



Burseraceae: a model for studying the Amazon flora

Burseraceae: um modelo para estudos da flora Amazônica

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Abstract

A well-studied group of plants can serve as a model for addressing issues in conservation, evolution, and biogeography, making it possible to assign conservation status with confidence and detecting not only those taxa that are most threatened but also those that represent basal, unique, and/or relictual members of entire lineages. Clarified higher-level phylogenetic relationships open the door to more refined systematics of clades without having to worry if they are para- or polyphyletic. A well-studied group can also be an excellent testing ground for new or under-utilized tools and independent data sets. Research on the Burseraceae, with over 100 taxa in the Amazon, is rapidly arriving at the point where the family can be used effectively both as a tool for conservation and as a model for studying the processes influencing the origin and maintenance of high diversity in the Amazonian flora. First, we are resolving higher-level phylogenies as well as species-level taxonomy in various clades, allowing comparative approaches. Second, the family occurs throughout Amazonia and is well-represented in most habitats overall, but most of the taxa are restricted in their distributions and/or habitats; this makes it possible to test the relative importance of geographic barriers vs. habitat diversity in the speciation process. The family is sufficiently large to provide adequate statistical power for hypothesis testing and yet small enough to achieve the necessary sampling intensity, allowing us to assess the relative impacts of morphological innovation, ecological opportunity, and biogeographic events on the diversification of Burseraceae and related groups.

Key words: Amazonia, Anacardiaceae, conservation, phylogeny.

Resumo

Um grupo bem estudado de plantas pode servir como modelo para abordar assuntos de conservação, evolução e biogeografia, possibilitando designar o status de conservação de táxons e detectando não somente os táxons que são mais ameaçados mas também os que constituem representantes basais, únicos e/ou relictuais de linhagens. Relacionamentos filogenéticos esclarecidos abrem a porta para uma sistemática mais refinada de clados sem se preocupar sobre grupos para- ou polifiléticos. Um grupo bem estudado pode também servir como base para ferramentas novas ou sub-utilizadas. Pesquisas sobre as Burseraceae, com mais de 100 táxons na Amazônia, está chegando rapidamente ao ponto em que a família pode ser utilizada com grande impacto tanto na conservação como em um modelo para estudar os processos que influenciam a origem e a manutenção da alta diversidade da flora Amazônica. Primeiro, estamos resolvendo a filogenia a níveis taxonômicos superiores assim como a taxonomia ao nível de espécie em vários clados, o que permite estudos comparativos. Segundo, estamos verificando que a família ocorre em toda a Bacia e é bem representada na maioria dos habitats, mas quase todos os táxons são restritos nas suas distribuições e/ou habitats ocupados; isto permite testar a importância relativa de barreiras geográficas *versus* diversidade de habitats no processo de especiação. A família tem tamanho adequado para provas estatísticas de hipóteses mas também suficientemente pequena para atingir intensidade necessária de amostragem, permitindo avaliar os impactos relativos de inovações morfológicas, oportunidades ecológicas e eventos biogeográficos na diversificação das Burseraceae e grupos aparentados.

Palavras-chave: Amazônia, Anacardiaceae, conservação, filogenia.

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Introduction

Why a Global Approach?

A well-studied group of plants can serve as a model for many different avenues of biological investigation, if the group's state of the art includes three main components: (1) a strong taxonomic foundation complemented by a molecular phylogeny; (2) thorough sampling, providing both morphological and molecular characters; and (3) parallel ecological, morphological, and physiological studies of representative species. We can use these well-studied groups to address issues in conservation, biogeography, and evolution, making it possible to assign conservation status with confidence and detecting not only those taxa that are most threatened but also those that represent basal, unique, and/or relictual members of entire lineages. For example, *Beiselia mexicana* Forman was recently proposed to constitute a distinct tribe basal to the rest of the Burseraceae (Thulin *et al.* 2008). Clarified higher-level phylogenetic relationships open the door to more refined systematics of clades without having to worry if they are para- or polyphyletic (a big obstacle for beginning graduate students in plant systematics). Well-supported phylogenies can be used to test hypotheses for a spectrum of issues, such as the origins and affinities of lineages, e.g., migrations involving South America, the Chocó, the Caribbean and Central America (Weeks *et al.* 2005); the evolution of plant-animal interactions, e.g., whether bat dispersal arose independently in more than one Protieae lineage; and habitat shifts, e.g., strong suggestions that parapatric speciation from clay to sandy soils took place a number of times in *Protium* Burm.f. and has contributed significantly to the overall diversification of the group (Fine *et al.* 2005; Fine *et al.*, in press).

A well-studied group can also be an excellent testing ground for new or under-utilized tools and independent data sets; as an example of this, to date we have prepared permanently mounted leaf clearings of 110 species of tribe Protieae in preparation for a detailed analysis of the value of leaf architecture for Burseraceae systematics (see Ellis *et al.* 2009).

Addressing these issues requires a densely sampled, well-supported phylogeny and a detailed study of the morphology and biogeography of the species. To maximize the utility of these studies, one must also have large numbers of specimens data-based and geo-referenced.

We cannot understand Amazonian Burseraceae (or any other group, for that matter) if all we know about is the Burseraceae of Amazonia. Comprehensive knowledge of a group of plants is important if only to know which names to use, i.e., which are valid and have priority, whether at generic or specific rank. For example, if it were determined that what are called *Protium* in Asia and in Amazonia are not monophyletic (i.e., not congeneric), the Amazonian taxa would have to be part of a Neotropical endemic genus, *Icica* Aubl. Similarly, if the Amazonian *Protium puncticulatum* J.F. Macbr. is found to be conspecific with Andean *P. macrophyllum* (H.B.K.) Engl. or Central American *P. glabrum* (Rose) Engl., the Andean name and then the Central American name have priority and all three would cease to be regional endemics. These issues extending beyond the limits of Amazonia also go well beyond nomenclature, because they affect conclusions about diversity, endemism, biogeography, and conservation.

The Burseraceae are rapidly arriving at the point where the family can be used effectively as a model for studying the Amazon, not only because we are resolving higher-level phylogenies as well as species-level taxonomy in various clades, but also because in Amazonia the family is highly diverse and most of the taxa are restricted in their distributions and/or habitats. The following discusses the current status of research on the family on several scales as it becomes one of the better studied families in Amazonia.

An Overview of Burseraceae Diversity

The Burseraceae comprise ca. 750 species of trees and shrubs in 19 genera, and the family is best known as the source of frankincense (*Boswellia* Roxb. ex Colebr.), the premier African timber tree okoumé (*Aucoumea* Pierre), copal (*Bursera* Jacq. ex L. and *Protium*), myrrh (*Commiphora* Jacq.), and the regionally important pili nut (*Canarium* L.) and African pear (*Dacryodes* Vahl). The latter four genera occur on at least two continents, and four genera in the family each have more than 100 species: *Protium*, *Commiphora*, *Bursera*, and *Canarium* (Daly *et al.* 2011)(Fig. 1).

The Burseraceae make up an important part of the structure and diversity of both humid and dry forests in many parts of the tropics, often accounting for 10–14% of the trees in species-rich lowland tropical moist forests. As an example, in a lowland forest in Sarawak, the Burseraceae

comprised the third most important tree family in relative density, second in basal area, and ninth in relative diversity, and it accounted for five of top 20 species in relative frequency (Lee *et al.* 2002).

The family is remarkable for having a high number of congeners in limited areas. As examples, there are 48 species of *Bursera* in the state of Guerrero, Mexico (Rzedowski *et al.* 2005); 8 of *Dacryodes* on 1 ha in Brunei, 17 of *Santiria* Blume on 50 ha in Sarawak (Lee *et al.* 2004), 33 of *Protium* on 70 ha near Manaus, and 29 spp. of *Protium*, *Crepidospermum* Benth. and *Tetragastris* Gaertn. in 67 0.1-ha plots spread over 25 km² in Amazonian Peru (Fine *et al.* 2005).

Towards a New Subfamilial Classification

Until recently, the subfamilial classification of the Bursereaceae was in a fascinating state of flux, but as molecular systematic investigations progress and the results are reconciled with morphology, the Mexican endemic *Beiselia* is indicated as a monotypic tribe basal to the rest of the family (Fig. 1).

In tribe Bursereae, *Bursera* moves toward absorbing *Commiphora*, as recent phylogenetic analyses are revealing new patterns within traditional lineages, with *Bursera* subgenus *Elaphrium* Jacq. sister to *Commiphora* + *Bursera* subgenus *Bursera*

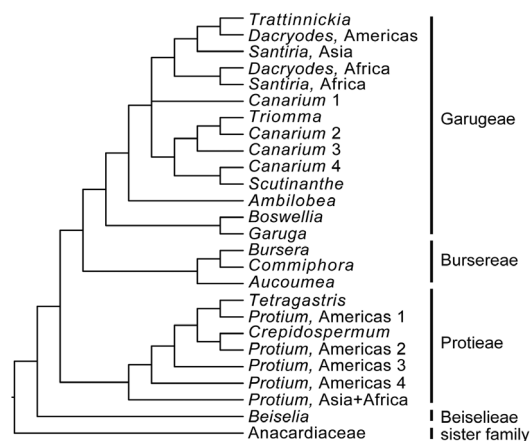


Figure 1 – Generalized phylogeny of Bursereaceae with expanded sample, but with similar methods and the same genes as reported in Weeks *et al.* (2005). Tribal names follow those as recommended by Thulin *et al.* (2008). Note that several genera are paraphyletic. Figure courtesy of A. Weeks.

(e.g., Weeks & Simpson 2007). There is surprising evidence for *B. inversa* from northern Colombia being the most common recent ancestor for *Commiphora*, a genus with all but two of its approx. 190 species distributed in the Old World. *Bursera tonkinensis* Guillaumin is also implicated as having a basal position in the clade (Weeks & Simpson 2007; Martínez-Habibe, unpublished results).

Molecular phylogeny and to a lesser extent morphology are changing the composition and structure of tribe Canarieae. The Bursereae-Boswelliinae are being confirmed as monophyletic – but sister to traditional tribe Canarieae instead of Bursereae, which may be absorbed by the former. Madagascan *Boswellia* has proven to be a new, endemic genus, *Ambilobeia* Thulin, Beier & Razafim., and firmly in Canarieae (Thulin *et al.* 2008). *Dacryodes* is pantropical as currently circumscribed but may prove to be polyphyletic (A. Weeks, pers. comm.). A number of Neotropical species in this latter genus have been found to have functionally perfect flowers (Daly & Martínez-Habibe 1992), but the monophyly of these species has yet to be tested.

With the removal of *Trattinnickia* Willd., *Garuga* Roxb., and later *Garuga*, the Protieae have remained intact as a tribe but internally unresolved. Accepting the unification of Madagascar/Mauritius *Marignia* Comm. ex Kunth and Neotropical *Icica* under Asian *Protium* by Marchand in 1867–1868, the broadly circumscribed *Protium* at present consists of ca. 175 species in the Neotropics plus one species each with non-overlapping distributions in Indonesia, continental tropical Asia, the Philippines, Papua New Guinea, Mauritius, and Madagascar. The remainder of the tribe comprises two small genera, *Crepidospermum* (6 species) and *Tetragastris* (10). The Protieae are examined in more detail below.

Molecular-based Phylogeny and Biogeographical Reconstruction

A well-sampled phylogeny can provide insights into the historical biogeography of a lineage. For example, work in the Malpighiaceae has revealed that the oldest members of the family are African and that colonization of South America occurred later, via a land bridge in the Miocene (Davis *et al.* 2002). The Bursereaceae are also thought to be a lineage that has migrated between the Old and New World via a Boreotropical landbridge (Weeks *et al.* 2005). Fossils of the Protieae, Canarieae and Bursereae have been found

in London and Florissant, Colorado, even though those lineages no longer occur in the Northern Hemisphere outside of the tropics. Reconstructions of biogeography using the phylogeny of the Burseraceae points to a Northern Hemisphere origin with subsequent migrations into Africa, Asia and the New World Tropics (Weeks *et al.* 2005).

As for the Protieae, our phylogeny in Figure 2 reveals a similar story. The oldest lineage appears to be the Old World clade (sections *Protium* and *Marignia*) that includes species from Madagascar, Mauritius, continental tropical Asia, the Philippines and Papua New Guinea. All other lineages are clades in the New World tropics – pointing to an ancient split at least 50 million years ago, when fossils of Protieae show that the lineage lived in London, in what was then a tropical Europe. Subsequent cooling and drying of the global climate caused two lineages of the Protieae to move south, one towards the Old World tropics and another towards South America. One of our most fascinating preliminary findings is that the most basal lineage of New World Protieae is the *Icicopsis* group – and its most basal taxon is *P. fragrans* (Rose) Urb., which occurs only in Cuba's Oriente rain forests near Baracoa. This is consistent with the hypothesis that that the common ancestor of *Protium fragrans* and all other New World Protieae lived in the New World tropics before the lineage ever arrived in the Amazon and began its spectacular radiation of over 100 species. All other Central American and Caribbean *Protium* (including the other four species that live in Cuba) occur in derived lineages of the clade (Fig. 2), pointing to more recent dispersal by lineages that radiated in the Amazon and then dispersed northward across the Caribbean Sea or the Darien Gap.

The trajectory of *Bursera* tells a very different story. Although the resolution of certain clades is still vague, it was possible to determine that the islands were colonized from Central America by two distinct lineages, and that most species are restricted endemics that radiated during the Middle Miocene to Pliocene (De-Nova *et al.* 2011, Martínez-Habibe, unpublished results).

The Importance of Sampling

It is important to be very cautious when making sweeping interpretations of biogeographic history when one does not have a comprehensive sample of all of the taxa (including extinct species). For example, if we did not have samples of *Protium fragrans* in the phylogeny, we would conclude that the basal lineage *Icicopsis* Engl. was

Amazonian, and that perhaps all Caribbean and Central American taxa were more derived – a story that we now hypothesize to be incorrect. Many of the taxa missing from our phylogeny in Figure 2 are from the Chocó biogeographic region on the Pacific side of the Andes, and these may either change the structure of the phylogeny or reveal that some subclades currently considered Amazonian are in fact trans-Andean, which could change our characterization of the dispersal and migrations of Protieae through the eons. Recent collections made in that region are being incorporated into a more complete molecular phylogeny (Fine *et al.* in prep.).

In *Bursera*, a broad sampling was important to determine the relationships of the Antillean species with their relatives in mainland Central and South America. It would be impossible to obtain an understanding of the evolutionary relationships of a region like the Antilles without both a molecular phylogeny and a thorough study of herbarium and living material.

Current Challenges – Global

For tribe Protieae as for so many groups of organisms, satisfactory internal resolution of the group's phylogeny hinges on obtaining samples for molecular studies of far-flung taxa possibly representing distinct lineages; this highlights both the need for both greatly increased field work and facilitation of access to silica-dried material from parts of the world that may be unstable and/or resistant to export of such material.

For the Burseraceae in general, most key geographic gaps are in the Malesian region, especially Borneo, the uplands of New Guinea, the Philippines, Vietnam and neighboring countries. Of greatest concern for the Protieae are the Chocó biogeographic region, the northern Andes, western Amazonia including the Andean piedmont, and various additional parts of Colombia. Between 2009-2011, we were able to sample lowland New Guinea, Vietnam, part of the Chocó biogeographic region of Colombia, and New Caledonia. As for key taxa, during the same period we were finally able to collect and sample several key taxa for the first time: *Haplolobus* H.J. Lam, "*Bursera*" *tonkinensis* Guillaumin (an apparent link between *Bursera* and *Commiphora*), Asian *Dacryodes*, *Bursera* sp. nov. from Goiás, Brazil (Daly, in press), and *Protium serratum* Engl. in Vietnam (of which *P. yunnanense* (Hu) Kalkman from S China proves to be a synonym), but some missing links still present

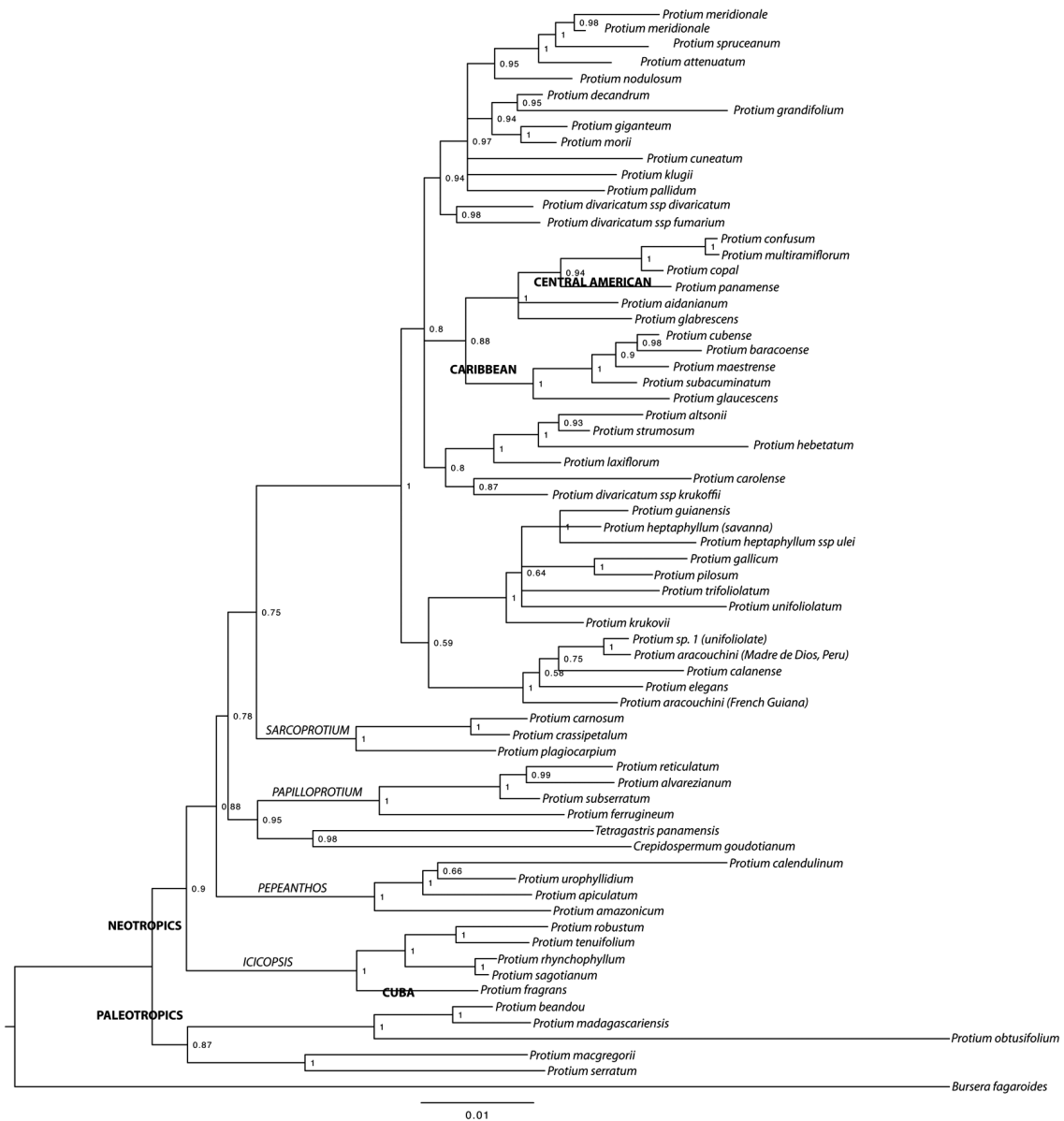


Figure 2 – Bayesian analysis of 66 Protieae taxa using a GTR + I + Gamma model in Mr. Bayes 3.1 (Huelsenbeck & Ronquist 2001) for one million generations (and after stationarity was achieved). Posterior probabilities (after burn-in generations were discarded) are listed at each node when over 50%. Named sections of *Protium* are written along the branches of the clades in italics. All species are South American unless otherwise indicated in bold capitals.

worrisome gaps for our higher-level phylogeny: *Pseudodacryodes* from Congo, *Rosselia* from eastern Papua New Guinea, and African *Santiria*.

Another challenge is posed by the large number of undescribed species in some genera and in some geographic regions. Pockets of new species and under- or unsampled lineages occur in the Chocó biogeographic region (various genera); Madagascar,

where the number of described species is increasing from 3 to 33 in *Canarium* (Daly & Raharimampionona in prep.) and from 28 to ca. 50 in *Commiphora*; and surprisingly parts of the Andes (mostly *Protium*), where some undescribed Burseraceae are proving to be local dominants (Daly *et al.* in press). Many of the new taxa worldwide are not yet represented by material adequate for publishing them.

Overview – Burseraceae in Amazonia

The Burseraceae comprise an excellent model for studying Amazonia because of its high diversity, ecological importance, diversity of habitats occupied, and habitat specificity. The family includes over 100 species in the Amazon, including at least 65 species in the Colombian Amazon. In their ecological importance, the Burseraceae are on a par with all of the great families of trees in Amazonia and the Guianas, but the manner in which this importance is achieved differs from one region to another. Overall, the Burseraceae score somewhat higher in relative density than in relative diversity (number of species) and far higher in relative density than in relative “dominance” (basal area), as they tend to be small to medium-sized trees. In eastern Amazonia and the Guianas, the importance of the Burseraceae is due primarily to their great numbers. In the western part, relative density is far lower but relative diversity far higher. In central Amazonia, the family is strikingly important under both these criteria.

As examples of some of these patterns, in a forest inventory in Amapá (E Amazonia), the Burseraceae were 4th in Family Importance Value and 3rd in relative density but only 7th in relative diversity (Mori *et al.* 1989), while in an inventory in W Amazonian Peru, the family was 11th in relative density but tied for 5th in relative diversity (Spichiger *et al.* 1996). In the Biological Dynamics of Forest Fragments project in Central Amazonia, the family was 2nd in relative diversity, with 49 species, and *Protium* was the most speciose genus (35 spp.) (Rankin-de-Morona *et al.* 1992), while at the same time the Burseraceae comprised 5838 or 9.82% of 59436 trees sampled over 10 cm DBH and one species of *Protium* was by far the most abundant tree species, with 2435 individuals or 4.1% of all the trees inventoried (S. Laurance, pers. comm. 2000).

The family is ecologically versatile overall, but individual species tend to show habitat preferences and a number are habitat specialists, although few species of Burseraceae are found as habitat specialists in flooded, poorly-drained or extremely poor soils; those that do are often restricted geographically. On 28 plots of 0.1 ha in the Colombian Amazon, Giraldo-Cañas (1999) found that the Burseraceae were represented in 12 of 15 vegetation types sampled, while on 95 plots of 0.1 ha, Duivenvoorden (1995) found that most Burseraceae show strong preferences against flooding, for drainage, and for nutrient-poor soils.

Almost three quarters of the 35 species investigated in the Peruvian Amazon by Fine *et al.* (2005) were restricted to only one of three edaphic habitats: white-sand forest, clay soil forest, or brown sand forest from eroded river terraces.

Molecular-based Phylogeny and Taxonomic Questions in Protieae

Generic limits and many relationships within Protieae historically have proven difficult to resolve based on morphology alone (e.g., Daly 1989; Harley & Daly 1996), although molecular studies to date provide strong support for a well-resolved Protieae clade (Fig. 2), and the results are remarkably congruent with higher-level, morphology-based taxonomy within the tribe, including virtually all published sections of *Protium* (the oversized sect. *Eu-Icica* excepted): *Protium*, *Marignia*, *Icicopsis*, *Sarcoprotium*, *Pepeanthos* and *Papilloprotium* (e.g., Daly 1989, 2007; Daly & Fine 2011). *Crepidosperrum* and *Tetragastris* are thus far both monophyletic but nested within *Protium*, so as it stands the tribe may end up being a single genus of ca. 190 species.

The molecular-based phylogeny has also contributed to the circumscription of these sections, including unusual taxa that were misplaced on first examination. For example, *Protium fragrans* from Cuba falls neatly within a well-supported *Icicopsis* clade, as originally proposed by Swart (1942) and, similarly, the Guianas endemic *P. plagiocarpium* Benoist belongs to a well-supported clade of section *Sarcoprotium* Daly species (Fig. 2).

Despite the large cluster of *Protium* species towards the top of Figure 2 that are unassigned to sections, it includes some well-supported groups that are united by morphological characters and thus could become new named sections in the future. For example, most if not all of the clade that includes *Protium altsonii* Sandwith, *P. hebetatum* Daly, *P. laxiflorum* Engl. and *P. strumosum* Daly is characterized by green fruits, suggesting bat dispersal (see Daly 1987).

Current Challenges in the Protieae

One issue that will be helped by molecular studies at (infra-)specific rank is the question of whether one or more clusters of names that have been synonymized are in fact complexes of closely related species; these include *Protium decandrum* (Aubl.) Marchand, *P. trifoliolatum* Engl., *P.*

aracouchini (Aubl.) Marchand, *P. heptaphyllum* (Aubl.) Marchand, *P. sagotianum* Marchand, and *P. unifoliolatum* Engl.; it is interesting to note that all but the latter were originally described from French Guiana.

An eternal question in Amazonian botany is which of the taxa we believe to be strict endemics or disjuncts are in fact artifacts of collecting; examples that appear to be disjunct between C or W Amazonia and the Guianas include *Protium krukovii* Swart, *P. occultum* Daly, *P. strumosum* Daly, *P. pallidum* Cuatrec., and *P. robustum* (Swart) D. M. Porter.

While *Bursera* is notorious for hybridizing (e.g., Weeks & Simpson 2004), especially *B. simaruba* (L.) Sarg., this has not yet been documented in *Protium*, but one complex that should be examined is Amazonian *P. guianense* (Aubl.) Marchand and the mostly Cerrado specialist *P. pilosissimum* Engl., between which intermediates are found in S Amazonia.

Finally, several groups present what have been intractable challenges among the Amazonian Burseraceae; the molecular-based phylogeny will aid in the untangling of species complexes and synonymy questions, but all require expanded botanical exploration. First, *Protium* sect. *Icicopsis*, an object of current revision, is both variable and repetitive vegetatively while the fruits rarely help; it is possible that hair types and surface features like lenticels will yield useful keys. Second, *Protium heptaphyllum* is a highly variable, widespread species ranging from Costa Rica to S Brazil that needs to be the subject of at least a master's thesis using morphometrics and molecular systematics. Third, the *Protium aracouchini*/*P. calanense* Cuatrec./*P. elegans* Engl./*P. leptostachyum* Cuatrec. complex is also widespread, and it is highly variable vegetatively, the flowers display few diagnostic characters, and the fruits of all are red above and green below at maturity. Finally, the species of *Protium* sect. *Sarcoprotium* can be distinguished rather easily with flowers present, or even with a petal or two persisting on the developing fruits, but sterile or with just fruits they are very difficult to separate. Surveying multiple populations of a species complex across its geographic range and assessing genetic variation within and between populations and comparing it to the amount of variation between morphologically distinct (and discrete) species is one way to begin to resolve these questions using genetic data.

Molecular Phylogeny and Speciation Mechanisms in Amazonian Protieae

An interesting application of molecular-based phylogenies is using sister-taxa relationships to infer speciation mechanisms. For example, lineages that are subdivided by a mountain range often include sister taxa that share elevational ranges suggesting allopatric speciation via barriers causing reproductive isolation (Coyne & Orr 2005). Alternatively, sister taxa can have parapatric ranges and specialize in different habitat types, indicating a very different mechanism (Moritz *et al.* 2000). In the Protieae, Fine *et al.* (2005) mapped soil type onto a phylogeny of 35 species of Protieae from the Peruvian Amazon and found that the five species that were associated with white-sand forests had each arisen independently in the phylogeny, consistent with a hypothesis of habitat heterogeneity promoting speciation.

Finer-scale studies of section *Papilloprotium* (Daly & Fine 2011; Fine *et al.* in press) have yielded interesting patterns with respect to habitat and phylogeny. The white-sand specialists *Protium reticulatum* (Engl.) Engl. and *P. alvarezianum* Daly & P. Fine are geographically separated and likely are a result of allopatric speciation between different white-sand areas, while *P. subserratum* (Engl.) Engl. includes multiple populations of two morphologically and genetically distinct entities that inhabit both white-sand forests and terra firme forests of more fertile soil types throughout the western Amazon, plus a third morphotype that is geographically isolated from the other populations in Amapá and French Guiana (Daly & Fine 2011; Fine *et al.*, in press). Future studies will quantify the level of gene flow that crosses habitat boundaries in order to directly test whether speciation-with-gene flow is occurring within *P. subserratum*.

Three additional groups of species merit similar investigations. As noted, one *Protium* clade consists possibly exclusively of species with large, globose fruits that at maturity are green without and white within, suggesting dispersal by bats; the implication is that bat dispersal may have arisen only once or at most a few times in *Protium*. Very few Neotropical Burseraceae are mostly or exclusively floodplain species (e.g., *P. krukovii* Swart, *P. meridionale* Swart, *P. puncticulatum* J.F. Macbr.), and it will be interesting to determine whether these arose parapatrically like the white-sand specialists. Finally, the surprising number of Andean *Protium* species, most of them recently discovered and still

undescribed, invite investigation as to whether colonization of montane habitats has occurred multiple times and relatively recently.

A Broader View of Amazonian Burseraceae

Our rapidly improving understanding of Burseraceae systematics and biogeography, combined with the family's diversity, ecological importance, and habitat specialization in the Amazon region, make it an excellent group for studying the Amazon flora. Diversification in the family occurs via multiple mechanisms, even within some clades, but in Amazonia, in the absence of obvious barriers to genetic exchange, divergence via habitat shifts is likely to be more prevalent than in other regions. Our results to date are compatible with the scenario of the Amazon flora as relatively young, with groups like the Burseraceae undergoing relatively recent and rapid speciation. It is impossible to decipher an Amazonian group without a global grasp of the group, particularly in adjacent floras. Thorough sampling is absolutely essential, as is a rigorous taxonomic foundation, and taxonomic revisions should be complemented by ecological and physiological studies. This sets the stage for the revealing analyses that can be conducted using molecular phylogenies.

Approaches – Tools and Independent Data Sets

Molecular approaches are already making inroads into some of the most stubborn problems in higher-level Burseraceae classification, and examples have been cited of issues where this will prove to be the case at lower ranks as well, but additional tools hold great promise. Pollen characters cast a good deal of light on tribe Protieae (Harley & Daly 1996), so we anticipate similar success with tribe Canarieae (Harley & Daly in prep.). Another traditional character set that inexplicably has been neglected to date in the family is leaf(let) anatomy, and we have begun to build a more extensive collection of liquid-preserved leaf material; one curious aspect of Burseraceae leaflet morphology is the pulvinulus, and lab studies are needed to determine its anatomical structure and whether these are “present” anatomically even when they are not visible in taxa normally characterized by them.

Leaf anatomy and leaf architecture have proven to be useful for better delimitation of

Antillean *Bursera*, helping in the construction of a solid taxonomic treatment for the region (including three new species). The union of molecular and morphological approaches allowed the discovery of, for example, the independent evolution of amphistomatic and simple leaves (Martínez-Habibe, unpublished results).

Barriers to Progress

The obstacles to progress in the study of the Burseraceae are those faced by all Amazonian botanists, but this does not make them any less damaging nor bring them closer to resolution. Botanical exploration and the number of botanical collections generated are both drastically down from the levels of activity ten years ago, and some high-profile but ill-conceived initiatives in Amazonia have proven to be expensive, ineffective in their geographic coverage, and wasteful in that they are producing large numbers of mostly useless sterile collections.

Meanwhile, there is still a severe shortage of professional and productive (in the sense of publications) botanists based in Amazonia; there are still campuses of federal universities that do not have a single Ph.D.-level vascular plant systematist on their faculties. Elsewhere, professors of botany have such heavy teaching loads that they have difficulty finding time to identify plants and conduct systematic research.

Encouraging Developments

Still, there is strong cause for hope. Access to biodiversity for researchers has improved, and there are some embryonic efforts at international cooperation in frontier regions of Amazonia; this includes Colombia, where very recently botanical exploration has become markedly safer and more feasible. The data-basing and digitization of Amazonian herbaria, using standardized software, are beginning to reduce duplication of effort and increase consistency in recorded identifications; Brazil's national flora checklist project and a small number of regional floristic projects are helping as well. These advances will further increase the value of well-studied plant groups as models for research on floristics, conservation, and speciation.

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