Trends in Ecology & Evolution

CellPress

Opinion

Maximising Synergy among Tropical Plant Systematists, Ecologists, and Evolutionary Biologists

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Closer collaboration among ecologists, systematists, and evolutionary biologists working in tropical forests, centred on studies within long-term permanent plots, would be highly beneficial for their respective fields. With a key unifying theme of the importance of vouchered collection and precise identification of species, especially rare ones, we identify four priority areas where improving links between these communities could achieve significant progress in biodiversity and conservation science: (i) increasing the pace of species discovery; (ii) documenting species turnover across space and time; (iii) improving models of ecosystem change; and (iv) understanding the evolutionary assembly of communities and biomes.

Trends

Key research questions are defined to foster closer collaboration between systematists, ecologists, and evolutionary biologists working in tropical forests.

Long-term plots are proposed as a focus of such collaborative studies.

Addressing the proposed questions will require a significant shift in how both individuals and institutions operate in the collection and curation of botanical specimens.

Linking Ecology and Systematics in the Tropics

Systematics (see Glossary) and ecology in the tropics each has a distinguished heritage, but there are significant bottlenecks to progress in both fields: for systematics, the slow pace of species discovery and description, and for ecologists, the difficulty of ensuring consistent and accurate species determinations within and among study sites. These problems prevent progress in addressing some of the most pressing questions in biodiversity science, such as how diversity is distributed in space, how it changes over time, and how it contributes to the resilience of tropical ecosystems to global change. Here we present a question-driven justification for bringing systematists, ecologists, and evolutionary biologists together, to complement recent work that has argued for specimen archiving [1,2] or highlighted problems with identifications within existing collections [3].

The questions we identify and discuss below fall into two categories. Our first question relates to **taxonomy**: completing the formal description of tree species in tropical forests. By contrast, answering the final three ecological and evolutionary questions depends on solving issues of species identification. Achieving consistent, precise, and accurate identifications among

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tropical forest sites has been greatly facilitated by an increasing number of field guides, local floras, annotated checklists, taxonomic revisions, and monographs (e.g., [4]). In particular, the availability of automated online tools that standardise spellings and catalogue synonyms for tropical plants has been a major step forward in improving datasets for large comparative analyses [5]. However, standardising spelling and nomenclature does not address the key assumption of comparative studies that species identifications are consistent and correct among sites. Uniform identifications are unlikely to be the case in many species-rich clades of tropical tree, even with a committed effort by the ecological community, because species identification, especially of sterile vouchers, can be challenging (Box 1). This problem limits our

Box 1. Evaluating Identification Success in Complex Groups of Tropical Trees

Consistent species identifications are challenging to maintain in dispersed networks of plots in diverse forests over time and space. This difficulty is related to variation in knowledge among field botanists in different regions and at different times, especially where new taxonomies have been published concurrently. Abundant, widespread species are likely to be identified successfully, particularly if they possess distinctive vegetative features that facilitate the identification of sterile collections (e.g., five of the ten most abundant species found in the RAINFOR plot network in Amazonia are arboreal palms [57], which are readily identified in the field). By contrast, rarer taxa present particular challenges, especially if they lack key diagnostic morphological characters. However, few studies examine whether identifications of such ‘difficult’ groups vary in space, or over time, and determination of whether current taxonomic knowledge has been appropriately applied is rare (e.g., [19]). We used an online image library hosted at ForestPlots.net [54] from tropical forest inventory plots in western Amazonia to explore uncertainties in identifications within eight clades of tropical trees that present difficulties in identification: *Andira*, *Apuleia*, *Inga*, *Parkia*, *Platymiscium*, *Poeppigia*, *Protium*, and *Tachigali*.

Specialists in each group assessed the accuracy of the identifications of collections that had been made for these genera by 18 different botanists across 60 plots during the past 30 years. In total, collections from 452 trees were examined online and their species-level identifications were assessed as correct or incorrect based on the voucher images. The collections were originally identified as 77 different species. Overall, the results were encouraging: even in taxonomically difficult groups where species are often very rare, 75% of trees were correctly identified (Figure I). However, some lineages clearly present greater difficulties than others: within *Andira* and *Tachigali*, approximately 50% of trees are apparently misidentified (Figure I). Successful identification is not clearly related to the diversity of the genera or the frequency of botanical collection of these species (Figure I). Rather, achieving high levels of correct identification within particular groups is more idiosyncratic. Undoubtedly, in some groups, identification is very difficult with sterile material (e.g., *Tachigali*). For other groups, it might reflect that all species occur at extremely low density and are therefore unfamiliar to many field ecologists (e.g., *Andira*). In other cases, relative success might depend on the availability and knowledge of recent taxonomic studies and existing links between ecologists and systematists to transfer this knowledge (e.g., *Protium*, *Inga*).

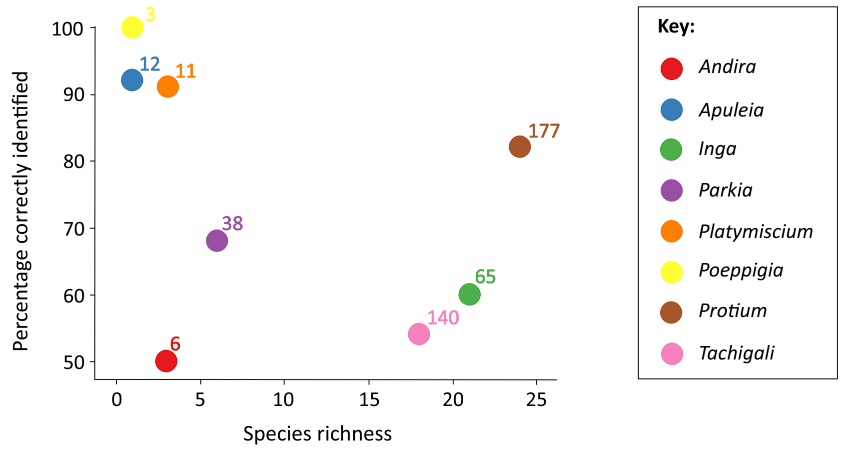

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Figure I. The percentage of correctly identified specimens within eight genera, as a function of the total number of species that were originally identified within the collections for each genus. The total number of collections examined in this study for each genus is also shown next to each point.

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capacity to make the reliable links, based on species names, among phylogenetic, **functional trait**, and inventory datasets that are required for large-scale comparative analyses. Overall, our broad aim is to suggest that the solution to these issues requires changes in how both individual researchers and collections-based institutions operate. We concentrate on tropical forest tree communities because they have been a focus of long-term ecological monitoring and their high species richness means that they are a priority for global biodiversity conservation. However, our arguments also apply more broadly to studies of other biomes and taxa, such as the diverse and poorly known grass flora of savannah ecosystems, taxonomically complex groups in temperate evergreen forests, and comparative studies of insect diversity.

Question 1: How Can We Increase the Pace of Species Discovery of Tropical Forest Trees?

It is an embarrassment that estimates of the tree species richness of tropical forest regions rest on large extrapolations [6]. Forest plot inventories contain *c.* 5000 tree species of ≥10 cm diameter in Amazonia [6] and in total ~11 600 tree species have been collected to date in this region [7]. However, based on extrapolations from plot data approximately 16 000 tree species are estimated to occur in Amazonia [6], which means that ~5000 tree species might await discovery. This proportion of undescribed species is consistent with recent taxonomic monographs of diverse neotropical rain forest tree genera where 20–40% of species are new to science (e.g., [8–10]). While some of these new species might be surprisingly abundant (e.g., *Drypetes gentryana* [11], *Brownea jaramilloi* [12]; Box 2), in many cases their population sizes are likely to be small: ter Steege *et al.* [6] estimate that 62% of Amazonian tree species collectively comprise only 0.12% of trees in the Amazon.

Locating new species is like searching for a needle in a haystack, particularly because defining new species fundamentally relies on reproductive structures. In other words, the challenge is not only to find species that occur at low population densities in hyperdiverse forests but also to collect these with flowers and/or fruit rather than sterile (i.e., in leaf only). Given the often short and unpredictable phenologies of many tropical tree species, botanical expeditions can easily miss the reproductive period of species. As a result, collecting in permanent inventory plots has much to offer for the discovery of tropical species (Box 2). In **long-term plots**, ecologists usually map and measure every individual tree above a certain diameter and collect specimens of rare and undescribed species. If permanent plots are revisited regularly over months and years, this increases the chance of collecting fertile specimens of previously collected sterile individuals – particularly if the interaction between ecologists and systematists encourages the search for fertile specimens of specific taxa. Long-term plots also have the benefit of yielding rich information on morphological and ecological traits (e.g., bark type, plant size, edaphic preferences) and how these vary with ontogeny. Further, these sites provide an accessible resource as the basis for studies of the population genetics of specific taxa (e.g., [13]), which might also assist in the delimitation of species, in understanding the nature of widespread species, and in uncovering cryptic taxa.

We emphasise that permanent plots are not the only solution to completing the biological inventory of the tropics. New species will doubtless emerge from collecting expeditions to poorly collected regions such as the interfluves of the southwestern Brazilian Amazon [7] or by detailed study of existing collections, including genetic analysis [14]. Emerging technologies offer additional solutions. For example, even if herbarium voucher specimens from plots lack flowers and fruit, DNA sequence data and the technique of near-IR (NIR) leaf spectroscopy now offer insights into species identification and both of these techniques can help improve taxonomic consistency among sites. In addition, although neither was initially intended as a tool in the taxonomic process of defining species, both might be able to contribute to it. For example, applying multilocus **DNA barcoding** [15–18] routinely across sites can help in

Glossary

Demographic rates: the rates, usually per year, of recruitment and/or mortality of individual trees within a site, species, or clade.

DNA barcoding: the use of sequences of standard regions of DNA as a tool for species identification. In plants, these regions are generally the plastid genes matK and rbcL [16].

Functional traits: the characteristics that influence individual plant survival and performance, such as how the plant delivers a specific function or responds to an external driver.

Long-term plot: permanent monitoring site where all trees of a defined minimum diameter are numbered, tree identity and diameters are recorded, and tree deaths and new recruits are noted in repeated censuses. For example, the RAINFOR, AfriTRON, and T-FORCES networks of permanent plots in Amazonian, African, and Southeast Asian tropical forests, respectively, focus on widely distributed and replicated 1-ha plots using a minimum diameter of 10 cm. The CTFS Forest-Geo network comprises a global network of large, typically 50-ha, forest plots that employ a minimum diameter of 1 cm. Monitoring networks can focus on a broad range of vegetation types, including dry biomes (e.g., the Terrestrial Ecosystem Research Network in Australia), or on management questions related to specific sites (e.g., the Three Parks Plot Network in Australia).

Morphospecies: distinct morphological entities generally recognised based on vegetative characters. Typically, morphospecies are recognised by an individual researcher at a given site, and morphospecies concepts are rarely standardised across researchers or sites.

Systematics: a commonly used definition of systematics is the study of the kinds and diversity of organisms and their evolutionary relationships. The terms taxonomy and systematics are often used interchangeably, but here we use taxonomy in a more restricted sense as the part of systematics that deals with the description and identification of species.

Taxonomy: see systematics.

Box 2. Using Networks of Long-Term Monitoring Sites to Increase Taxonomic Knowledge

There are several examples of the value of closely linking long-term monitoring with taxonomic studies to increase the pace of species discovery in tropical forests. For example, at the Jenaro Herrera Research Centre in Peru, two permanent plots – one 9-ha arboretum in upland forest and one 6-ha arboretum in seasonally flooded forest – have been established since the 1980s. In subsequent decades, numerous researchers have collected specimens from these sites. This repeated collection effort has resulted in the description of 26 new tree species (Table 1 and Figure II) (E. Honorio, MSc thesis, University of Edinburgh, 2006). The descriptions of these new taxa have been based on specimens that have been archived in herbaria internationally, which made them widely accessible to the taxonomic community. A similar example comes from permanent plots established as part of a forest fragmentation project near Manaus, Brazil, where a taxonomic specialist identified potential new species of Sapotaceae from sterile plot vouchers in the early 1990s. The ecologists responsible for the plots revisited them annually and finally collected these trees with flowers and fruit over the subsequent decade, resulting in the publication of 10 species new to science [58].

Most of the species that remain to be described are likely to be rare, but some might be both widespread and surprisingly common. For example, *Drypetes gentryana* was described in 2014 from a permanent plot in the Yanachaga Chemillén National Park on the eastern flank of the Andes in central Peru [11]. Previously collected sterile vouchers collected from other permanent plots have since demonstrated that this species is also found in aseasonal and seasonal forests spanning >1000 km in lowland Peruvian Amazonia. The plot data also demonstrate that this species occurs with local abundances of two or more stems per hectare, which would classify the species as an 'oligarchic' taxon: both locally common (abundance of one or more stems per hectare) and widespread [59]. This example demonstrates the benefit to taxonomists of working with distributed permanent plots: the plot data provide information on the distribution and local abundance of new taxa, which contributes to assessments of their ecology and conservation status.

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Figure II. (A) *Pourouma herrerensis*, a new tree species described from material from (B) the 9-ha arboretum at Jenaro Herrera, Peru.

Trait-based vegetation model: the traditional approach to including variation in species composition in vegetation models has been through parameterising a limited number of different kinds, or functional types, of plant (e.g., evergreen and deciduous trees, C4 and C3 grasses). Such models typically simulate abrupt shifts in ecosystem function that correspond to sudden changes in vegetation type. More recently, a range of models have been developed that represent plant biodiversity in a community by incorporating the distribution of key traits, such as leaf nitrogen concentration and wood density, that are represented in that community. By linking these traits to key processes such as photosynthetic rate and mortality, the effect of more subtle changes in species composition as expressed by changes in the traits of the community can be explored, and potentially validated using permanent plot records. Such an approach promises to yield more nuanced predictions of the resilience and sensitivity of forests, tropical or otherwise, to climate change.

highlighting potentially new species. DNA barcode data or sequences from other loci can also be incorporated by systematists into detailed molecular phylogenetic studies of specific clades, which routinely result in the clarification of species boundaries and the discovery of new species (e.g., [19]). Although currently accepted standard barcode loci [20] might not always discriminate among closely related tropical plant species [21,22], such problems can be overcome by the application of additional, more variable loci derived from next-generation sequencing techniques, which also have the benefit of being able to work with highly degraded DNA from preserved plant specimens [23]. NIR might offer better species-level discrimination of tropical tree species than DNA barcoding [24] and works well with dried specimens, but assessing how useful it can be as a taxonomic tool requires further sampling of widespread species across their distributions. Such sampling is well suited to permanent plot networks that sample broad environmental gradients.

Question 2: How Does Species Composition Vary across Space and Time?

Determining how diversity varies within and among tropical forests is a key question for the definition of conservation priorities and understanding of how the taxonomic composition of

Table 1. The 26 New Species of Tree Described Using Herbarium Vouchers Collected in Jenaro Herrera, Peru

Family	Species	Type citation
Anacardiaceae	*Thyrsodium herrerense* Encarn.	[60]
Annonaceae	*Klarobelia inundata* Chatrou	L.W. Chatrou, PhD thesis, Utrecht University, 1998
Araliaceae	*Schefflera megacarpa* A.H. Gentry	[61]
Arecaceae	*Oenocarpus balickii* F. Kahn	[62]
Calophyllaceae	*Haploclathra cordata* R. Vásquez	[63]
Caryocaraceae	*Caryocar harlingii* Prance & Encarn.	[64]
Ebenaceae	*Diospyros nanay* B. Walln.	[65]
Humiriaceae	*Vantanea spichigeri* A.H. Gentry	[66]
Lauraceae	*Endlicheria argentea* Chanderb.	[67]
Lauraceae	*Endlicheria citriodora* van der Werff	[68]
Lauraceae	*Mezilaurus opaca* Kubitzki & van der Werff	[69]
Lauraceae	*Ocotea immersa* van der Werff	[70]
Lauraceae	*Pleurothyrium acuminatum* van der Werff	[71]
Magnoliaceae	*Talauma rimachii*[a] Lozano	[72]
Melastomataceae	*Miconia spichigeri* Wurdack	[73]
Melastomataceae	*Votomita pubescens* Morley	[74]
Meliaceae	*Carapa vasquezii* Kenfack	[75]
Meliaceae	*Trichilia tenuifructa* T.D. Penn.	[76]
Moraceae	*Naucleopsis herrerensis* C.C. Berg	[77]
Ochnaceae	*Froesia diffusa* Gereau & R. Vásquez	[78]
Ochnaceae	*Quiina attenuata* J.V. Schneid. & Zizka	[79]
Primulaceae	*Cybianthus spichigeri* Pipoly	[80]
Rubiaceae	*Platycarpum loretensis* N. Dávila & Kin.-Gouv.	[81]
Sapotaceae	*Micropholis bochidodroma* T.D. Penn.	[82]
Sapotaceae	*Pouteria sessilis* T.D. Penn.	[82]
Urticaceae	*Pourouma herrerensis* C.C. Berg	[83]

[a] This name is now the basionym of *Magnolia rimachii* (Lozano) Govaerts.

these ecosystems might change in the future [25]. Addressing these issues requires consistent identifications among sites, both for all named species and for the inevitable proportion of stems within diverse tropical forests identified as **morphospecies** [26]. Of course, for ecological analyses of variables such as alpha diversity that focus on individual sites, documenting the patterns does not require standardisation of names across sites. However, comparative studies of composition and traits among sites require standardisation of both species concepts and nomenclature.

Studies of species turnover have typically dealt with these uncertainties by focusing on well-curated, relatively small-scale datasets [27] omitting poorly identified trees [28] or using higher taxonomic ranks, such as genera [29]. However, increasing the accuracy and consistency of species determinations would substantially improve our understanding of variation in the geographic distribution of individual clades and allow us to explore whether climate change and disturbance are causing the taxonomic composition of intact tropical forests to converge, or diverge, among sites over time [25]. For example, even low error rates in identifications can shift our understanding of the spatial patterns of species turnover within species-rich clades, such as the legume genus *Inga* [19]. At the community level, linking changes in taxonomic diversity with associated changes in functional and phylogenetic diversity might allow us to understand the ecological mechanisms that are driving shifts, or maintaining stasis, in different dimensions of the biodiversity of tropical forests [30,31].

Question 3: How Can We Ensure that Trait-Based Models of Tropical Forests Are Correctly Calibrated?

A key challenge in forecasting the future of tropical forests is predicting their resilience to climate change: will forest structure and composition be able to bounce back from short-term climatic extremes such as droughts and keep pace with longer-term changes in temperature? Dynamic global **vegetation models** that have been used to address this question at broad scales provide a range of very different perspectives, hinting at either extensive 'dieback' [32] or an overall resilience of tropical forest carbon stocks to predicted climate change [33]. Biodiversity will play a vital role in determining which scenario is most accurate because different species show a wide range of adaptations that might allow ecosystems to persist as climates change [34–36]. For example, over decadal timescales gradual changes in the abundances of different species might buffer forests from abrupt changes in structure related to changing environmental conditions: in tropical forests in Ghana, an increase in the abundance of species adapted to drier climates during a 30-year drought led to an increase in overall forest biomass [37]. New modelling approaches seek to incorporate such effects of biodiversity by using distributions of functional traits, rather than a small number of artificial fixed functional types, to capture how variation in species composition affects ecosystem function [35,38]. Successful implementation of this approach therefore hinges on the effective use of field data from long-term plots and other measurements that collate quantitative information on plant function and performance (e.g., size, growth and mortality rates, foliar and wood structure and chemistry) of the full diversity of species. Fundamentally this requires a key focus on naming species consistently, because data on species abundances and traits might come from a range of independent sources (e.g., the TRY Plant Trait Database [39]) that are linked by species names. It is particularly important to ensure that rare species are consistently named, as they might have rare traits that do not confer dominance under existing environmental conditions but might provide resilience in the face of climate change. For example, among tropical forest trees in French Guiana and seedling communities in tropical forests in China, locally rare species have distinctive functional traits [40,41] and make a disproportionate contribution to functional diversity [42].

Question 4: What Are the Processes that Determine Community Assembly and the Evolutionary History of Tropical Forests?

Accurate and consistent taxonomic naming of both common and rare species among disparate datasets is also required to advance studies of the mechanisms underlying community assembly and the evolutionary history of tropical forests. Phylogenies form an essential part of these studies and long-term plot networks first provide a resource of well-identified trees to facilitate sampling for the reconstruction of phylogenetic relationships among species [17]. Subsequently linking phylogenetic and functional data with information on species distributions within plots allows inferences about the role of niche-based processes or dispersal limitation in determining community composition [30,43]. However, such studies require accurate and consistent identification of species. Studies of a single or small number of sites can avoid this problem by collecting the full suite of trait, phylogenetic, and abundance data from each site [30,43] but this strategy is unlikely to be possible or desirable for large comparative studies.

Analyses of trait evolution and diversification also require accurate identifications of all species in phylogenies to score them with trait values. For example, multiple lineages of Amazonian trees possess evolutionarily conserved characteristics such as short generation times [44] that are associated with high diversification rates [45], and the evolution of particular traits, such as preferences for different soil types, is associated with speciation in some species-rich clades, such as *Protium* [46]. Understanding whether these relationships are consistent across all tropical regions and clades of trees [47] requires consistent identifications among phylogenetic and trait datasets as well as among long-term plots, as they provide data for some of the key traits, such as **demographic rates** and species maximum size.

Finally, long-term plots have much to offer to our understanding of the nature of tropical tree species and speciation. For example, variation in breeding systems has fundamental effects on gene flow but remains poorly understood for many taxa of tropical trees [48] and there is a great need for more studies to understand whether congeneric tropical tree species can hybridise [49] and whether the resulting hybrid offspring are fertile. Long-term plots are ideal sites for such studies, which would ultimately shed light on the nature of tropical speciation and the maintenance of species coexistence in diverse communities [50].

Achieving These Goals

We have argued that greater collaboration among systematists, ecologists, and evolutionary biologists working in permanent inventory plots can speed the process of plant species discovery in the tropics and address key scientific questions about species turnover, the resilience of tropical forests to climate change, and the evolution of species-rich tropical floras 1 to 4.

Addressing the Challenge of Curating Ecological Vouchers

Better interdisciplinary collaboration is key to addressing all of the scientific questions raised in the first part of this Opinion article, but central to all of them is a need for accurate delimitation and identification of species, especially those that are rare. Reliable identifications will require the archiving of high-quality voucher specimens representing all species in plots; that is, a reference library of herbarium specimens that needs to be openly accessible to the scientific community. This will require a significant cultural shift by ecologists, systematists, and collection managers. Ecologists need to focus on preparing high-quality collections, while systematists and herbarium curators need to be more open to the creation of secure, long-term archives for ecological vouchers, which are often sterile, in major herbaria. The difficulty of lodging vouchers from inventory plots in herbaria has created an unsatisfactory situation where ecologists are forced to keep vouchers in unsuitable conditions outside formal collections (e.g., in their offices) where their long-term safety and endurance as voucher specimens cannot be assured. Further, such vouchers are not openly accessible, resulting in their identification being much less likely to be verified by taxonomists. If the ecological vouchers were openly available (as mounted specimens in major herbaria and as digitised images online, linked to the plot records), taxonomists could more easily highlight individuals of particular interest – for example, those representing possible new species or those connected to DNA barcode sequences and/or archived tissue samples – that should be a priority for future collection when found in flower and/or fruit.

Several of the authors of this Opinion article work in collections-based institutions and are well aware that adding an additional burden of ecological voucher specimens to collections would have considerable resource implications. In our view the numbers of vouchers to be archived are well within the capabilities of some major collections based on their recorded growth in previous decades. For example, archiving a voucher representing every species in 321 plots monitored as part of the RAINFOR network [51], which has a mean richness of 152 species

[52], would total just under 50 000 vouchers. This is a very small number when put in the context of the growth of the world's leading herbaria for tropical plants; for example, the Missouri Botanical Garden grew from 2 million specimens in 1970 to 6 million in 2006. Images of vouchers can be made freely available online (see below), which might help to address the issue of accommodating vouchers in regional tropical herbaria, in particular. Overall, our purpose is to highlight the significant scientific benefits of archiving plot-based vouchers – fertile or sterile. Accommodating vouchers from long-term plots should become a higher priority given the value of these specimens to systematists, ecologists, and evolutionary biologists alike. We are not advocating that all ecological vouchers should be archived, but that priority should be given to those from long-term, established monitoring networks. For other ecological projects, decisions on whether to archive vouchers will need to be made on a case-by-case basis by ecologists, evolutionary biologists, and collections managers. Our hope is that this Opinion article will facilitate such collaborative discussions.

If more herbaria would accept ecological vouchers, even if sterile, this might encourage a cultural change among ecologists resulting in the preparation of better herbarium specimens and thus ensuring that their research includes the funding required to collect them and to incorporate them into formal collections. Collections managers often comment that specimens from ecologists are poorly prepared and lack adequate field data on their labels. However, ecological labels almost always have precise geographic data and thereby reduce uncertainty in descriptions of species distributions. If more herbaria were to accept ecological vouchers, this could encourage collection of specimens by ecologists that are well prepared before acceptance by herbarium curators. Additionally, the presence of ecological vouchers in collections would encourage more taxonomists to visit plots, where they can easily locate numerous mapped and tagged individuals of species to study intra- and interspecific morphological variation.

Using Digital Images to Cross-Check Identifications

A key issue for the scientific questions we highlight is not just accurate identification of specimens from a single plot, but the consistency of identifications across plots and studies, which requires side-by-side comparison of voucher specimens. In this way, even if a species cannot be named (because, e.g., it has not yet been described) one could be confident that two or more plots contain the same unidentified morphospecies. This suggests considerable advantages in concentrating voucher specimens in just a few major herbaria. However, this might not be necessary given that high-resolution specimen images are increasingly available online. Herbaria globally have invested heavily in imaging specimens (e.g., https://plants.jstor.org/) but with understandable initial emphasis on important historical collections, especially nomenclatural type specimens. Some plot networks have also started to place voucher images online [53,54]. Development of workflows and software that can allow on-screen comparison of multiple high-resolution plot voucher specimens and images of living plants is an area ripe for collaboration between ecologists and systematists.

Concluding Remarks

We have been arguing for the high value of housing voucher specimens from long-term plots and we have focused exclusively on plants, especially trees, that are long lived. However, the same logic would apply to herbaceous plants and other organisms in these plots (e.g., insects [55]), with the caveat that re-collection of the same individual organism might be much more difficult or impossible for non-sessile organisms. We therefore extend our plea for the archiving of vouchers from long-term ecological inventory plots to other types of biological collections. Finally, we have focused here on tropical forests, where biodiversity and ecosystem processes are perhaps least well understood (see Outstanding Questions), but our arguments apply in principle to all other forest types and even non-forest biomes. For example, consistently

Outstanding Questions

How many species remain unidentified within existing long-term permanent plots in tropical forests?

How is the species composition of intact tropical forests changing over time as a result of climate change?

How much do rare species contribute to the resilience of tropical forests to climate change?

Are there consistent ecological processes that have promoted diversification across clades and regions?

identified herbarium specimens from a wide range of sites have been critical for our understanding of how shifts in functional traits, particularly C3 and C4 physiology, impact the breadth and dimensions of ecological niches [56]. We therefore advocate collecting and housing voucher specimens from long-term ecological studies across diverse biomes for the benefit of the broader communities of all ecologists, systematists, and evolutionary biologists.

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