of the development of the ovary wall only.

4.4.2   Capsules and berries in Datureae and other Solanaceae

Capsules and berries in Datureae do not present the entire suite of characters that distinguish the two types in other species in Solanaceae. Pabon-Mora ([164]) studied the fruit development of six representative taxa in Solanaceae, the capsules of *Nicotiana sylvestris*, *Petunia hybrida* and *Datura inoxia*, and the berries of *Solanum lycopersicum*, *Iochroma fuchsioides*, and *Cestrum diurnum*. Both *N. sylvestris* and *P.* x *hybrida* belong to lineages which have retained the pleisiomorphic state of capsules, and they present the following character states: constant number of cell layers in the ovary wall and pericarp throughout development, sclerified endocarp, elongation of the epidermal cells of the placenta, dehiscence zones delineated by discontinuities of the sclerified endocarp, and fruit dehiscence. The major difference between these and the capsules of *Datura*, as pointed out by Pabon-Mora ([164]), is the lack of a sclerified endocarp in the latter. This may relate to the fact that *Datura* capsules have recently transitioned from berries, fruits that do not develop such a specialized endocarp. Pabon-Mora ([164]) concluded that the capsules of *D. inoxia* were the excep-

tion when it comes to capsule anatomy in Solanaceae (see also Dave [38]). The berries produced by *S. lycopersicum*, *I. fuchsioides*, and *C. diurnum* show an increase in the number of layers of the pericarp following fertilization, fruit growth due to cell expansion, collenchyma in the mesocarp, expansion of the endocarp into the locules, and plasticity in mature fruit size (Pabon-Mora [164]). By comparison, *Brugmansia* and *Trompettia* berries lack the expansion of the endocarp tissue. Furthermore, the capsules of *Datura* have at least two of the characters listed as characteristic of berries, collenchyma in the mesocarp (Fig. 4.4, blue arrows), expansion of the endocarp into the locules (Fig. 4.4 l); and berries of *Brugmansia* and *Trompettia* present what looks like a sclerified endocarp (innermost layer of cells, Fig. 4.4 a, d, e).

Said overlap in anatomical characters of *Datura* capsules and berries in Solanaceae could be an indication of the different ways to make and open a capsule. While *Datura* capsules are not as sclerified as those of *Nicotiana* and *Petunia* (Dave [38]; Pabon-Mora [164]), the fruits in *Datura* still present effective dehiscence mechanisms, regular and irregular, as described here. Indeed, *D. ceratocaula* fruits have few fiber bundles on the mesocarp (due to the lack of spines on its fruit wall), a demonstration that capsules in Datureae that do not rely solely on the hardening of the fruit wall to open. *Datura ceratocaula* fruits could make use of the continued growth of the mesocarp without accompanying growth in the endocarp, which ultimately creates suture regions in the endocarp (as suggested by Dave [38]).

4.4.3   Vascular system as the tissue of resistance in fruit wall of *Datura* capsules

Datura fruits dehisce differently than those of Petunia and Nicotiana. The fruit dehiscence mechanism in *Petunia* and *Nicotiana* relies heavily on the extensive lignification of the inner cell layers of the fruit, and on the delimitation of dehiscence zones at the junction of the septum and pericarp. These zones constitute a gap in the lignified tissue, making those the weak points in the fruit wall (Pabon-Mora [164]). *Datura* fruits, on the other hand, appear to open using a different mechanism. The lack of lignification in the endocarp, or the lack of cell layers with thinner cell walls to define dehiscence zones, differentiates the dehiscence mechanism of *Datura* from *Petunia*

and *Nicotiana.* Here we propose that the vascular tissue is one of the main components of the dehiscence mechanism in *Datura.* Along with the structure provided by the observed sub-epidermal collenchyma (Fig. 4.4 g, h, j, k, n, o), the vascular tissue creates a tissue of resistance that may increase the tension within the fruit wall while it dries out. Variations in the organization of the vascular tissue of the fruit wall and the different levels of vascular bundle differentiation (well-developed amphicribral bundles vs. underdeveloped) are tied to the two types of dehiscence, regular and irregular. Thicker vascular bundles, with a large number of lignified xylem cell layers results in a tissue that resists to the deformation as the pericarp cells lose water, resulting in regular dehiscence.

The development of amphicribral vascular bundles in fruits of *Datura* is not an innovation, however. The carpels of multiple genera in Solanaceae present amphicribral vascular bundles (Murray [148]). These bundles seem to be common in the flower gynoecium, where bicollateral vascular bundles transition to amphicribral bundles that can be found in the placenta (more commonly) and later in parts of the pericarp (Roth [195]). These bundles have also been described in the berries of *Capsicum annuum* (although their structural function, if any, is not discussed) (Roth [195]), and an underdeveloped version seems to be common in berries in Solanaceae (Pabon-Mora [164]). Nevertheless, this co-option (and further development) of the vascular tissue as a key feature in capsule dehiscence in *Datura* appears to be unique in Solanaceae, and rare in other families (but see Kriebel [108]).

4.4.4 Seed dispersal in Datureae

Fruit type transitions in Datureae are likely associated with differences in modes of seed dispersal. All species in *Datura*, except for *D. quercifolia* and *D. stramonium*, produce seeds with elaiosomes. These fleshy seed structures take on the role of attracting animal dispersers, usually ants. Seed dispersal in *Datura* is primarily done by ants, and water serves as a secondary disperser (O'Dowd [157]; Marussich [130]). The seeds have a thin but present corky outer layer that makes them float, and *Datura* specimens have been observed growing along or near riverbeds (J. Dupin

pers. obs.). In contrast, the dispersal mechanisms in *Brugmansia* and *Trompettia* are unknown. There are no reports of animal dispersal in any of these genera, but both produce corky seeds, making water a potential disperser. In addition, *Brugmansia* fruits tend to rot on the plant, and the pericarp is completely removed, leaving behind the net of vascular tissue holding the seeds (J. Dupin, pers. obs.). Notably, while *Brugmansia* fruits have always been classified as fleshy and indehiscent, a rare instance of a *Brugmansia* fruit showing signs of desiccation and dehiscence has been observed (Pabon-Mora pers. comm.). This could be an example where the usual thick, fleshy pericarp was not developed well enough to resist the tension caused by the net of amphicribral bundles. The large size of *Brugmansia* fruits (elongated fruits of length between 10 and 25 cm) and the lack of records about dispersers could indicate that the main animal disperser of these fruits has gone extinct. In the case of *Trompettia*, the lack of records is likely a product of the rarity of this species. *Trompettia* is restricted to dry intermountain regions along the Andes of southern Bolivia, making the study of the biology of this species challenging.

4.5　　Conclusion and future directions

Our results demonstrate the relevance of phylogenetic context when reconstructing the evolution of complex traits. We found that the re-evolution of capsules in *Datura* fruits is due to different character changes when compared to other genera that produce capsules in Solanaceae. *Petunia* and *Nicotiana*, not only retained the ancestral state in the family but they also have about a 70-million-year headstart on *Datura* (Särkinen [200]) when it comes to producing capsules, once we consider that the ancestor of Solanaceae and Convolvulaceae (its sister group; Magallón [127]) likely produced capsules too. The overlap of characters between the capsules of *Datura* and berries may represent the signature of common ancestry, given that the ancestral state in Datureae is a berry. Our study of the reversal in fruit type in *Datura* also shows that the making of capsules in Solanaceae is variable. Consider the dehiscence patterns of *D. ceratocaula*, we conclude that high levels of sclerification of the endocarp are not required for dehiscent capsules, as the tension within the fruit wall can be a product of the resistance in other tissues, such as the vascular and

the collenchyma tissues. As a matter of fact, the dehiscence in *D. ceratocaula* capsules merits an independent study given that the fruits rupture while the pericarp is still fleshy.

The results presented here provide a foundation for future studies of the drivers of transitions among fruit types in Solanaceae, and other plant families. For example, different fruit types have often been associated with different habitat types (e.g. Givnish [70]; Chen [26]) and Datureae fits this pattern in being distributed among both mesic and arid areas. Indeed, the transition to capsules coincides with long distance dispersal from South America to North America in *Datura* (see Chapter 3). Transitions in fruits have also been reported as being associated with type of dispersers, where fleshy fruits (or fruits with fleshy appendices) tend to be dispersed by animals (Bremer [17]; Lorts [121]), and dry fruits by abiotic factors such as wind (reviewed in Howe [87]). The results of such correlated analysis can be put in context and compared with causes of transitions in other plant families to tests for broad patterns of association between specific fruit types and a given environment or disperser. As we consider how habitat transitions, changes in dispersal mode, and other selective factors that might influence fruit evolution, we have to incorporate the phylogenetic framework. For studies to determine ancestral and derived states and directionality of transitions, it is crucial to determine how closely related species are, and the overall amount of time available for transitions in a given clade.

4.6   Tables and figures

Table 4.1. Characters at late stage of fruit development of species of *Brugmansia*, *Datura* and *Trompettia*.

Figure 4.1. Fruit types in Datureae. Fleshy fruits (berries) of: a, *Brugmansia versicolor*; and b, *Trompettia cardenasiana*; dry fruits (capsules) of c, *Datura quercifolia*; d, *D. discolor*; e, *D. ceratocaula*. Capsules are shown with a picture of their dehisced state. Images are representative of the relative sizes of fruits.

Figure 4.2. Differences in fruit septa in the different genera in Datureae. *Brugmansia* and *Trompettia* berries have two locules along the whole extension of the fruit, while *Datura* fruits,

up to the middle, have a fake septa (arrows) that comes from the placenta and that creates four locules in the fruits bottom half. Horizontal lines represent position of cross section. Dark, full circles mark the dorsal veins of the two fused carpels that form the fruit. Fruits and sections not to scale.

Figure 4.3. Cell layer organization in Datureae fruits. From top to bottom, the exocarp corresponds to the outer most layer of cells; mesocarp all layers between the exocarp and the vascular bundles (these included), and the endocarp corresponds to the remaining layers below the mesocarp.

Figure 4.4. Anatomical images of berries and capsules in Datureae at their late stage of development. All images are arranged in the same fashion, with the exocarp on the top and the endocarp towards the bottom. Reference scale indicates 200 μm in all images. Arrows indicate the layers of collenchyma tissue, circles highlight some of the intercellular spaces. Red coloration indicate lignified cell walls. a-c *Brugmansia versicolor*, in c a close-up of vascular bundle; d-e, *Trompettia cardenasiana*; f-i, *Datura quercifolia*, in f one of the fruits spines with the fibers that help form it; j-m, *D. discolor*, in l expansion of the endocarp cells into the locule, in m a close-up of vascular bundle; n-q, *D. ceratocaula*, in p one of the amphicribral vascular bundles found in the septa, in q a close-up of vascular bundle.

Figure 4.5. Anatomy and morphology of the dehiscence process in the regualrly dehisced fruits of *Datura quercifolia*. The order of the images begins with the earlies stage at top left, moving counterclockwise towards maturity. a, detail of *D. quercifolia* fruit seen from the top (left), section of the fruit apex (middle) showing the separation of the septa (in the center) from the fruit wall, and the horizontal lines of cells (marked with asterisks) from the fruit tip that mark two out of the four dehiscence zones, half way the fruit wall (cross section seen on the right picture) showing the continuity of the dehiscence zones (lines). b, anatomical detail of the dehiscence zones focusing on the middle portion of the fruit and the connection points between the septa and the false septa with the fruit wall (diagram on the left), in the middle images we see the moment right before the dehiscence zones start rupturing, and on the right advanced stages of dehiscence where the

innermost layer of cell is discontinuous which triggers the degradation of cells in those regions. c, *D. quercifolia* fruits completely dry, arrows point to the massive vascular bundles (same ones showed in b) that delimit the four valves that are formed once the fruits dehiscence is complete.

Figure 4.6. Results of the compression tests on regularly dehisced fruits of *Datura quercifolia* and *D. stramonium*, and irregularly dehisced fruits of *D. discolor* and *D. wrightii*. The distribution of the points in space is concordant with dehiscence type. Regularly dehisced fruits require less load, and deform less, before a crack happens on the fruit wall, when compared to irregularly dehisced fruits. Pictures show how the compression test was set up on the Instron machine, on the left a fruit of *D. quercifolia*, on the right, one of *D. wrightii*.

Figure 4.7. Stepwise reversal to regularly dehisced capsules in Datureae. 1. loss of endocarp collenchyma and gain of mesocarp fibers; 2. production of large concentric vascular bundles in the pericarp.

Figure 4.8. Ancestral state reconstruction for six characters: fruit type, dehiscence type, presence of intercellular spaces, presence of sclerenchyma in mesocarp, and placement concentric vascular bundles.

Table 4.1: Characters at late stage of fruit development of species of *Brugmansia*, *Datura* and *Trompettia*.

Species	Fruit type	Dehiscence type	Intercellular spaces in pericarp	Mesocarp collenchyma	Endocarp collenchyma	Mesocarp sclerenchyma	Endocarp sclerenchyma	Placement concentric vascular bundles
B. versicolor	Berry	None	+	+	+	-	-	Pericarp, septa
B. sanguinea	Berry	None	+	+	+	-	-	Pericarp, septa
Trompettia	Berry	None	-	+	+	-	-	None
D. quercifolia	Capsule	Regular	+	+	-	+	-	Pericarp, septa
D. stramonium	Capsule	Regular	+	+	-	+	-	Pericarp, septa
D. discolor	Capsule	Irregular	+	+	-	+	-	Septa
D. lanosa	Capsule	Irregular	+	+	-	+	-	Septa
D. wrightii	Capsule	Irregular	+	+	-	+	-	Septa
D. ceratocaula	Capsule	Irregular	+	+	-	-	-	Septa

Figure 4.1: Fruit types in Datureae. Fleshy fruits (berries) of: a, *Brugmansia versicolor*; and b, *Trompettia cardenasiana*; dry fruits (capsules) of c, *Datura quercifolia*; d, *D. discolor*; e, *D. ceratocaula*. Capsules are shown with a picture of their dehisced state. Images are representative of the relative sizes of fruits.

Figure 4.2: Differences in fruit septa in the different genera in Datureae. *Brugmansia* and *Trompettia* berries have two locules along the whole extension of the fruit, while *Datura* fruits, up to the middle, have a fake septa (arrows) that comes from the placenta and that creates four locules in the fruits bottom half. Horizontal lines represent position of cross section. Dark, full circles mark the dorsal veins of the two fused carpels that form the fruit. Fruits and sections not to scale.

Figure 4.3: Cell layer organization in Datureae fruits. From top to bottom, the exocarp corresponds to the outer most layer of cells; mesocarp all layers between the exocarp and the vascular bundles (these included), and the endocarp corresponds to the remaining layers below the mesocarp.

Figure 4.4: Anatomical images of berries and capsules in Datureae at their late stage of development. All images are arranged in the same fashion, with the exocarp on the top and the endocarp towards the bottom. Reference scale indicates 200 μm in all images. Arrows indicate the layers of collenchyma tissue, circles highlight some of the intercellular spaces. Red coloration indicate lignified cell walls. a-c *Brugmansia versicolor*, in c a close-up of vascular bundle; d-e, *Trompettia cardenasiana*; f-i, *Datura quercifolia*, in f one of the fruits spines with the fibers that help form it. (continues on next page)
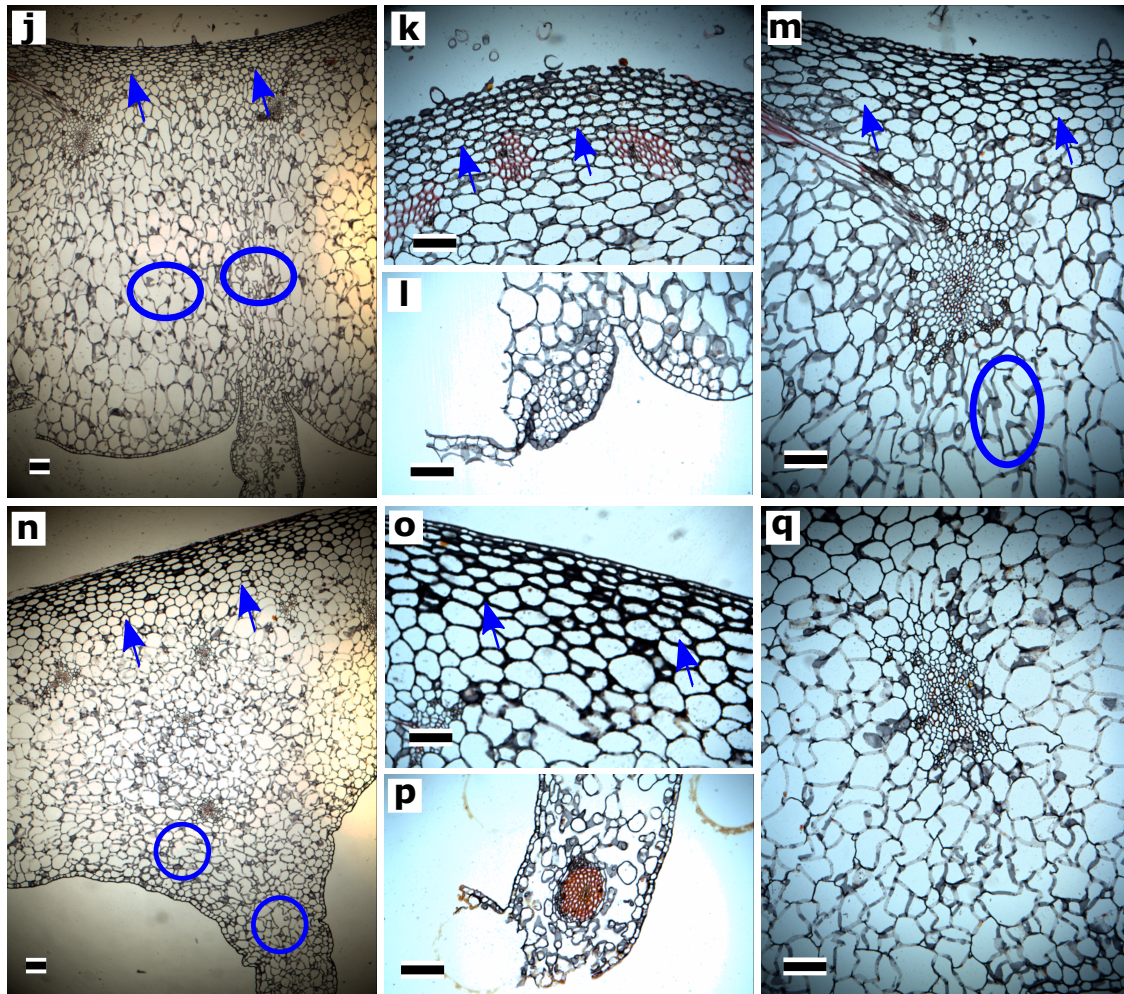
(continued) j-m, *D. discolor*, in l expansion of the endocarp cells into the locule, in m a close-up of vascular bundle; n-q, *D. ceratocaula*, in p one of the amphicribral vascular bundles found in the septa, in q a close-up of vascular bundle.

Figure 4.5: Anatomy and morphology of the dehiscence process in the regualrly dehisced fruits of *Datura quercifolia*. The order of the images begins with the earlies stage at top left, moving counterclockwise towards maturity. a, detail of *D. quercifolia* fruit seen from the top (left), section of the fruit apex (middle) showing the separation of the septa (in the center) from the fruit wall, and the horizontal lines of cells (marked with asterisks) from the fruit tip that mark two out of the four dehiscence zones, half way the fruit wall (cross section seen on the right picture) showing the continuity of the dehiscence zones (lines). b, anatomical detail of the dehiscence zones focusing on the middle portion of the fruit and the connection points between the septa and the false septa with the fruit wall (diagram on the left), in the middle images we see the moment right before the dehiscence zones start rupturing, and on the right advanced stages of dehiscence where the innermost layer of cell is discontinuous which triggers the degradation of cells in those regions. c, *D. quercifolia* fruits completely dry, arrows point to the massive vascular bundles (same ones showed in b) that delimit the four valves that are formed once the fruits dehiscence is complete.

Figure 4.6: Results of the compression tests on regularly dehisced fruits of *Datura quercifolia* and *D. stramonium*, and irregularly dehisced fruits of *D. discolor* and *D. wrightii*. The distribution of the points in space is concordant with dehiscence type. Regularly dehisced fruits require less load, and deform less, before a crack happens on the fruit wall, when compared to irregularly dehisced fruits. Pictures show how the compression test was set up on the Instron machine, on the left a fruit of *D. quercifolia*, on the right, one of *D. wrightii*.

Figure 4.7: Stepwise reversal to regularly dehisced capsules in Datureae. 1. loss of endocarp collenchyma and gain of mesocarp fibers; 2. production of large concentric vascular bundles in the pericarp.

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Appendix A

Supporting information to Chapter 1

This appendix contains supporting information for Chapter 1.

A.1 Supplementary tables and algorithm validation

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SUPPORTING INFORMATION

Bayesian estimation of the global biogeographical history of the Solanaceae.

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Appendix S1. Supplementary tables, Dispersal multiplier matrices and Algorithm validation for Biogeographical Stochastic Mapping in 'BioGeoBEARS'

Supplementary tables

Table S1.1. Species list from Solanaceae phylogeny (Särkinen *et al*., 2013) that were pruned due to cultivation or duplicates, and that had their names corrected according to more recent literature.

Cultivated taxa pruned	*Capsicum annuum* *Nicotiana rustica* *Nicotiana tabacum* *Solanum lycopersicum* *Solanum mammosum* *Solanum melongena* *Solanum pseudocapsicum* *Solanum tuberosum*
Synomyms (pruned = kept)	*Datura bernhardii = Datura stramonium* *Datura ferox = Datura quercifolia* *Datura laevis = Datura stramonium* *Datura rosei = Brugmansia sanguinea* *Metternichia sp = Metternichia princeps* *Nicotiana digluta = artificial polyploid* *Nicotiana eastii = artificial polyploid* *Nicotiana palmeri = Nicotiana obtusifolia* *Nicotiana picilla = Nicotiana plumbaginifolia* *Nicotiana trigonophylla = Nicotiana obtusifolia* *Lycium duplicatum* = unresolved species *Solanum aggregatum = Solanum guineense* *Solanum bukasovii = Solanum candolleanum* *Solanum capsicastrum = Solanum pseudocapsicum* *Solanum kurzii = Solanum violaceum* *Solanum marginatum = Solanum candolleanum* *Solanum nakurense = Solanum terminale* *Solanum ovigerum = Solanum melongena* *Solanum panduriforme = Solanum campylacanthum* *Solanum rigescentoides = Solanum humile* *Solanum sessilistellatum = Solanum nigriviolaceum* *Solanum tundalomense = Solanum colombianum* *Vestia lycioides = Vestia foetida*
Taxa renamed	*Cestrum megalophyllum -> Cestrum schlechtendalii* *Datura leichhardtii -> Datura pruinosa* *Leucophysalis viscosa -> Schraderanthus sp* *Mandragora autumnalis -> Mandragora officinalis* *Solanum adhaerens -> Solanum volubile* *Solanum circaeifolium -> Solanum stipuloideum*

	Solanum cumingii -> Solanum insanum *Solanum drymophilum -> Solanum ensifolium* *Solanum kwebense -> Solanum tettense* *Solanum megistacrolobum -> Solanum boliviense* *Solanum quadrangulare -> Solanum africanum* *Solanum thruppii -> Solanum coagulans* *Solanum tredecimgranum -> Solanum furcatum* *Solanum tridynamum -> Solanum houstonii*

Table S1.2. Solanaceae species distribution today according to a seven-area coding. Distribution scoring: South America (SAm), Central America (CAm), the Caribbean (Car), North America (NAm), Africa (AF), Eurasia (EU), and Australia (OZ). The x=12 clade (marked with an asterisk on Fig. 2) includes the clades Solaneae, Capsiceae, Physaleae, "Salpichroina", Datureae, *Mandragora*, Juanulloeae, *Nicandra*, *Exodeconus*, "Atropina" and Nicotianoideae

Taxon	Clade	Distribution
Acnistus arborescens	Physaleae	SAm&CAm&Car
Anisodus acutangulus	Atropina	EU
Anisodus carniolicoides	Atropina	EU
Anisodus luridus	Atropina	EU
Anisodus tanguticus	Atropina	EU
Anthocercis angustifolia	Nicotianoideae	OZ
Anthocercis gracilis	Nicotianoideae	OZ
Anthocercis ilicifolia	Nicotianoideae	OZ
Anthocercis intricata	Nicotianoideae	OZ
Anthocercis littorea	Nicotianoideae	OZ
Anthocercis myosotidea	Nicotianoideae	OZ
Anthocercis racemosa	Nicotianoideae	OZ
Anthocercis sylvicola	Nicotianoideae	OZ
Anthocercis viscosa	Nicotianoideae	OZ
Anthotroche blackii	Nicotianoideae	OZ
Anthotroche myoporoides	Nicotianoideae	OZ
Anthotroche pannosa	Nicotianoideae	OZ
Anthotroche walcottii	Nicotianoideae	OZ
Athenaea pogogena	Physaleae	SAm
Athenaea sp	Physaleae	SAm
Atropa belladonna	Atropina	EU
Atropa komarovii	Atropina	EU
Atropanthe sinensis	Atropina	EU
Aureliana fasciculata	Physaleae	SAm
Benthamiella patagonica	Benthamielleae	SAm
Benthamiella skottsbergii	Benthamielleae	SAm
Bouchetia anomala	Petunieae	SAm
Bouchetia erecta	Petunieae	NAm&CAm
Brachistus stramoniifolius	Physaleae	NAm&CAm
Browallia eludens	Cestroideae	NAm&CAm
Browallia speciosa	Cestroideae	SAm&CAm
Brugmansia arborea	Datureae	SAm
Brugmansia aurea	Datureae	SAm
Brugmansia sanguinea	Datureae	SAm
Brunfelsia americana	Petunieae	Car
Brunfelsia uniflora	Petunieae	SAm

Calibrachoa parviflora	Petunieae	SAm&Nam
Calibrachoa pygmaea	Petunieae	SAm
Calibrachoa sellowiana	Petunieae	SAm
Capsicum baccatum	Capsiceae	SAm
Capsicum campylopodium	Capsiceae	SAm
Capsicum cardenasii	Capsiceae	SAm
Capsicum ceratocalyx	Capsiceae	SAm
Capsicum chacoense	Capsiceae	SAm
Capsicum chinense	Capsiceae	SAm&CAm
Capsicum ciliatum	Capsiceae	NAm&SAm&CAm
Capsicum coccineum	Capsiceae	SAm
Capsicum eximium	Capsiceae	SAm
Capsicum flexuosum	Capsiceae	SAm
Capsicum frutescens	Capsiceae	NAm&SAm&CAm
Capsicum galapagoense	Capsiceae	SAm
Capsicum geminifolium	Capsiceae	SAm
Capsicum hunzikerianum	Capsiceae	SAm
Capsicum lanceolatum	Capsiceae	NAm&CAm
Capsicum lycianthoides	Capsiceae	SAm
Capsicum minutiflorum	Capsiceae	SAm
Capsicum pereirae	Capsiceae	SAm
Capsicum pubescens	Capsiceae	SAm
Capsicum recurvatum	Capsiceae	SAm
Capsicum rhomboideum	Capsiceae	SAm
Capsicum schottianum	Capsiceae	SAm
Capsicum tovarii	Capsiceae	SAm
Capsicum villosum	Capsiceae	SAm
Cestrum acutifolium	Cestroideae	Car
Cestrum aurantiacum	Cestroideae	NAm&CAm
Cestrum chiriquianum	Cestroideae	CAm
Cestrum dasyanthum	Cestroideae	CAm
Cestrum diurnum	Cestroideae	NAm&CAm&Car
Cestrum elegans	Cestroideae	NAm
Cestrum endlicheri	Cestroideae	NAm
Cestrum fasciculatum	Cestroideae	NAm
Cestrum fragile	Cestroideae	CAm
Cestrum fulvescens	Cestroideae	NAm

Cestrum glanduliferum	Cestroideae	NAm&CAm
Cestrum guatemalense	Cestroideae	NAm&CAm
Cestrum inclusum	Cestroideae	Car
Cestrum irazuense	Cestroideae	CAm
Cestrum laxum	Cestroideae	NAm
Cestrum luteovirescens	Cestroideae	NAm&CAm
Cestrum macrophyllum	Cestroideae	SAm&CAm&Car
Cestrum schlechtendalii	Cestroideae	NAm&SAm&CAm&Car
Cestrum milciomejiae	Cestroideae	Car
Cestrum miradorense	Cestroideae	NAm
Cestrum mortonianum	Cestroideae	CAm
Cestrum nocturnum	Cestroideae	NAm&SAm&CAm&Car
Cestrum oblongifolium	Cestroideae	NAm
Cestrum pacayense	Cestroideae	CAm
Cestrum pittieri	Cestroideae	CAm
Cestrum poasanum	Cestroideae	CAm
Cestrum regelii	Cestroideae	NAm&CAm
Cestrum rigidum	Cestroideae	SAm
Cestrum roseum	Cestroideae	NAm
Cestrum sphaerocarpum	Cestroideae	Car
Cestrum strigilatum	Cestroideae	CAm&SAm
Cestrum thyrsoideum	Cestroideae	NAm
Cestrum tomentosum	Cestroideae	SAm&CAm
Cestrum tuerckheimii	Cestroideae	Car
Cestrum violaceum	Cestroideae	Car
Cestrum virgaurea	Cestroideae	Car
Chamaesaracha coronopus	Physaleae	NAm
Chamaesaracha sordida	Physaleae	NAm
Coeloneurum ferrugineum	Goetzeoideae	Car
Combera paradoxa	Benthamielleae	SAm
Crenidium spinescens	Nicotianoideae	OZ
Cuatresia exiguiflora	Physaleae	SAm&CAm
Cuatresia riparia	Physaleae	SAm&CAm
Cyphanthera albicans	Nicotianoideae	OZ
Cyphanthera anthocercidea	Nicotianoideae	OZ
Cyphanthera microphylla	Nicotianoideae	OZ
Cyphanthera odgersii	Nicotianoideae	OZ
Datura ceratocaula	Datureae	NAm
Datura discolor	Datureae	NAm
Datura inoxia	Datureae	NAm&CAm
Datura pruinosa	Datureae	Nam
Datura metel	Datureae	NAm&CAm
Datura quercifolia	Datureae	NAm

Datura stramonium	Datureae	NAm&CAm
Deprea bitteriana	Physaleae	SAm
Deprea orinocensis	Physaleae	SAm&CAm
Deprea paneroi	Physaleae	SAm
Deprea sylvaticum	Physaleae	SAm&CAm
Discopodium penninervium	Physaleae	AF
Duboisia hopwoodii	Nicotianoideae	OZ
Duboisia leichhardtii	Nicotianoideae	OZ
Duboisia myoporoides	Nicotianoideae	OZ
Duckeodendron cestroides	Duckeodendron	SAm
Dunalia brachyacantha	Physaleae	SAm
Dunalia obovata	Physaleae	SAm
Dunalia solanacea	Physaleae	SAm
Dunalia spathulata	Physaleae	SAm
Dunalia spinosa	Physaleae	SAm
Dyssochroma viridiflora	Juanulloeae	SAm
Eriolarynx fasciculata	Physaleae	SAm
Eriolarynx lorentzii	Physaleae	SAm
Espadaea amoena	Goetzeoideae	Car
Exodeconus miersii	Exodeconus	SAm
Fabiana imbricata	Petunieae	SAm
Goetzea ekmanii	Goetzeoideae	Car
Goetzea elegans	Goetzeoideae	Car
Grammosolen dixonii	Nicotianoideae	OZ
Grammosolen truncatus	Nicotianoideae	OZ
Henoonia myrtifolia	Goetzeoideae	Car
Heteranthia decipiens	Schwenckieae	SAm
Hunzikeria texana	Petunieae	NAm
Hyoscyamus albus	Atropina	EU&AF
Hyoscyamus aureus	Atropina	EU&AF
Hyoscyamus desertorum	Atropina	EU
Hyoscyamus leptocalyx	Atropina	EU
Hyoscyamus muticus	Atropina	EU&AF
Hyoscyamus niger	Atropina	EU
Hyoscyamus pusillus	Atropina	EU
Hyoscyamus turcomanicus	Atropina	EU
Iochroma australe	Physaleae	SAm
Iochroma calycinum	Physaleae	SAm
Iochroma cardenasianum	Datureae	SAm
Iochroma confertiflorum	Physaleae	SAm
Iochroma cornifolium	Physaleae	SAm
Iochroma cyaneum	Physaleae	SAm
Iochroma edule	Physaleae	SAm

Iochroma ellipticum	Physaleae	SAm
Iochroma fuchsioides	Physaleae	SAm
Iochroma gesnerioides	Physaleae	SAm
Iochroma grandiflorum	Physaleae	SAm
Iochroma lehmannii	Physaleae	SAm
Iochroma loxense	Physaleae	SAm
Iochroma nitidum	Physaleae	SAm
Iochroma parvifolium	Physaleae	SAm
Iochroma salpoanum	Physaleae	SAm
Iochroma squamosum	Physaleae	SAm
Iochroma stenanthum	Physaleae	SAm
Iochroma umbellatum	Physaleae	SAm
Ipomoea	Outgroup	NAm&SAm&CAm&Car&EU&OZ&AF
Jaborosa integrifolia	Atropina	SAm
Jaborosa sativa	Atropina	SAm
Jaborosa squarrosa	Atropina	SAm
Jaltomata andersonii	Solaneae	SAm
Jaltomata antillana	Solaneae	Car
Jaltomata aspera	Solaneae	SAm
Jaltomata auriculata	Solaneae	SAm
Jaltomata bernardelloana	Solaneae	SAm
Jaltomata bicolor	Solaneae	SAm
Jaltomata biflora	Solaneae	SAm
Jaltomata bohsiana	Solaneae	NAm
Jaltomata cajacayensis	Solaneae	SAm
Jaltomata chihuahuensis	Solaneae	NAm
Jaltomata chotanae	Solaneae	SAm
Jaltomata contumacensis	Solaneae	SAm
Jaltomata darcyana	Solaneae	CAm
Jaltomata dendroidea	Solaneae	SAm
Jaltomata dentata	Solaneae	SAm
Jaltomata grandiflora	Solaneae	NAm
Jaltomata guillermoguerrae	Solaneae	SAm
Jaltomata herrerae	Solaneae	SAm
Jaltomata lanata	Solaneae	SAm
Jaltomata leivae	Solaneae	SAm
Jaltomata lezamae	Solaneae	SAm
Jaltomata lojae	Solaneae	SAm
Jaltomata lomana	Solaneae	SAm
Jaltomata mionei	Solaneae	SAm
Jaltomata nigricolor	Solaneae	SAm
Jaltomata oppositifolia	Solaneae	SAm
Jaltomata paneroi	Solaneae	SAm

Jaltomata procumbens	Solaneae	NAm&SAm&CAm
Jaltomata repandidentata	Solaneae	NAm&SAm&CAm
Jaltomata sagastegui	Solaneae	SAm
Jaltomata salpoensis	Solaneae	SAm
Jaltomata sanchezvegae	Solaneae	SAm
Jaltomata sinuosa	Solaneae	SAm
Jaltomata tayabambae	Solaneae	SAm
Jaltomata truxillana	Solaneae	SAm
Jaltomata umbellata	Solaneae	SAm
Jaltomata ventricosa	Solaneae	SAm
Jaltomata viridiflora	Solaneae	SAm
Jaltomata weberbaueri	Solaneae	SAm
Jaltomata yacheri	Solaneae	SAm
Jaltomata yungayensis	Solaneae	SAm
Juanulloa mexicana	Juanulloeae	NAm&SAm&CAm
Larnax dilloniana	Physaleae	SAm
Larnax hawkesii	Physaleae	SAm
Larnax nieva	Physaleae	SAm
Larnax parviflora	Physaleae	SAm
Larnax peruviana	Physaleae	SAm
Larnax psilophyta	Physaleae	SAm
Larnax purpurea	Physaleae	SAm
Larnax sachapapa	Physaleae	SAm
Larnax subtriflora	Physaleae	SAm
Larnax suffruticosa	Physaleae	SAm
Larnax sylvarum	Physaleae	SAm&CAm
Latua pubiflora	Atropina	SAm
Leptoglossis darcyana	Petunieae	SAm
Leucophysalis grandiflora	Physaleae	NAm
Leucophysalis nana	Physaleae	NAm
Schraderanthus sp	Physaleae	CAm
Lycianthes acapulcensis	Capsiceae	NAm
Lycianthes acutifolia	Capsiceae	SAm
Lycianthes amatitlanensis	Capsiceae	NAm&SAm&CAm
Lycianthes asarifolia	Capsiceae	SAm
Lycianthes beckneriana	Capsiceae	CAm
Lycianthes biflora	Capsiceae	EU
Lycianthes ciliolata	Capsiceae	NAm&CAm
Lycianthes dejecta	Capsiceae	NAm
Lycianthes denticulata	Capsiceae	EU
Lycianthes fasciculata	Capsiceae	SAm
Lycianthes furcatistellata	Capsiceae	CAm
Lycianthes geminiflora	Capsiceae	NAm&CAm

Lycianthes glandulosa	Capsiceae	SAm
Lycianthes heteroclita	Capsiceae	NAm&CAm
Lycianthes inaequilatera	Capsiceae	SAm
Lycianthes jalicensis	Capsiceae	NAm
Lycianthes jelskii	Capsiceae	SAm
Lycianthes lenta	Capsiceae	NAm&CAm&Car
Lycianthes lycioides	Capsiceae	SAm
Lycianthes lysimachioides	Capsiceae	EU
Lycianthes moziniana	Capsiceae	NAm
Lycianthes multiflora	Capsiceae	CAm&NAm
Lycianthes nitida	Capsiceae	NAm&SAm&CAm
Lycianthes peduncularis	Capsiceae	NAm
Lycianthes pringlei	Capsiceae	NAm
Lycianthes pseudolycioides	Capsiceae	SAm
Lycianthes radiata	Capsiceae	SAm
Lycianthes rantonnei	Capsiceae	SAm
Lycianthes rzedowskii	Capsiceae	NAm
Lycianthes saltensis	Capsiceae	SAm
Lycianthes sanctaeclarae	Capsiceae	CAm
Lycianthes shanesii	Capsiceae	OZ
Lycianthes stephanocalyx	Capsiceae	NAm&CAm
Lycianthes surotatensis	Capsiceae	NAm
Lycianthes synanthera	Capsiceae	NAm&SAm&CAm
Lycianthes tricolor	Capsiceae	NAm&CAm
Lycium acutifolium	Atropina	AF
Lycium afrum	Atropina	AF
Lycium ameghinoi	Atropina	SAm
Lycium americanum	Atropina	SAm&Car
Lycium amoenum	Atropina	AF
Lycium andersonii	Atropina	NAm
Lycium arenicola	Atropina	AF
Lycium athium	Atropina	SAm
Lycium australe	Atropina	OZ
Lycium barbarum	Atropina	EU
Lycium berlandieri	Atropina	NAm
Lycium boerhaviifolium	Atropina	NAm&SAm
Lycium bosciifolium	Atropina	AF
Lycium brevipes	Atropina	NAm
Lycium californicum	Atropina	NAm
Lycium carolinianum	Atropina	Nam
Lycium cestroides	Atropina	SAm
Lycium chanar	Atropina	SAm
Lycium chilense	Atropina	SAm

Lycium chinense	Atropina	EU
Lycium ciliatum	Atropina	SAm
Lycium cinereum	Atropina	AF
Lycium cooperi	Atropina	NAm
Lycium cuneatum	Atropina	SAm
Lycium dasystemum	Atropina	EU
Lycium decumbens	Atropina	AF
Lycium depressum	Atropina	EU
Lycium deserti	Atropina	SAm
Lycium eenii	Atropina	AF
Lycium elongatum	Atropina	SAm
Lycium europaeum	Atropina	EU
Lycium exsertum	Atropina	NAm
Lycium ferocissimum	Atropina	AF
Lycium fremontii	Atropina	NAm
Lycium fuscum	Atropina	SAm
Lycium gariepense	Atropina	AF
Lycium gilliesianum	Atropina	SAm
Lycium grandicalyx	Atropina	AF
Lycium hirsutum	Atropina	AF
Lycium horridum	Atropina	AF
Lycium infaustum	Atropina	SAm
Lycium macrodon	Atropina	NAm
Lycium microphyllum	Atropina	SAm
Lycium minimum	Atropina	SAm
Lycium minutifolium	Atropina	SAm
Lycium morongii	Atropina	SAm
Lycium nodosum	Atropina	SAm
Lycium oxycarpum	Atropina	AF
Lycium pallidum	Atropina	NAm
Lycium parishii	Atropina	NAm
Lycium pilifolium	Atropina	AF
Lycium puberulum	Atropina	NAm
Lycium pumilum	Atropina	AF
Lycium rachidocladum	Atropina	SAm
Lycium ruthenicum	Atropina	EU
Lycium sandwicense	Atropina	OZ
Lycium schizocalyx	Atropina	AF
Lycium schweinfurthii	Atropina	AF
Lycium shawii	Atropina	AF
Lycium shockleyi	Atropina	NAm
Lycium stenophyllum	Atropina	SAm
Lycium strandveldense	Atropina	AF

Lycium tenue	Atropina	AF
Lycium tenuispinosum	Atropina	SAm
Lycium tetrandrum	Atropina	AF
Lycium texanum	Atropina	NAm
Lycium torreyi	Atropina	NAm
Lycium truncatum	Atropina	EU
Lycium villosum	Atropina	AF
Lycium vimineum	Atropina	SAm
Lycium yunnanense	Atropina	EU
Mandragora officinalis	Mandragora	EU&AF
Mandragora caulescens	Mandragora	EU
Mandragora chinghaiensis	Mandragora	EU
Mandragora officinarum	Mandragora	EU&AF
Mandragora turcomanica	Mandragora	EU
Markea panamensis	Juanulloeae	CAm
Markea ulei	Juanulloeae	SAm
Melananthus guatemalensis	Schwenckieae	SAm&CAm
Mellissia begoniifolia	Physaleae	AF
Merinthopodium neuranthum	Juanulloeae	CAm
Metternichia princeps	Goetzeoideae	SAm
Nectouxia formosa	Salpichroina	NAm
Nicandra physalodes	Nicandra	SAm
Nicotiana acaulis	Nicotianoideae	SAm
Nicotiana acuminata	Nicotianoideae	SAm
Nicotiana africana	Nicotianoideae	AF
Nicotiana alata	Nicotianoideae	SAm
Nicotiana amplexicaulis	Nicotianoideae	OZ
Nicotiana arentsii	Nicotianoideae	SAm
Nicotiana benavidesii	Nicotianoideae	SAm
Nicotiana bonariensis	Nicotianoideae	SAm
Nicotiana cavicola	Nicotianoideae	OZ
Nicotiana clevelandii	Nicotianoideae	NAm
Nicotiana cordifolia	Nicotianoideae	SAm
Nicotiana corymbosa	Nicotianoideae	SAm
Nicotiana excelsior	Nicotianoideae	OZ
Nicotiana exigua	Nicotianoideae	OZ
Nicotiana forgetiana	Nicotianoideae	SAm
Nicotiana forsteri	Nicotianoideae	OZ
Nicotiana glauca	Nicotianoideae	SAm
Nicotiana glutinosa	Nicotianoideae	SAm
Nicotiana goodspeedii	Nicotianoideae	OZ
Nicotiana gossei	Nicotianoideae	OZ
Nicotiana kawakamii	Nicotianoideae	SAm

Nicotiana knightiana	Nicotianoideae	SAm
Nicotiana langsdorffii	Nicotianoideae	SAm
Nicotiana linearis	Nicotianoideae	SAm
Nicotiana longiflora	Nicotianoideae	SAm
Nicotiana maritima	Nicotianoideae	OZ
Nicotiana megalosiphon	Nicotianoideae	OZ
Nicotiana miersii	Nicotianoideae	SAm
Nicotiana nesophila	Nicotianoideae	NAm
Nicotiana noctiflora	Nicotianoideae	SAm
Nicotiana nudicaulis	Nicotianoideae	NAm
Nicotiana obtusifolia	Nicotianoideae	NAm
Nicotiana occidentalis	Nicotianoideae	OZ
Nicotiana otophora	Nicotianoideae	SAm
Nicotiana paniculata	Nicotianoideae	SAm
Nicotiana pauciflora	Nicotianoideae	SAm
Nicotiana petunioides	Nicotianoideae	SAm
Nicotiana plumbaginifolia	Nicotianoideae	NAm&SAm&CAm
Nicotiana quadrivalvis	Nicotianoideae	NAm
Nicotiana raimondii	Nicotianoideae	SAm
Nicotiana repanda	Nicotianoideae	NAm&CAm&Car
Nicotiana rosulata	Nicotianoideae	OZ
Nicotiana rotundifolia	Nicotianoideae	OZ
Nicotiana simulans	Nicotianoideae	OZ
Nicotiana solanifolia	Nicotianoideae	SAm
Nicotiana spegazzinii	Nicotianoideae	SAm
Nicotiana stocktonii	Nicotianoideae	NAm
Nicotiana suaveolens	Nicotianoideae	OZ
Nicotiana sylvestris	Nicotianoideae	SAm
Nicotiana thyrsiflora	Nicotianoideae	SAm
Nicotiana tomentosa	Nicotianoideae	SAm
Nicotiana tomentosiformis	Nicotianoideae	SAm
Nicotiana umbratica	Nicotianoideae	OZ
Nicotiana undulata	Nicotianoideae	SAm
Nicotiana velutina	Nicotianoideae	OZ
Nicotiana wigandioides	Nicotianoideae	SAm
Nierembergia andina	Petunieae	SAm
Nierembergia angustifolia	Petunieae	SAm
Nierembergia aristata	Petunieae	SAm
Nierembergia boliviana	Petunieae	SAm
Nierembergia browallioides	Petunieae	SAm
Nierembergia calycina	Petunieae	SAm
Nierembergia ericoides	Petunieae	SAm
Nierembergia graveolens	Petunieae	SAm

Nierembergia hatschbachii	Petunieae	SAm
Nierembergia hippomanica	Petunieae	SAm
Nierembergia linariifolia	Petunieae	SAm
Nierembergia micrantha	Petunieae	SAm
Nierembergia pinifolia	Petunieae	SAm
Nierembergia pulchella	Petunieae	SAm
Nierembergia repens	Petunieae	SAm
Nierembergia rigida	Petunieae	SAm
Nierembergia rivularis	Petunieae	SAm
Nierembergia scoparia	Petunieae	SAm
Nierembergia spathulata	Petunieae	SAm
Nierembergia tucumanensis	Petunieae	SAm
Nierembergia veitchii	Petunieae	SAm
Nolana acuminata	Atropina	SAm
Nolana adansonii	Atropina	SAm
Nolana albescens	Atropina	SAm
Nolana aplocaryoides	Atropina	SAm
Nolana arequipensis	Atropina	SAm
Nolana aticoana	Atropina	SAm
Nolana baccata	Atropina	SAm
Nolana balSAmiflua	Atropina	SAm
Nolana carnosa	Atropina	SAm
Nolana cerrateana	Atropina	SAm
Nolana chancoana	Atropina	SAm
Nolana chapiensis	Atropina	SAm
Nolana clivicola	Atropina	SAm
Nolana coelestis	Atropina	SAm
Nolana confinis	Atropina	SAm
Nolana coronata	Atropina	SAm
Nolana crassulifolia	Atropina	SAm
Nolana diffusa	Atropina	SAm
Nolana divaricata	Atropina	SAm
Nolana elegans	Atropina	SAm
Nolana filifolia	Atropina	SAm
Nolana flaccida	Atropina	SAm
Nolana galapagensis	Atropina	SAm
Nolana gayana	Atropina	SAm
Nolana humifusa	Atropina	SAm
Nolana incana	Atropina	SAm
Nolana inflata	Atropina	SAm
Nolana intonsa	Atropina	SAm
Nolana johnstonii	Atropina	SAm
Nolana laxa	Atropina	SAm

Nolana leptophylla	Atropina	SAm
Nolana lezamae	Atropina	SAm
Nolana linearifolia	Atropina	SAm
Nolana lycioides	Atropina	SAm
Nolana mollis	Atropina	SAm
Nolana onoana	Atropina	SAm
Nolana pallida	Atropina	SAm
Nolana paradoxa	Atropina	SAm
Nolana parviflora	Atropina	SAm
Nolana peruviana	Atropina	SAm
Nolana pilosa	Atropina	SAm
Nolana plicata	Atropina	SAm
Nolana pterocarpa	Atropina	SAm
Nolana ramosissima	Atropina	SAm
Nolana rostrata	Atropina	SAm
Nolana rupicola	Atropina	SAm
Nolana salsoloides	Atropina	SAm
Nolana scaposa	Atropina	SAm
Nolana sedifolia	Atropina	SAm
Nolana sessiliflora	Atropina	SAm
Nolana spathulata	Atropina	SAm
Nolana sphaerophylla	Atropina	SAm
Nolana stenophylla	Atropina	SAm
Nolana tarapacana	Atropina	SAm
Nolana thinophila	Atropina	SAm
Nolana tocopillensis	Atropina	SAm
Nolana tomentella	Atropina	SAm
Nolana urubambae	Atropina	SAm
Nolana villosa	Atropina	SAm
Nolana volcanica	Atropina	SAm
Nolana weissiana	Atropina	SAm
Nolana werdermannii	Atropina	SAm
Nolana willeana	Atropina	SAm
Nothocestrum latifolium	Physaleae	OZ
Nothocestrum longifolium	Physaleae	OZ
Oryctes nevadensis	Physaleae	NAm
Pantacantha ameghinoi	Benthamielleae	SAm
Petunia altiplana	Petunieae	SAm
Petunia axillaris	Petunieae	SAm
Petunia bonjardinensis	Petunieae	SAm
Petunia exserta	Petunieae	SAm
Petunia integrifolia	Petunieae	SAm
Petunia littoralis	Petunieae	SAm

Petunia mantiqueirensis	Petunieae	SAm
Petunia reitzii	Petunieae	SAm
Petunia saxicola	Petunieae	SAm
Petunia scheideana	Petunieae	SAm
Petunia secreta	Petunieae	SAm
Physalis acutifolia	Physaleae	NAm
Physalis alkekengi	Physaleae	EU
Physalis angulata	Physaleae	NAm&SAm&CAm&Car
Physalis angustifolia	Physaleae	NAm
Physalis angustiphysa	Physaleae	NAm&CAm
Physalis arborescens	Physaleae	NAm
Physalis arenicola	Physaleae	NAm
Physalis campanulata	Physaleae	NAm
Physalis carpenteri	Physaleae	NAm
Physalis caudella	Physaleae	NAm
Physalis cinerascens	Physaleae	NAm
Physalis cordata	Physaleae	NAm&CAm&Car
Physalis coztomatl	Physaleae	NAm
Physalis crassifolia	Physaleae	NAm
Physalis glutinosa	Physaleae	NAm
Physalis greenmanii	Physaleae	NAm
Physalis hederifolia	Physaleae	NAm
Physalis heterophylla	Physaleae	NAm
Physalis ignota	Physaleae	CAm&Car
Physalis lagascae	Physaleae	NAm&SAm&CAm&Car
Physalis lanceolata	Physaleae	NAm
Physalis lassa	Physaleae	NAm&CAm
Physalis longifolia	Physaleae	NAm
Physalis melanocystis	Physaleae	NAm&CAm
Physalis microcarpa	Physaleae	NAm&CAm&Car
Physalis microphysa	Physaleae	NAm
Physalis minima	Physaleae	AF&EU
Physalis minimaculata	Physaleae	NAm
Physalis mollis	Physaleae	NAm
Physalis nicandroides	Physaleae	NAm&CAm
Physalis patula	Physaleae	NAm
Physalis peruviana	Physaleae	SAm
Physalis philadelphica	Physaleae	NAm
Physalis pruinosa	Physaleae	NAm&SAm&CAm
Physalis pubescens	Physaleae	NAm&SAm&CAm
Physalis pumila	Physaleae	NAm
Physalis sordida	Physaleae	NAm
Physalis virginiana	Physaleae	NAm

Physalis viscosa	Physaleae	NAm&SAm
Physalis walteri	Physaleae	NAm
Physochlaina infundibularis	Atropina	EU
Physochlaina orientalis	Atropina	EU
Physochlaina physaloides	Atropina	EU
Physochlaina praealta	Atropina	EU
Plowmania nyctaginoides	Petunieae	CAm
Protoschwenkia mandonii	Cestroideae	SAm
Przewalskia tangutica	Atropina	EU
Quincula lobata	Physaleae	NAm
Reyesia sp	Reyesia	SAm
Salpichroa origanifolia	Salpichroina	SAm
Salpiglossis sinuata	Cestroideae	SAm
Saracha punctata	Physaleae	SAm
Saracha quitensis	Physaleae	SAm
Schizanthus alpestris	Schizanthus	SAm
Schizanthus candidus	Schizanthus	SAm
Schizanthus grahamii	Schizanthus	SAm
Schizanthus hookeri	Schizanthus	SAm
Schizanthus integrifolius	Schizanthus	SAm
Schizanthus lacteus	Schizanthus	SAm
Schizanthus laetus	Schizanthus	SAm
Schizanthus litoralis	Schizanthus	SAm
Schizanthus parvulus	Schizanthus	SAm
Schizanthus pinnatus	Schizanthus	SAm
Schizanthus porrigens	Schizanthus	SAm
Schizanthus tricolor	Schizanthus	SAm
Schultesianthus leucanthus	Juanulloeae	CAm&SAm
Schultesianthus megalandrus	Juanulloeae	SAm
Schwenckia glabrata	Schwenckieae	SAm
Schwenckia lateriflora	Schwenckieae	SAm&CAm
Sclerophylax adnatifolia	Atropina	SAm
Sclerophylax gilliesii	Atropina	SAm
Sclerophylax sp	Atropina	SAm
Sclerophylax spinescens	Atropina	SAm
Scopolia carniolica	Atropina	EU
Scopolia japonica	Atropina	EU
Scopolia lutescens	Atropina	EU
Scopolia parviflora	Atropina	EU
Sessea corymbiflora	Cestroideae	SAm
Sessea stipulata	Cestroideae	SAm
Sessea vestita	Cestroideae	SAm
Solandra brachycalyx	Juanulloeae	CAm

Solandra grandiflora	Juanulloeae	CAm&Car
Solanum absconditum	Solaneae	SAm
Solanum abutiloides	Solaneae	SAm
Solanum acanthodapis	Solaneae	OZ
Solanum acaule	Solaneae	SAm
Solanum accrescens	Solaneae	CAm&SAm
Solanum acerifolium	Solaneae	NAm&SAm&CAm
Solanum achacachense	Solaneae	SAm
Solanum acroscopicum	Solaneae	SAm
Solanum aculeastrum	Solaneae	AF
Solanum aculeatissimum	Solaneae	SAm
Solanum acutilobum	Solaneae	SAm
Solanum volubile	Solaneae	NAm&SAm&CAm&Car
Solanum adscendens	Solaneae	SAm
Solanum aethiopicum	Solaneae	AF
Solanum agrarium	Solaneae	SAm&Car
Solanum agrimonifolium	Solaneae	NAm&CAm
Solanum alandiae	Solaneae	SAm
Solanum albicans	Solaneae	SAm
Solanum albidum	Solaneae	SAm
Solanum aligerum	Solaneae	NAm&SAm&CAm
Solanum allophyllum	Solaneae	SAm&CAm
Solanum amblymerum	Solaneae	OZ
Solanum americanum	Solaneae	NAm&Car&SAm&CAm
Solanum amygdalifolium	Solaneae	SAm
Solanum anceps	Solaneae	SAm
Solanum andreanum	Solaneae	SAm
Solanum anguivi	Solaneae	AF
Solanum angustialatum	Solaneae	SAm
Solanum angustifolium	Solaneae	NAm
Solanum annuum	Solaneae	SAm
Solanum aphyodendron	Solaneae	SAm&CAm&NAm
Solanum appendiculatum	Solaneae	NAm&CAm
Solanum arachnidanthum	Solaneae	SAm
Solanum arboreum	Solaneae	SAm&CAm
Solanum argentinum	Solaneae	SAm
Solanum argopetalum	Solaneae	OZ
Solanum arnezii	Solaneae	SAm
Solanum arundo	Solaneae	AF
Solanum asperolanatum	Solaneae	SAm
Solanum asperum	Solaneae	SAm&CAm
Solanum asterophorum	Solaneae	SAm
Solanum asteropilodes	Solaneae	SAm

Solanum asymmetriphyllum	Solaneae	OZ
Solanum atropurpureum	Solaneae	SAm
Solanum aturense	Solaneae	SAm
Solanum aviculare	Solaneae	OZ
Solanum avilesii	Solaneae	SAm
Solanum bahamense	Solaneae	NAm&Car
Solanum batoides	Solaneae	AF
Solanum beaugleholei	Solaneae	OZ
Solanum berthaultii	Solaneae	SAm
Solanum betaceum	Solaneae	SAm
Solanum bicorne	Solaneae	NAm
Solanum bolivianum	Solaneae	SAm
Solanum bonariense	Solaneae	SAm
Solanum brevicaule	Solaneae	SAm
Solanum brevifolium	Solaneae	SAm
Solanum brownii	Solaneae	OZ
Solanum buddleifolium	Solaneae	SAm
Solanum bulbocastanum	Solaneae	NAm
Solanum bumeliifolium	Solaneae	AF
Solanum cacosmum	Solaneae	SAm
Solanum caesium	Solaneae	SAm
Solanum cajanumense	Solaneae	SAm
Solanum calileguae	Solaneae	SAm
Solanum CAmpanulatum	Solaneae	OZ
Solanum CAmpylacanthum	Solaneae	AF
Solanum candidum	Solaneae	SAm&CAm
Solanum candolleanum	Solaneae	SAm
Solanum capense	Solaneae	AF
Solanum capsiciforme	Solaneae	OZ
Solanum capsicoides	Solaneae	SAm
Solanum cardiophyllum	Solaneae	NAm
Solanum carduiforme	Solaneae	OZ
Solanum caricifolium	Solaneae	SAm
Solanum caripense	Solaneae	SAm&CAm
Solanum carolinense	Solaneae	NAm
Solanum cataphractum	Solaneae	OZ
Solanum centrale	Solaneae	OZ
Solanum cerasiferum	Solaneae	AF
Solanum chacoense	Solaneae	SAm
Solanum chamaepolybotryon	Solaneae	SAm
Solanum cheesmaniae	Solaneae	SAm
Solanum chenopodinum	Solaneae	OZ
Solanum chenopodium	Solaneae	OZ

Solanum chilense	Solaneae	SAm
Solanum chippendalei	Solaneae	OZ
Solanum chmielewskii	Solaneae	SAm
Solanum chomatophilum	Solaneae	SAm
Solanum chrysotrichum	Solaneae	NAm&CAm&SAm
Solanum cinereum	Solaneae	OZ
Solanum stipuloideum	Solaneae	SAm
Solanum circinatum	Solaneae	SAm&CAm
Solanum citrullifolium	Solaneae	NAm
Solanum clandestinum	Solaneae	SAm
Solanum clarkiae	Solaneae	OZ
Solanum clarum	Solaneae	NAm&CAm
Solanum cleistogamum	Solaneae	OZ
Solanum coactiliferum	Solaneae	OZ
Solanum colombianum	Solaneae	SAm
Solanum comarapanum	Solaneae	SAm
Solanum comptum	Solaneae	SAm
Solanum conditum	Solaneae	SAm
Solanum confusum	Solaneae	SAm
Solanum conicum	Solaneae	SAm
Solanum cookii	Solaneae	OZ
Solanum cordovense	Solaneae	NAm&CAm&SAm
Solanum coriaceum	Solaneae	SAm
Solanum corifolium	Solaneae	OZ
Solanum crinitipes	Solaneae	SAm
Solanum crinitum	Solaneae	SAm
Solanum crispum	Solaneae	SAm
Solanum crotonoides	Solaneae	Car
Solanum insanum	Solaneae	EU
Solanum cunninghamii	Solaneae	OZ
Solanum curvicuspe	Solaneae	OZ
Solanum cyaneopurpureum	Solaneae	AF
Solanum cylindricum	Solaneae	SAm
Solanum dasyphyllum	Solaneae	AF
Solanum davisense	Solaneae	NAm
Solanum decompositiflorum	Solaneae	SAm
Solanum delitescens	Solaneae	SAm
Solanum demissum	Solaneae	NAm&CAm
Solanum densevestitum	Solaneae	OZ
Solanum dianthophorum	Solaneae	OZ
Solanum dimorphispinum	Solaneae	OZ
Solanum dioicum	Solaneae	OZ
Solanum diphyllum	Solaneae	NAm&CAm
Solanum diploconos	Solaneae	SAm
Solanum discolor	Solaneae	OZ
Solanum dissectum	Solaneae	OZ
Solanum ditrichum	Solaneae	OZ
Solanum diversiflorum	Solaneae	OZ
Solanum doddsii	Solaneae	SAm
Solanum donianum	Solaneae	NAm&CAm&Car
Solanum ensifolium	Solaneae	Car
Solanum dulCAmara	Solaneae	EU&AF
Solanum echinatum	Solaneae	OZ
Solanum ehrenbergii	Solaneae	NAm
Solanum elachophyllum	Solaneae	OZ
Solanum elaeagnifolium	Solaneae	NAm&SAm
Solanum ellipticum	Solaneae	OZ
Solanum enantiophyllanthum	Solaneae	SAm
Solanum endopogon	Solaneae	SAm
Solanum esuriale	Solaneae	OZ
Solanum etuberosum	Solaneae	SAm
Solanum evolvulifolium	Solaneae	SAm&CAm
Solanum exiguum	Solaneae	SAm
Solanum fallax	Solaneae	SAm
Solanum felinum	Solaneae	SAm
Solanum ferocissimum	Solaneae	OZ
Solanum fiebrigii	Solaneae	SAm
Solanum fraxinifolium	Solaneae	SAm&CAm
Solanum fructotecto	Solaneae	NAm
Solanum furfuraceum	Solaneae	OZ
Solanum fusiforme	Solaneae	SAm
Solanum gabrielae	Solaneae	OZ
Solanum galapagense	Solaneae	SAm
Solanum gardneri	Solaneae	SAm
Solanum giganteum	Solaneae	AF&EU
Solanum glabratum	Solaneae	AF&EU
Solanum glaucophyllum	Solaneae	SAm
Solanum glutinosum	Solaneae	SAm
Solanum goetzei	Solaneae	AF
Solanum grayi	Solaneae	NAm
Solanum guerreroense	Solaneae	NAm
Solanum guineense	Solaneae	AF
Solanum gympiense	Solaneae	OZ
Solanum habrochaites	Solaneae	SAm
Solanum hapalum	Solaneae	OZ
Solanum hasslerianum	Solaneae	SAm

Solanum havanense	Solaneae	Car
Solanum hayesii	Solaneae	SAm&CAm
Solanum heinianum	Solaneae	AF
Solanum herculeum	Solaneae	EU&AF
Solanum heterodoxum	Solaneae	NAm
Solanum heteropodium	Solaneae	OZ
Solanum hexandrum	Solaneae	SAm
Solanum hibernum	Solaneae	SAm
Solanum hieronymi	Solaneae	SAm
Solanum hindsianum	Solaneae	NAm
Solanum hirtum	Solaneae	SAm&CAm
Solanum hjertingii	Solaneae	NAm
Solanum hoehnei	Solaneae	SAm
Solanum hoplopetalum	Solaneae	OZ
Solanum horridum	Solaneae	OZ
Solanum hougasii	Solaneae	NAm
Solanum humile	Solaneae	AF
Solanum hyporhodium	Solaneae	SAm
Solanum hystrix	Solaneae	OZ
Solanum immite	Solaneae	SAm
Solanum inaequilaterum	Solaneae	OZ
Solanum inCAmayoense	Solaneae	SAm
Solanum incanum	Solaneae	AF&EU
Solanum incarceratum	Solaneae	SAm
Solanum incompletum	Solaneae	OZ
Solanum incurvum	Solaneae	SAm
Solanum inelegans	Solaneae	SAm
Solanum infundibuliforme	Solaneae	SAm
Solanum innoxium	Solaneae	OZ
Solanum iopetalum	Solaneae	NAm
Solanum jabrense	Solaneae	SAm
Solanum jamaicense	Solaneae	NAm&Car&SAm&CAm
Solanum jamesii	Solaneae	NAm
Solanum johnsonianum	Solaneae	OZ
Solanum johnstonii	Solaneae	NAm
Solanum jucundum	Solaneae	OZ
Solanum juglandifolium	Solaneae	SAm
Solanum juvenale	Solaneae	SAm
Solanum kurtzianum	Solaneae	SAm
Solanum tettense	Solaneae	AF
Solanum laciniatum	Solaneae	OZ
Solanum lamprocarpum	Solaneae	AF
Solanum lanceifolium	Solaneae	NAm&SAm&CAm&Car

Solanum lanceolatum	Solaneae	NAm&CAm
Solanum lasiocarpum	Solaneae	EU
Solanum lasiophyllum	Solaneae	OZ
Solanum latens	Solaneae	OZ
Solanum latiflorum	Solaneae	SAm
Solanum laxissimum	Solaneae	SAm
Solanum laxum	Solaneae	SAm
Solanum leopoldense	Solaneae	OZ
Solanum lepidotum	Solaneae	SAm&CAm
Solanum leptophyes	Solaneae	SAm
Solanum lichtensteinii	Solaneae	AF
Solanum lidii	Solaneae	AF
Solanum lignicaule	Solaneae	SAm
Solanum limitare	Solaneae	OZ
Solanum linearifolium	Solaneae	OZ
Solanum linnaeanum	Solaneae	AF
Solanum longiconicum	Solaneae	CAm
Solanum lucani	Solaneae	OZ
Solanum lumholtzianum	Solaneae	NAm
Solanum luteoalbum	Solaneae	SAm
Solanum lycocarpum	Solaneae	SAm
Solanum lycopersicoides	Solaneae	SAm
Solanum lyratum	Solaneae	EU
Solanum lythrocarpum	Solaneae	OZ
Solanum macoorai	Solaneae	OZ
Solanum macrocarpon	Solaneae	AF
Solanum maglia	Solaneae	SAm
Solanum mahoriense	Solaneae	AF
Solanum mapiriense	Solaneae	SAm
Solanum marginatum	Solaneae	AF
Solanum maternum	Solaneae	SAm
Solanum mauritianum	Solaneae	SAm
Solanum megalonyx	Solaneae	SAm
Solanum boliviense	Solaneae	SAm
Solanum melanospermum	Solaneae	OZ
Solanum melissarum	Solaneae	SAm
Solanum microdontum	Solaneae	SAm
Solanum microphyllum	Solaneae	Car
Solanum mitchellianum	Solaneae	OZ
Solanum mite	Solaneae	SAm
Solanum mitlense	Solaneae	NAm
Solanum monachophyllum	Solaneae	SAm
Solanum monarchostemon	Solaneae	SAm

Solanum montanum	Solaneae	SAm
Solanum morelliforme	Solaneae	NAm&CAm&SAm
Solanum mortonii	Solaneae	SAm
Solanum moscopanum	Solaneae	SAm
Solanum moxosense	Solaneae	SAm
Solanum multifidum	Solaneae	SAm
Solanum multiinterruptum	Solaneae	SAm
Solanum multispinum	Solaneae	SAm
Solanum multivenosum	Solaneae	OZ
Solanum muricatum	Solaneae	SAm
Solanum myoxotrichum	Solaneae	AF
Solanum myriacanthum	Solaneae	NAm&CAm
Solanum nemophilum	Solaneae	OZ
Solanum nemorense	Solaneae	SAm
Solanum neoanglicum	Solaneae	OZ
Solanum neorickii	Solaneae	SAm
Solanum nigriviolaceum	Solaneae	AF
Solanum nigrum	Solaneae	EU&AF
Solanum nitidum	Solaneae	SAm
Solanum nobile	Solaneae	OZ
Solanum nummularium	Solaneae	OZ
Solanum obliquum	Solaneae	SAm
Solanum occultum	Solaneae	SAm
Solanum ochranthum	Solaneae	SAm
Solanum ochrophyllum	Solaneae	SAm
Solanum oedipus	Solaneae	OZ
Solanum okadae	Solaneae	SAm
Solanum oldfieldii	Solaneae	OZ
Solanum oligacanthum	Solaneae	OZ
Solanum opacum	Solaneae	OZ
Solanum oplocense	Solaneae	SAm
Solanum orbiculatum	Solaneae	OZ
Solanum oxycarpum	Solaneae	NAm
Solanum oxyphyllum	Solaneae	SAm
Solanum palinacanthum	Solaneae	SAm
Solanum palitans	Solaneae	SAm
Solanum pallidum	Solaneae	SAm
Solanum paludosum	Solaneae	SAm
Solanum palustre	Solaneae	SAm
Solanum pampasense	Solaneae	SAm
Solanum pancheri	Solaneae	OZ
Solanum paniculatum	Solaneae	SAm
Solanum papaverifolium	Solaneae	OZ

Solanum paposanum	Solaneae	SAm
Solanum paraibanum	Solaneae	SAm
Solanum pascoense	Solaneae	SAm
Solanum pectinatum	Solaneae	SAm&CAm
Solanum pedemontanum	Solaneae	SAm
Solanum pendulum	Solaneae	SAm
Solanum pennellii	Solaneae	SAm
Solanum peruvianum	Solaneae	SAm
Solanum petraeum	Solaneae	OZ
Solanum petrophilum	Solaneae	OZ
Solanum phaseoloides	Solaneae	CAm&SAm
Solanum phlomoides	Solaneae	OZ
Solanum physalifolium	Solaneae	SAm
Solanum pimpinellifolium	Solaneae	SAm
Solanum pinetorum	Solaneae	SAm
Solanum pinnatisectum	Solaneae	NAm
Solanum piurae	Solaneae	SAm
Solanum platense	Solaneae	SAm
Solanum pluviale	Solaneae	CAm
Solanum poinsettiifolium	Solaneae	SAm
Solanum polyadenium	Solaneae	NAm
Solanum polytrichum	Solaneae	SAm
Solanum prinophyllum	Solaneae	OZ
Solanum proteanthum	Solaneae	SAm
Solanum pseudolulo	Solaneae	SAm
Solanum ptychanthum	Solaneae	NAm
Solanum pubigerum	Solaneae	NAm&CAm
Solanum pungetium	Solaneae	OZ
Solanum pyracanthos	Solaneae	AF
Solanum africanum	Solaneae	AF
Solanum quadriloculatum	Solaneae	OZ
Solanum quitoense	Solaneae	SAm
Solanum raphanifolium	Solaneae	SAm
Solanum reductum	Solaneae	SAm
Solanum reflexiflorum	Solaneae	SAm
Solanum refractum	Solaneae	NAm
Solanum repandum	Solaneae	OZ
Solanum reptans	Solaneae	SAm
Solanum retroflexum	Solaneae	AF
Solanum rhytidoandrum	Solaneae	SAm
Solanum riojense	Solaneae	SAm
Solanum rixosum	Solaneae	OZ
Solanum robustum	Solaneae	SAm

Solanum roseum	Solaneae	SAm
Solanum rostratum	Solaneae	NAm
Solanum rovirosanum	Solaneae	CAm&NAm
Solanum rudepannum	Solaneae	NAm&CAm
Solanum rugosum	Solaneae	SAm&CAm
Solanum rupincola	Solaneae	SAm
Solanum sandwicense	Solaneae	OZ
Solanum santolallae	Solaneae	SAm
Solanum savanillense	Solaneae	SAm
Solanum scabrifolium	Solaneae	SAm
Solanum scabrum	Solaneae	AF
Solanum schenckii	Solaneae	NAm
Solanum schimperianum	Solaneae	AF
Solanum schlechtendalianum	Solaneae	SAm&CAm
Solanum schomburgkii	Solaneae	SAm
Solanum sciadostylis	Solaneae	SAm
Solanum sejunctum	Solaneae	OZ
Solanum semiarmatum	Solaneae	OZ
Solanum sendtnerianum	Solaneae	SAm
Solanum serpens	Solaneae	OZ
Solanum sessiliflorum	Solaneae	SAm
Solanum shirleyanum	Solaneae	OZ
Solanum sibundoyense	Solaneae	SAm
Solanum simile	Solaneae	OZ
Solanum sisymbriifolium	Solaneae	SAm
Solanum sitiens	Solaneae	SAm
Solanum sparsipilum	Solaneae	SAm
Solanum spegazzinii	Solaneae	SAm
Solanum stagnale	Solaneae	SAm
Solanum stellativelutinum	Solaneae	SAm
Solanum stelligerum	Solaneae	OZ
Solanum stenandrum	Solaneae	SAm
Solanum stenophyllidium	Solaneae	NAm
Solanum stenopterum	Solaneae	OZ
Solanum stoloniferum	Solaneae	NAm
Solanum stramoniifolium	Solaneae	SAm&CAm&Car
Solanum stuckertii	Solaneae	SAm
Solanum stupefactum	Solaneae	OZ
Solanum sturtianum	Solaneae	OZ
Solanum subinerme	Solaneae	SAm
Solanum subpanduratum	Solaneae	SAm
Solanum sucrense	Solaneae	SAm
Solanum supinum	Solaneae	AF

Solanum symonii	Solaneae	OZ
Solanum taeniotrichum	Solaneae	CAm
Solanum talarense	Solaneae	SAm
Solanum tampicense	Solaneae	NAm&CAm&SAm&Car
Solanum tarijense	Solaneae	SAm
Solanum tegore	Solaneae	SAm
Solanum tenuipes	Solaneae	NAm
Solanum tenuisetosum	Solaneae	SAm
Solanum tenuispinum	Solaneae	SAm
Solanum terminale	Solaneae	AF
Solanum ternatum	Solaneae	SAm
Solanum tetramerum	Solaneae	Car
Solanum tetrathecum	Solaneae	OZ
Solanum thelopodium	Solaneae	SAm
Solanum thomasiifolium	Solaneae	SAm
Solanum coagulans	Solaneae	AF
Solanum tobagense	Solaneae	SAm
Solanum toliaraea	Solaneae	AF
Solanum tomentosum	Solaneae	AF
Solanum torvum	Solaneae	SAm&CAm&Car
Solanum furcatum	Solaneae	SAm
Solanum tribulosum	Solaneae	NAm
Solanum houstonii	Solaneae	NAm
Solanum triflorum	Solaneae	NAm&SAm
Solanum tripartitum	Solaneae	SAm
Solanum trisectum	Solaneae	AF
Solanum tudununggae	Solaneae	OZ
Solanum turneroides	Solaneae	SAm
Solanum ugentii	Solaneae	SAm
Solanum uncinellum	Solaneae	SAm
Solanum unilobum	Solaneae	SAm
Solanum ursinum	Solaneae	SAm
Solanum urticans	Solaneae	SAm
Solanum vaccinioides	Solaneae	OZ
Solanum valdiviense	Solaneae	SAm
Solanum vansittartense	Solaneae	OZ
Solanum vernei	Solaneae	SAm
Solanum verrucosum	Solaneae	NAm
Solanum vescum	Solaneae	OZ
Solanum vespertilio	Solaneae	AF
Solanum vestissimum	Solaneae	SAm
Solanum viarum	Solaneae	SAm
Solanum vicinum	Solaneae	OZ

Solanum villosum	Solaneae	AF&EU
Solanum	Solaneae	SAm
Solanum violaceum	Solaneae	EU
Solanum viridifolium	Solaneae	OZ
Solanum wallacei	Solaneae	NAm
Solanum wendlandii	Solaneae	CAm&NAm
Solanum whalenii	Solaneae	SAm
Solanum wrightii	Solaneae	SAm
Solanum yungasense	Solaneae	SAm
Streptosolen jamesonii	Cestroideae	SAm
Symonanthus aromaticus	Nicotianoideae	OZ
Symonanthus bancroftii	Nicotianoideae	OZ
Trianaea sp	Juanulloeae	SAm
Trianaea speciosa	Juanulloeae	SAm
Tsoala tubiflora	Goetzeoideae	AF
Tzeltalia amphitricha	Physaleae	NAm&CAm
Tzeltalia calidaria	Physaleae	CAm
Vassobia breviflora	Physaleae	SAm
Vassobia dichotoma	Physaleae	SAm
Vestia foetida	Cestroideae	SAm
Withania coagulans	Physaleae	EU
Withania somnifera	Physaleae	AF&EU
Witheringia cuneata	Physaleae	CAm
Witheringia macrantha	Physaleae	CAm
Witheringia meiantha	Physaleae	CAm
Witheringia solanacea	Physaleae	CAm&Car&SAm

Table S1.3. Biogeographical models tested in this study, along with estimated parameters, log-likelihoods and AIC values. Models were classified according to the number of free parameters and whether the input dispersal multiplier matrices included time-stratified (TS) probabilities of dispersal between areas. Model suitability was examined using AIC comparisons. Model 16 (in bold italics) is the best model and the estimated parameters under that model were used for the Biogeographical Stochastic Mappings. Default values for j and w when they were not free are 0 and 1, respectively. $j = 0$ means founder-events were not allowed, while $w = 1$ means the dispersal multiplier matrices have an exponent of 1.

#	Models	Dispersal multipliers	Free parameters Number	$d^{(1)}$	$e^{(2)}$	$j^{(3)}$	$w^{(4)}$	Log-Likelihood	AIC	Δ AIC	AIC weights
	Basic Models										
1	DEC_NonTS	Non-TS	2	0.011	0.000	0.000	1.000	-1341.413	2686.826	317.604	0.000
2	DIVALIKE_NonTS	Non-TS	2	0.013	0.000	0.000	1.000	-1401.936	2807.871	438.648	0.000
3	BayAreaLIKE_NonTS	Non-TS	2	0.009	0.049	0.000	1.000	-1528.828	3061.656	692.433	0.000
	Time-Stratified Models										
4	DEC_TS	TS	2	0.025	0.000	0.000	1.000	-1210.832	2425.663	56.441	0.000
5	DIVALIKE_TS	TS	2	0.029	0.000	0.000	1.000	-1252.831	2509.661	140.438	0.000
6	BayAreaLIKE_TS	TS	2	0.023	0.044	0.000	1.000	-1430.614	2865.227	496.004	0.000
	+j Models										
7	DEC_ NonTS _j	Non-TS	3	0.010	0.000	0.003	1.000	-1324.525	2655.050	285.828	0.000
8	DIVALIKE_NonTS_ j	Non-TS	3	0.011	0.000	0.003	1.000	-1387.768	2781.536	412.313	0.000
9	BayAreaLIKE_NonTS_ j	Non-TS	3	0.007	0.004	0.009	1.000	-1335.728	2677.457	308.234	0.000
10	DEC_TS_ j	TS	3	0.022	0.000	0.008	1.000	-1191.907	2389.813	20.590	0.000
11	DIVALIKE_ TS_ j	TS	3	0.025	0.000	0.007	1.000	-1239.123	2484.246	115.024	0.000
12	BayAreaLIKE_ TS_ j	TS	3	0.015	0.001	0.020	1.000	-1213.992	2433.984	64.762	0.000
	+w Models										
13	DEC_TS_w	TS	3	0.026	0.000	0.000	1.114	-1204.980	2415.960	46.738	0.000
14	DIVALIKE_ TS_w	TS	3	0.032	0.000	0.000	1.201	-1250.615	2507.231	138.008	0.000
15	BayAreaLIKE_ TS_w	TS	3	0.026	0.045	0.000	1.307	-1425.518	2857.036	487.813	0.000
	+j +w Models										
16	*DEC_TS_j_w*	*TS*	*4*	*0.029*	*0.000*	*0.009*	*1.887*	*-1180.611*	*2369.223*	*0.000*	*0.999*
17	DIVALIKE_TS_ j_w	TS	4	0.027	0.000	0.007	1.344	-1221.864	2451.729	82.506	0.000
18	BayAreaLIKE_TS_ j_w	TS	4	0.016	0.001	0.021	1.117	-1210.247	2428.494	59.271	0.000

(1) rate of range expansion
(2) rate of range contraction
(3) relative per-event weight of jump dispersal
(4) exponent on manual dispersal multipliers (modifies d and j)

Table S1.4. Species richness, within-area speciation events, and dispersal events estimated for each of the seven delimited areas. The mean numbers of events were calculated from the 100 stochastic maps. Areas are ranked from highest to lowest numbers of species per area in the phylogeny. The number of species within each area in the phylogeny and in the entire family are given for comparison. *The number of species in each area is a rough approximation based on expert opinion, existing floristic treatments, and monographs. The raw species counts underlying this estimate is available from the authors upon request.

Area	Overall number of species per area in the family; proportion of total*	Number of species per area in the phylogeny; proportion of total in the phylogeny	Mean within-area speciation events / Events per species in the phylogeny / Proportion of total within-area events estimated	Mean dispersal events from the area / Events per species in the phylogeny / Proportion of total dispersal events estimated
South America	1624; 63.5%	584; 55.9 %	529.3 / 0.90 / 60.2%	119.7 / 0.20 / 47%
North America	208; 8.1%	186; 17.8 %	98.2 / 0.53 / 11.1%	53.21 / 0.29 /20%
Australia	240; 9.4%	145; 13.9 %	133.1 / 0.92 / 15.1%	2.53 / 0.02 / 1%
Central America	315; 12.3%	126; 12.1 %	17.6 / 0.14 / 2.0%	45.62 / 0.32 / 18%
Africa	143; 5.6%	79; 7.6 %	59.5 / 0.75 / 6.8%	14.31 / 0.18 / 6%
Eurasia	119; 4.7%	56; 5.4 %	33.8 / 0.60 / 3.8%	11.51 / 0.34 / 4%
Caribbean	99; 3.9%	45; 4.3 %	8.8 / 0.20 / 0.9%	8.97 / 0.20 / 4%

Table S1.5. Vicariant events estimated from BSM. In 'BioGeoBEARS', vicariance events involve the split of an ancestral range comprising two or more regions into descendant ranges that are subsets of the ancestral range (Appendix S2). The mean number of each type of event (row in the table) and standard deviation was computed from the 100 stochastic maps.

Ancestral range	Daughter species ranges	Mean number of events (StDev)
South America+North America	South America; North America	10.94 (2.81)
South America+Central America+North America	South America; Central America+North America	4.62 (1.28)
South America+Central America	South America; Central America	4.45(1.04)
South America+Caribbean	South America; Caribbean	2.89 (0.57)
South America+Africa	South America; Africa	2.01(1.32)
South America+Australia	South America; Australia	1.69 (0.46)
Central America+North America	Central America; North America	1.64 (1.02)
Africa+Eurasia	Africa; Eurasia	1.56 (1.44)
North America+Eurasia	North America; Eurasia	1.41 (1.94)
South America+Africa+Australia	South America +Australia; Africa	1.2 (2.88)
South America+Eurasia	South America; Eurasia	1.17 (2.56)
Africa+Australia	Africa; Australia	1 (4.22)

Table S1.6. Transoceanic dispersals in Solanaceae from New World to Old World inferred from BSM. These events happened either within the clade or along its ancestral branch. See Fig. 3 (orange branches and nodes) and Appendix S2 for full ancestral state reconstruction.

Clade	Number of transoceanic dispersals
Anthocercidae	1
Hyoscyameae	1
Lycianthes	1
Lycium	2
Mandragora	1
Physalis	2
Solanum	8
Tsoala	1
Withaninae	1
Others	2
TOTAL	20

Table S1.7. Solanaceae species that presented range expansions, description of the major terrestrial ecoregions of the areas they occupy today, and their fruit type (dry or fleshy according to Knapp, 2002). Ecoregions retrieved from the World Wildlife Foundation database, http://www.worldwildlife.org/. Solanaceae are found in three of the six ecoregions: tropical dry (deserts, shrublands, grasslands), tropical wet, and temperate (including Mediterranean); they are not found in boreal forests, tundra, or mangroves. The species listed below represent 5% (14 of 263) of the total of species with dry fruits in the tree and 14% (109 of 803) of the species with fleshy fruits (i.e., berries, drupes, or pyrenes) in the tree.

Species	Distribution	Ecoregion	Fruit type
Acnistus arborescens	SAm&CAm&Car	Tropical Dry	Fleshy
Bouchetia erecta	NAm&CAm	Tropical Dry	Dry
Brachistus stramoniifolius	NAm&CAm	Tropical Wet	Fleshy
Browallia eludens	NAm&CAm	Tropical Dry	Dry
Browallia speciosa	SAm&CAm	Tropical Wet	Dry
Calibrachoa parviflora	SAm&NAm	Tropical Dry	Dry
Capsicum chinense	SAm&CAm	Tropical Wet	Fleshy
Capsicum ciliatum	NAm&SAm&CAm	Tropical Wet	Fleshy
Capsicum frutescens	NAm&SAm&CAm	Tropical Wet	Fleshy
Capsicum lanceolatum	NAm&CAm	Tropical Wet	Fleshy
Cestrum aurantiacum	NAm&CAm	Tropical Wet	Fleshy
Cestrum diurnum	NAm&CAm&Car	Tropical Wet	Fleshy
Cestrum glanduliferum	NAm&CAm	Tropical Wet	Fleshy
Cestrum guatemalense	NAm&CAm	Tropical Wet	Fleshy
Cestrum luteovirescens	NAm&CAm	Tropical Wet	Fleshy
Cestrum macrophyllum	SAm&CAm&Car	Tropical Wet	Fleshy
Cestrum nocturnum	NAm&SAm&CAm&Car	Tropical Wet	Fleshy
Cestrum regelii	NAm&CAm	Tropical Wet	Fleshy
Cestrum schlechtendalii	NAm&SAm&CAm&Car	Tropical Wet	Fleshy
Cestrum strigilatum	CAm&SAm	Tropical Wet	Fleshy
Cestrum tomentosum	SAm&CAm	Tropical Wet	Fleshy
Cuatresia exiguiflora	SAm&CAm	Tropical Wet	Fleshy
Cuatresia riparia	SAm&CAm	Tropical Wet	Fleshy
Datura inoxia	NAm&CAm	Tropical Dry	Dry
Datura metel	NAm&CAm	Tropical Dry	Dry
Datura stramonium	NAm&CAm	Tropical Dry	Dry
Deprea orinocensis	SAm&CAm	Tropical Wet	Fleshy
Deprea sylvaticum	SAm&CAm	Tropical Wet	Fleshy
Hyoscyamus albus	EU&AF	Tropical Dry	Dry
Hyoscyamus aureus	EU&AF	Tropical Dry	Dry
Hyoscyamus muticus	EU&AF	Tropical Dry	Dry
Jaltomata procumbens	NAm&SAm&CAm	Tropical Wet	Fleshy
Jaltomata repandidentata	NAm&SAm&CAm	Tropical Wet	Fleshy
Juanulloa mexicana	NAm&SAm&CAm	Tropical Wet	Fleshy
Larnax sylvarum	SAm&CAm	Tropical Wet	Fleshy
Lycianthes amatitlanensis	NAm&SAm&CAm	Tropical Wet	Fleshy
Lycianthes ciliolata	NAm&CAm	Tropical Wet	Fleshy
Lycianthes geminiflora	NAm&CAm	Tropical Wet	Fleshy

Lycianthes heteroclita	NAm&CAm	Tropical Wet	Fleshy
Lycianthes lenta	NAm&CAm&Car	Tropical Wet	Fleshy
Lycianthes multiflora	CAm&NAm	Tropical Wet	Fleshy
Lycianthes nitida	NAm&SAm&CAm	Tropical Wet	Fleshy
Lycianthes stephanocalyx	NAm&CAm	Tropical Wet	Fleshy
Lycianthes synanthera	NAm&SAm&CAm	Tropical Wet	Fleshy
Lycianthes tricolor	NAm&CAm	Tropical Wet	Fleshy
Lycium americanum	SAm&Car	Tropical Wet	Fleshy
Lycium boerhaviifolium	NAm&SAm	Tropical Dry	Fleshy
Mandragora officinalis	EU&AF	Tropical Dry	Fleshy
Mandragora officinarum	EU&AF	Tropical Dry	Fleshy
Melananthus guatemalensis	SAm&CAm	Tropical Wet	Dry
Nicotiana plumbaginifolia	NAm&SAm&CAm	Tropical Wet	Dry
Nicotiana repanda	NAm&CAm&Car	Tropical Dry	Dry
Physalis angulata	NAm&SAm&CAm&Car	Tropical Wet	Fleshy
Physalis angustiphysa	NAm&CAm	Tropical Wet	Fleshy
Physalis cordata	NAm&CAm&Car	Tropical Wet	Fleshy
Physalis ignota	CAm&Car	Tropical Wet	Fleshy
Physalis lagascae	NAm&SAm&CAm&Car	Tropical Wet	Fleshy
Physalis lassa	NAm&CAm	Tropical Wet	Fleshy
Physalis melanocystis	NAm&CAm	Tropical Wet	Fleshy
Physalis microcarpa	NAm&CAm&Car	Tropical Wet	Fleshy
Physalis minima	AF&EU	Tropical Dry	Fleshy
Physalis nicandroides	NAm&CAm	Tropical Wet	Fleshy
Physalis pruinosa	NAm&SAm&CAm	Tropical Wet	Fleshy
Physalis pubescens	NAm&SAm&CAm	Tropical Wet	Fleshy
Physalis viscosa	NAm&SAm	Tropical Wet	Fleshy
Schultesianthus leucanthus	CAm&SAm	Tropical Wet	Fleshy
Schwenckia lateriflora	SAm&CAm	Tropical Wet	Dry
Solandra grandiflora	CAm&Car	Tropical Wet	Fleshy
Solanum accrescens	CAm&SAm	Tropical Wet	Fleshy
Solanum acerifolium	NAm&SAm&CAm	Tropical Wet	Fleshy
Solanum agrarium	SAm&Car	Tropical Wet	Fleshy
Solanum agrimonifolium	NAm&CAm	Tropical Wet	Fleshy
Solanum aligerum	NAm&SAm&CAm	Tropical Wet	Fleshy
Solanum allophyllum	SAm&CAm	Tropical Wet	Fleshy
Solanum americanum	NAm&Car&SAm&CAm	Tropical Wet	Fleshy
Solanum aphyodendron	SAm&CAm&NAm	Tropical Wet	Fleshy
Solanum appendiculatum	NAm&CAm	Tropical Wet	Fleshy
Solanum arboreum	SAm&CAm	Tropical Wet	Fleshy
Solanum asperum	SAm&CAm	Tropical Wet	Fleshy
Solanum bahamense	NAm&Car	Tropical Wet	Fleshy
Solanum candidum	SAm&CAm	Tropical Wet	Fleshy
Solanum caripense	SAm&CAm	Tropical Wet	Fleshy
Solanum chrysotrichum	NAm&CAm&SAm	Tropical Wet	Fleshy
Solanum circinatum	SAm&CAm	Tropical Wet	Fleshy
Solanum clarum	NAm&CAm	Tropical Wet	Fleshy

Solanum cordovense	NAm&CAm&SAm	Tropical Wet	Fleshy
Solanum demissum	NAm&CAm	Tropical Dry	Fleshy
Solanum diphyllum	NAm&CAm	Tropical Wet	Fleshy
Solanum donianum	NAm&CAm&Car	Tropical Wet	Fleshy
Solanum dulcamara	EU&AF	Temperate	Fleshy
Solanum elaeagnifolium	NAm&SAm	Tropical Dry	Fleshy
Solanum evolvulifolium	SAm&CAm	Tropical Wet	Fleshy
Solanum fraxinifolium	SAm&CAm	Tropical Wet	Fleshy
Solanum giganteum	AF&EU	Temperate	Fleshy
Solanum glabratum	AF&EU	Tropical Dry	Fleshy
Solanum hayesii	SAm&CAm	Tropical Wet	Fleshy
Solanum herculeum	EU&AF	Tropical Dry	Fleshy
Solanum hirtum	SAm&CAm	Tropical Wet	Fleshy
Solanum incanum	AF&EU	Tropical Wet	Fleshy
Solanum jamaicense	NAm&Car&SAm&CAm	Tropical Wet	Fleshy
Solanum lanceifolium	NAm&SAm&CAm&Car	Tropical Wet	Fleshy
Solanum lanceolatum	NAm&CAm	Tropical Wet	Fleshy
Solanum lepidotum	SAm&CAm	Tropical Wet	Fleshy
Solanum morelliforme	NAm&CAm&SAm	Tropical Wet	Fleshy
Solanum myriacanthum	NAm&CAm	Tropical Wet	Fleshy
Solanum nigrum	EU&AF	Temperate	Fleshy
Solanum pectinatum	SAm&CAm	Tropical Wet	Fleshy
Solanum phaseoloides	CAm&SAm	Tropical Wet	Fleshy
Solanum pubigerum	NAm&CAm	Tropical Wet	Fleshy
Solanum rovirosanum	CAm&NAm	Tropical Wet	Fleshy
Solanum rudepannum	NAm&CAm	Tropical Wet	Fleshy
Solanum rugosum	SAm&CAm	Tropical Wet	Fleshy
Solanum schlechtendalianum	SAm&CAm	Tropical Wet	Fleshy
Solanum stramoniifolium	SAm&CAm&Car	Tropical Wet	Fleshy
Solanum tampicense	NAm&CAm&SAm&Car	Tropical Wet	Fleshy
Solanum torvum	SAm&CAm&Car	Tropical Wet	Fleshy
Solanum triflorum	NAm&SAm	Temperate	Fleshy
Solanum villosum	AF&EU	Tropical Dry	Fleshy
Solanum volubile	NAm&SAm&CAm&Car	Tropical Wet	Fleshy
Solanum wendlandii	CAm&NAm	Tropical Wet	Fleshy
Tzeltalia amphitricha	NAm&CAm	Tropical Wet	Fleshy
Withania somnifera	AF&EU	Temperate	Fleshy
Witheringia solanacea	CAm&Car&SAm	Tropical Wet	Fleshy

Dispersal Multiplier Matrices

Dispersal probability multiplier matrices were first introduced in the program Lagrange (Ree & Smith, 2008), and they are commonly used as a way to represent relative connectivity between regions in particular time periods. Despite their popularity, one criticism is that dispersal probability multipliers are typically determined subjectively. If it is certain that dispersal was either possible or impossible, the multipliers are clear (1 or 0), but usually there is some nonzero probability of long-distance dispersal between disconnected regions. One might therefore put a dispersal multiplier of 0.1 between regions that are disconnected but nearby (for example, North America and Asia), and a dispersal multiplier of 0.01 between regions that are very far apart (North America and Australia). However, the actual values of the multipliers are subjective and somewhat arbitrary, such that multipliers of 0.5 and 0.001, for instance, might be equally plausible. Thus, we can include, in our model fitting, parameters that modify the values of the matrix, e.g., multiplying or dividing all of the dispersal probabilities or raising them to a power. Here we introduce "w" parameter, which is incorporated into 'BioGeoBEARS'. In $+ w$ models, each dispersal probability multiplier is raised to the power w. The parameter w can be fixed to its default, 1, which replicates the traditional Lagrange approach, keeping the dispersal probability multipliers unchanged. If w is 0, all dispersal probability multipliers are converted to 1, and thus the model converts to a "unconstrained" model with equal rates of dispersal between regions. Alternatively, w can be made a free parameter and estimated via ML, along with all other free parameters (Matzke, 2014). Estimates of $w < 1$ indicate that a better fit to the data is obtained if the differences between user-specified dispersal probability multipliers are reduced; estimates of $w > 1$ indicate that the differences between multipliers should be increased. While there is still subjectivity in determining the base dispersal probability multiplier matrix, its influence on results is much reduced in $+w$ models, and all of the standard tools of statistical model choice (e.g., Likelihood Ratio Test, Akaike Information Criterion (AIC); Burnham & Anderson, 2002) may be applied.

Among our set of 18 biogeographical models for Solanaceae, we tested those with and without dispersal multiplier matrices ("_TS" in Table S1.3). For those models with dispersal multiplier matrices, we then estimated models with and without w. The base dispersal multiplier matrices used in this study (shown below) represent three time strata: 50 to 24 Ma, 24 to 10 Ma and 10 Ma to present. Rows represent areas from where the taxon is moving and columns to where they are dispersing. Movements between the Americas, for instance, become more probable towards the present with the formation of the Panama Isthmus. We set the probability of moving between the Old World and New World lower toward the present as the areas become more widely separated over time. The best model included dispersal multiplier matrices with a w of 1.88, suggesting that the best-fit dispersal multipliers between areas are unequal, and the differences are somewhat more extreme than those selected in the base matrices (below).

50 to 24 Ma

	SAm	CAm	Car	NAm	AF	EU	OZ
SAm	1	0.4	0.4	0.2	0.1	0.1	0.1
CAm	0.4	1	0.7	0.4	0.1	0.1	0.1
Car	0.4	0.7	1	0.4	0.1	0.1	0.1
NAm	0.2	0.4	0.4	1	0.7	1	0.3
AF	0.1	0.1	0.1	0.7	1	0.7	0.3
EU	0.1	0.1	0.1	0.8	0.7	1	0.3
OZ	0.1	0.1	0.1	0.3	0.3	0.3	1

24 to 10 Ma

	SAm	CAm	Car	NAm	AF	EU	OZ
SAm	1	0.6	0.5	0.5	0.1	0.2	0.1
CAm	0.6	1	0.7	0.6	0.1	0.1	0.1
Car	0.5	0.7	1	0.5	0.1	0.1	0.1
NAm	0.5	0.6	0.5	1	0.4	0.5	0.1
AF	0.1	0.1	0.1	0.4	1	1	0.3
EU	0.2	0.1	0.1	0.5	1	1	0.5
OZ	0.1	0.1	0.1	0.1	0.3	0.5	1

10 Ma to Present

	SAm	CAm	Car	NAm	AF	EU	OZ
SAm	1	1	0.75	1	0.1	0.2	0.1
CAm	1	1	0.7	1	0.1	0.1	0.1
Car	0.75	0.7	1	0.8	0.1	0.1	0.1
NAm	1	1	0.8	1	0.1	0.2	0.1
AF	0.1	0.1	0.1	0.1	1	1	0.7
EU	0.2	0.1	0.1	0.2	1	1	0.7
OZ	0.1	0.1	0.1	0.1	0.7	0.7	1

Time

Algorithm Validation for Biogeographical Stochastic Mapping in 'BioGeoBEARS'

Biogeographical Stochastic Mapping: Algorithm and Validation

As with traditional stochastic mapping (Nielsen, 2002; Huelsenbeck et al., 2003), biogeographical stochastic mapping (BSM) is a straightforward application of the Markov models used to calculate the likelihood of the data on the tree and the ancestral state probabilities. Here, the term "states" and "geographical ranges" are used interchangeably, because in Lagrange/BioGeoBEARS-type models, every geographical range is a just a state in a very large state space.

The BSM algorithm is as follows:

(1) The conditional probabilities calculated during the downpass likelihood calculation are saved.

(2) The ancestral state at the root is randomly sampled from the ancestral state probabilities.

(3) A cladogenetic range inheritance scenario is sampled conditional on the ancestral state, the downpass likelihoods at the bottom of each branch just after speciation, and the probability of each cladogenesis scenario according to the model parameters; the range inheritance scenario automatically specifies the states just after cladogenesis. This step is the only one that differs from traditional stochastic mapping.

(4) The states at the top of each of the two descendant branches are drawn, conditional on the downpass likelihoods and the probabilities passed up conditional on the states at the bottom of each branch.

(5) With the states now "known" at the bottom and top of each branch (for this particular stochastic mapping realisation), the history of range expansion and contraction events along the branch is simulated, starting from the branch bottom. Simulations that fail to

produce the known state at the top of the branch are discarded. The process is repeated until a

successful simulation occurs.

(6) Steps 2-5 are repeated for each node in the tree, moving from the root up to the

tips.

The result of this procedure is a sample from the Bayesian posterior distribution of

possible histories, conditional on the data, the tree, and the model. It constitutes one of many

possible exact histories. By sampling many BSM realisations (at least 50), and counting the

number of events of each type in each BSM, estimates of the frequency of each event are

easily produced, along with the uncertainty in these estimates. The BSM can be run across a

posterior sample of trees (e.g., from a Bayesian phylogenetic analysis) in order to incorporate

phylogenetic uncertainty. This procedure is thus superior to counts of events produced by

"eyeballing" a plot of ancestral states under the ML model; while the latter procedure will

bear some resemblance to the actual event counts, it will tend to underestimate the actual

number of events, and it tends to ignore the fact that some nodes may have ancestral states

that are highly uncertain.

The 'BioGeoBEARS' BSM procedure was validated in several ways. First, for any

given biogeographical model, averaging many BSMs should reproduce the ancestral state

probabilities calculated analytically under ML, within the stochastic uncertainty determined

by the number of BSMs. As the number of BSMs increases, the ancestral state probabilities

should become increasingly close to the analytic estimates. Second, the same should apply in

time-stratified analyses, which are programmed separately in 'BioGeoBEARS'. Time-

stratified and non-stratified analyses should also produce identical results when "dummy"

dispersal multiplier matrices (all 1s) are used in the time stratification. Third, a special case of

the 'BioGeoBEARS' supermodel, "BAYAREALIKE+a", is identical to traditional

morphological models, and thus can be compared to the ancestral state probabilities and

stochastic maps produced by another R package, phytools (Revell, 2012). For all of these tests, 1:1 correlation plots indicate a successful result. 'BioGeoBEARS' passed all of the above-described tests; the results are available in the online 'BioGeoBEARS' documentation at: http://phylo.wikidot.com/biogeobears-validation. The comparison of ML and BSM state probabilities was also repeated on the ML model for the Solanaceae dataset.

Validation of BSM for DEC+j+w model

Linear regression of the ML ancestral range probabilities with the mean of BSMs for the Solanaceae dataset under the DEC+j+w model (Figure S2.1) gave strong verification that the two are equivalent (slope=1, 95% CI=0.000203; p=0; R^2=0.999).
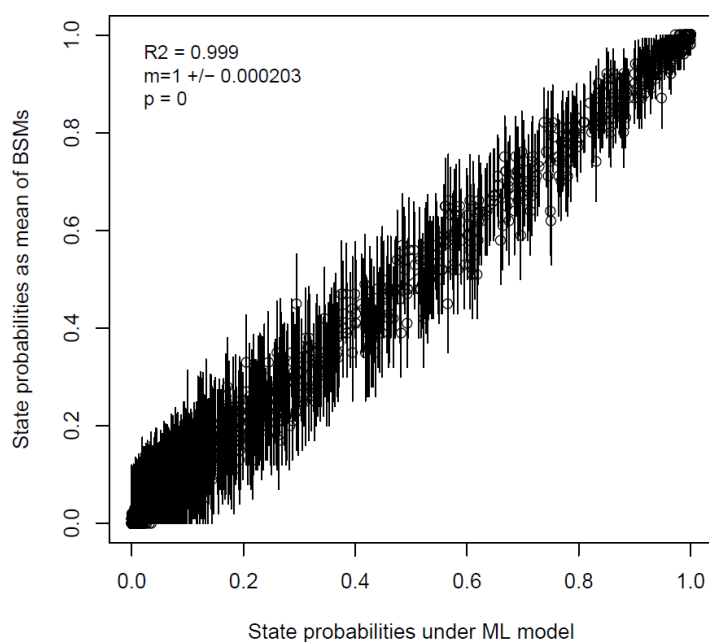
Figure S2.1. Validation of the 'BioGeoBEARS' stochastic mapping algorithm when comparing the estimated state probabilities under ML model versus estimated state probabilities as mean of BSMs. Vertical lines are the 95% confidence intervals on the mean BSM probabilities, as calculated using the R package MultinomialCI.

Revell, L.J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, **3**, 217–223.

A.2 Maximum likelihood ancestral range estimates

This material cannot be displayed in this document, please see files on the online version of the journal paper at `http://onlinelibrary.wiley.com/doi/10.1111/jbi.12898/full`

A.3 Example of a BSM realization

This material cannot be displayed in this document, please see files on the online version of the journal paper at `http://onlinelibrary.wiley.com/doi/10.1111/jbi.12898/full`

Appendix B

Supporting information to Chapter 2

This appendix contains supporting information for Chapter 2

B.1   Voucher information

B.1 Voucher information

genus	species epithet	authority	country	largest political subdivision	collector(s) and collector number	herbarium
Brugmansia	*arborea*	(L.) Lagerh.	-	Cultivated in Botanic Garden Munich, Germany	*2012/2883w7*	(MSB)
Brugmansia	*arborea*	(L.) Lagerh.	Peru	Pasco	*Smith 545*	-
Brugmansia	*aurea*	Lagerh.	Ecuador	Pichincha	*Dupin 42*	(QCA)
Brugmansia	*aurea*	Lagerh.	-	Cultivated in Botanic Garden Munich, Germany	*2012/2880w*	(MSB)
Brugmansia	*sanguinea*	(Ruiz & Pav.) D. Don	Ecuador	Pichincha	*Dupin 43*	(QCA)
Brugmansia	*sanguinea*	(Ruiz & Pav.) D. Don	-	Cultivated in Botanic Garden Munich, Germany	*2012/2888*	(MSB)
Brugmansia	*suaveolens*	(Humb. & Bonpl. ex Willd.) Sweet	Costa Rica	San Jose	*Dupin 2*	(COLO)
Brugmansia	*suaveolens*	(Humb. & Bonpl. ex Willd.) Sweet	-	Cultivated in Botanic Garden Munich, Germany	*2012/2889*	(MSB)

Brugmansia	*versicolor*	Lagerh.	Ecuador	Cultivated in Huntington Botanical Gardens, CA	*43862*	(HNT)
Brugmansia	*versicolor*	Lagerh.	-	Cultivated in Botanic Garden Munich, Germany	*2012/2890*	(MSB)
Datura	*arenicola*	Gentry ex Bye & Luna-Cavazos	Mexico	Baja California Sur	*H.S. Gentry 7881*	(RSA)
Datura	*ceratocaula*	Ortega	Mexico	Jalisco	*Dupin 50*	(COLO)
Datura	*ceratocaula*	Ortega	Mexico	Jalisco	*Dupin 51*	(COLO)
Datura	*ceratocaula*	Ortega	Mexico	Hidalgo	*A. Ventura A. 91*	(WIS)
Datura	*ceratocaula*	Ortega	Mexico	Durango	*Wieder, Bennett, Dunn & Torke 208*	(WIS)
Datura	*discolor*	Bernh.	USA	California	*S.D. White 11262*	(RSA)
Datura	*inoxia*	Mill.	USA	California	*M. DeDecker 2669*	(RSA)
Datura	*inoxia*	Mill.	Mexico	Jalisco	*Dupin 52*	(COLO)
Datura	*kymatocarpa*	A.S. Barclay	Mexico	Michoacan	*J.M. Porter & V.W. Steinmann 14726*	(RSA)
Datura	*kymatocarpa*	A.S. Barclay	Mexico	Guerrero	*J. C. Soto 14914*	(MEXU)

Datura	lanosa	Barclay ex Bye	Mexico	Sonora	A.L. Reina G 96-542	(RSA)
Datura	lanosa	Barclay ex Bye	Mexico	Chihuahua	R. Bye & E. Linares 14252	(MEXU)
Datura	lanosa	Barclay ex Bye	Mexico	Sonora	R. Bye 28391	(MEXU)
Datura	leichhardtii ssp. pruinosa	(Greenm.) A.S. Barclay ex K. Hammer	Mexico	Puebla	J. Dupin 38	(COLO)
Datura	leichhardtii ssp. pruinosa	(Greenm.) A.S. Barclay ex K. Hammer	Mexico	Oaxaca	R. Bye & L. Cervantes	(MEXU)
Datura	leichhardtii ssp. pruinosa	(Greenm.) A.S. Barclay ex K. Hammer	Mexico	Oaxaca	A. Mendoza	(WIS)
Datura	metel	L.	Mexico	Michoacan	J. Soto Nunez, A. R. Soto & F. Soto 7080	(MEXU)
Datura	metel	L.	Mexico	Mexico	R. Bye 26964	(MEXU)
Datura	quercifolia	Kunth	USA	California	A.C. Sanders 5337	(RSA)

Datura	*quercifolia*	Kunth	Mexico	Aguascalientes	*G. Garcia5004*	(MEXU)
Datura	*quercifolia*	Kunth	Mexico	Guanajuato	*E. Martinez 39665*	(MEXU)
Datura	*quercifolia*	Kunth	-	-	*J. Dupin 53*	(COLO)
Datura	*reburra*	A.S. Barclay	Mexico	Sonora	*Gentry, Barclay& Arguelles 19249*	(COLO)
Datura	*reburra*	A.S. Barclay	Mexico	Sinaloa	*Gentry, Barclay& Arguelles 19442*	(COLO)
Datura	*reburra*	A.S. Barclay	Mexico	Sinaloa	*B. Templeton 7079*	(RSA)
Datura	*stramonium*	L.	USA	California	*B. Ertter 8885*	(RSA)
Datura	*stramonium*	L.	USA	Kansas	*J. Dupin 54*	(COLO)
Datura	*wrightii*	Regel	USA	Nebraska	*J. Dupin 35*	(COLO)
Datura	*wrightii*	Regel	USA	Arizona	*J. Dupin 48*	(COLO)
Datura	*wrightii*	Regel	USA	Utah	*J. Dupin 49*	(COLO)
Trompettia	*cardenasiana*	(Hunz.) J. Dupin	Bolivia	Potosi	*S. Smith 383*	(WIS)
Trompettia	*cardenasiana*	(Hunz.) J. Dupin	Bolivia	Potosi	*S. Smith 385*	(WIS)
Capsicum	*lycianthoides*	Bitter	Ecuador	Pichincha	*S. Smith 203*	(WIS)
Juanulloa	*speciosa*	(Miers) Dunal	Colombia	Tolima	*J. Ng 023*	(COLO)

Lycium	*tenue*	Willd.	South Africa	Western Cape	*R. Olmstead 99-13*	(WTU)
Mandragora	*chinghaiensis*	Kuang & A.M. Lu	China	Qinghai	*Z.Y. Zhang 089*	(HNWP)
Mandragora	*chinghaiensis*	Kuang & A.M. Lu	China	Qinghai	*T. Tu Tu521-1*	-
Nicandra	*physalodes*	(L.) Gaertn.	Peru	Cultivated in Beal Botanical Garden, Michigan State University	*R. Olmstead S-38*	(WTU)
Physalis	*peruviana*	L.	Ecuador	Pichincha	*S. Smith 217*	(WIS)
Solanum	*demissum*	Lindl.	-	-	-	(PI-545757)
Nicotiana	*tabacum*	L.	-	-	-	(AYMY00000000.1)

B.2 *lfy* primers designed for this study

All primers with an F (forward) in the name are placed on the exon 2 of *lfy*, the ones with an R (reverse) are found on the exon 3; and the one with Ri (reverse, internal) is placed on the intro II.

B.2 *lfy* primers designed for this study

Primer name	Sequence 5' - 3'
LFYDatF1	GATTACTTGTTCCATCTCTATGAGCAATGC
LFYDatF2	AGGGAGCATCCGTTTATCGTGACG
LFYDatF3	TATCAACGAGGGCGGAGGAGGAGGAGTAAGC
LFYDatF4	AGGAGGACGATGAAACGGAGGAATTAGG
LFYDatF5	GGAAATAATGGTGAGAGGAAGAAGGC
LFYDatR1	GTTTATGTAGCTTGCCCCTGCCTTCTTCGCG
LFYDatR2	GGAGCCATCCTCGTCAAGACAATGAAGTGCG
LFYDatR3	CCTTGTCGAGCAGCTATGGCTACCAGGGGC
LFYDatR4	ACTGCAAAACTGAACCTGAGTCG
LFYDatR5	AACACAATCAGACTAACCATCCAACGC
LFYDatRi6	TTGAGTGGAAGTACAAATGGAGTAATGGGC

B.3 starBEAST2 analysis of *Datura*

Analysis from starBEAST2 of *Datura* (showing only results for the ingroup). Nodes with an asterisk have a *pp* of 1.00.

B.4 Divergence times with confidence intervals for Datureae and outgroups

Divergence times with confidence intervals for Datureae and outgroups. (MRCA = most recent common ancestor)
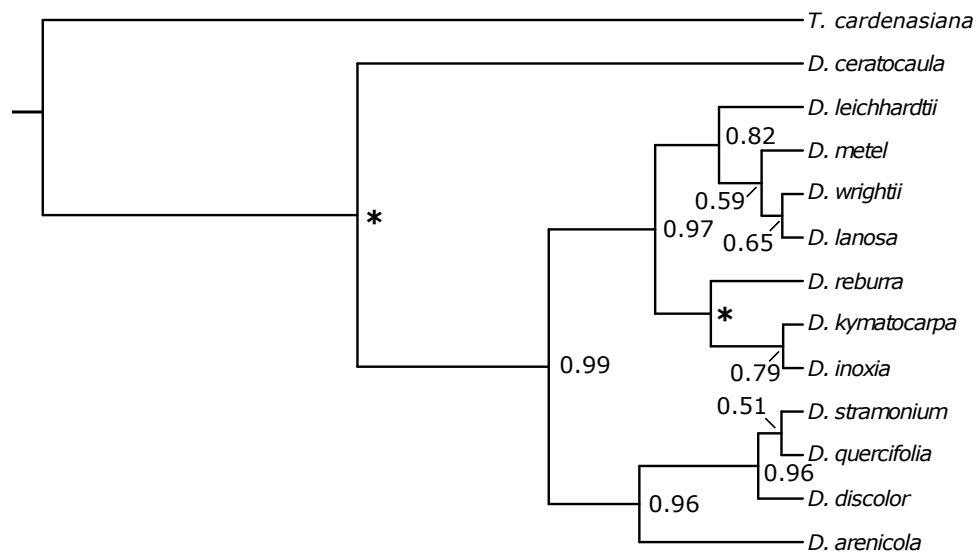
B.3 starBEAST2 analysis of *Datura*

B.4 Divergence times with confidence intervals for Datureae and outgroups. (1) MRCA = most recent common ancestor.

MRCA (1)	Median age (Ma)	95% CI (Ma)
Brugmansia	18.4	27.5, 10.8
Brugmansia arborea + B. sanguinea	12	20.2, 5.1
Brugmansia aurea + B. suaveolens	9.3	15.7, 4.4
Datura	14.2	20.6, 8.8
Datura arenicola + D. stramonium	11.4	16.1, 6.4
Datura kymatocarpa + D. leichhardtii	10.7	16.6, 7.1
Datura + Brugmansia	28.5	39.2, 18.7
Datureae	34.7	46.9, 23.8
Datureae + *Nicandra*	42.7	55.5, 30.6
Solanoideae	54.1	67.4, 52.2

Appendix C

Supporting information to Chapter 3

This appendix contains supporting information for Chapter 3.

C.1   Biogeographical models tested in this study

Biogeographical models tested in this study, along with estimated free parameters, log-likelihoods, AIC values and Akaike weights. Models were classified according to the time periods chosen depending on the reported date of the closure of the Panama isthmus: 3.5 Ma, 12 Ma or 20 Ma. Model suitability was examined using AIC comparisons. Models that included the j parameter presented better AIC values and, consequently, higher Akaike weights, but there was no significant difference between the six values that do included J as a free parameter. $j = 0$ means founder-events were not allowed. (1) rate of range expansion. (2) rate of range contraction. (3) exponent on manual dispersal multipliers (modifies d and j). (4) relative per-event weight of jump dispersal.

C.1 Biogeographical models tested in this study

Model name	Log-Likelihood	Free parameters				AIC	Akaike weights
		$d(1)$	$e(2)$	$w(3)$	$j(4)$		
DEC_3.5	-10.81	2.60E-03	0.00	1.32	0.00	27.62	0.032
DEC+j_3.5	-07.89	1.00E-07	0.00	2.39	0.14	23.78	0.221
DIVALIKE_3.5	-10.48	7.20E-03	0.00	1.36	0.00	26.96	0.045
DIVALIKE+j_3.5	-08.30	1.00E-07	0.00	1.60	0.09	24.60	0.147
DEC_12	-10.95	1.10E-03	0.00	0.38	0.00	27.90	0.028
DEC+j_12	-08.12	1.00E-07	0.00	10.0	0.43	24.24	0.176
DIVALIKE_12	-10.71	4.60E-03	0.00	0.66	0.00	27.42	0.036
DIVALIKE+j_12	-08.90	1.00E-07	0.00	0.94	0.05	25.80	0.080
DEC_20	-10.94	1.20E-03	0.00	0.59	0.00	27.88	0.028
DEC+j_20	-08.71	1.00E-07	0.00	0.77	0.04	25.42	0.097
DIVALIKE_20	-10.72	4.70E-03	0.00	0.80	0.00	27.44	0.035
DIVALIKE+j_20	-08.99	1.00E-07	0.00	0.94	0.05	25.98	0.073

C.2   List of environmental variables considered for this study

Initial list of environmental variables considered for this study, their sources and final 12 selected (marked with asterisk) to be used in subsequent pPCA after collinearity test. Numbers by soil variables represent the depth of the measurement. 'Worldclim' is from [81], 'SoilGrids 1km' is from [79].

C.2 List of environmental variables considered for this study

Variable	Source
Annual Mean Temperature	Worldclim
Mean Temperature Warmest Quarter	Worldclim
Mean Temperature Coldest Quarter	Worldclim
Annual Precipitation	Worldclim
Precipitation Wettest Month	Worldclim
Precipitation Driest Month	Worldclim
Precipitation Seasonality	Worldclim
Precipitation Wettest Quarter	Worldclim
Precipitation Driest Quarter	Worldclim
Precipitation Warmest Quarter	Worldclim
Precipitation Coldest Quarter	Worldclim
Mean Diurnal Range	Worldclim
Isothermality	Worldclim
Temperature Seasonality	Worldclim
Max Temperature Warmest Month	Worldclim
Min Temperature Coldest Month	Worldclim
Temperature Annual Range	Worldclim
Mean Temperature Wettest Quarter	Worldclim
Mean Temperature Driest Quarter	Worldclim
Soil bulk 0.3m	SoilGrids 1km
Soil bulk 0m	SoilGrids 1km
Soil bulk 1m	SoilGrids 1km
Soil clay 0.3m	SoilGrids 1km
Soil clay 0m	SoilGrids 1km
Soil clay 1m	SoilGrids 1km
Soil fragment 0.3m	SoilGrids 1km
Soil fragment 0m	SoilGrids 1km
Soil fragment 1m	SoilGrids 1km
Soil sand 0.3m	SoilGrids 1km
Soil sand 0m	SoilGrids 1km
Soil sand 1m	SoilGrids 1km
Soil silt 0.3m	SoilGrids 1km
Soil silt 0m	SoilGrids 1km
Soil silt 1m	SoilGrids 1km