

# *arnoldia*

*The Magazine of the Arnold Arboretum*

VOLUME 77 • NUMBER 1



# arnoldia

The Magazine of the Arnold Arboretum

VOLUME 77 • NUMBER 1 • 2019

*Arnoldia* (ISSN 0004-2633; USPS 866-100) is published quarterly by the Arnold Arboretum of Harvard University. Periodicals postage paid at Boston, Massachusetts.

Subscriptions are \$20.00 per calendar year domestic, \$25.00 foreign, payable in advance. Remittances may be made in U.S. dollars, by check drawn on a U.S. bank; by international money order; or by Visa, Mastercard, or American Express. Send orders, remittances, requests to purchase back issues, change-of-address notices, and all other subscription-related communications to Circulation Manager, *Arnoldia*, Arnold Arboretum, 125 Arborway, Boston, MA 02130-3500. Telephone 617.524.1718; fax 617.524.1418; e-mail [arnoldia@arnarb.harvard.edu](mailto:arnoldia@arnarb.harvard.edu)

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Postmaster: Send address changes to  
*Arnoldia* Circulation Manager  
The Arnold Arboretum  
125 Arborway  
Boston, MA 02130-3500

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*Front and back cover:* Cedar Creek, the namesake of the Cedar Creek Ecosystem Science Reserve, winds through a transitional zone between tallgrass prairie and mixed woodlands, about thirty miles north of Minneapolis, Minnesota. The site provides opportunities for long-term observation on how ecosystems function, including research described by Jake Grossman. Photo by Jacob Miller, Cedar Creek Ecosystem Science Reserve (CC BY-SA 4.0).

*Inside front cover:* "As it grows on the prairies of western Louisiana it is a striking and very attractive object," Charles Sprague Sargent wrote of the blueberry hawthorn (*Crataegus brachyacantha*). Sargent predicted that the species would become "a valuable ornament of gardens and parks." This illustration was prepared by Charles Edward Faxon for the fourth volume of Sargent's *Silva of North America*, published in 1892. The species is one of the parents for the unusual hybrid known as Stern's medlar ( $\times$ *Crataemespilus canescens*). Photo from Arnold Arboretum Archives.

*Inside back cover:* While an artwork may be considered a masterpiece from the day it arrives at a museum (if not before), trees at the Arnold Arboretum grow into that status. One of these undisputed masterpieces is an old painted maple (*Acer mono*, accession 5358\*A) along Meadow Road. Photo by Jon Hetman.

## Valuing Biodiversity

*Jake J. Grossman*

Lying on my side, I inspect each leaf of a four-year-old red maple (*Acer rubrum*) sapling. It is midsummer in central Minnesota, and, despite the hot weather, the leaves of this tree and most of its neighbors are covered in brown spots. These spots are a symptom of maple anthracnose, which is caused by infection with any of several ascomycete fungi. Especially in small trees, like the one I am inspecting, anthracnose can slow growth by impairing photosynthesis in damaged leaves and make them more vulnerable to other infections. I finish grading the infected leaves on my tree of interest, record the measurements on my clipboard, and roll over to check its nearest neighbor, also a red maple. Planted only 50 cm (about a foot and a half) apart from each other, these trees are part of the Forests and Biodiversity (FAB) experiment at the Cedar Creek Ecosystem Science Reserve, a long-term research site funded by the National Science Foundation. These trees are in a red maple monoculture plot, meaning each tree has only other red maples as neighbors. Many of these trees are covered in leaf anthracnose, probably because the fungal pathogens that cause it overwinter in the layer of dead leaves, or litter, of infected trees and emerge in the spring to reinfect new growth. Having so many red maples around seems to make any given tree more likely to develop anthracnose.

But when I stand up and walk only a few feet away from this maple monoculture, which only reaches my mid-thigh after several years of growth, I encounter a markedly different part of the FAB experiment. On entering a “biculture,” or two-species plot, of red maple and jack pine (*Pinus banksiana*), I am surrounded by pines that exceed my own height and maples that reach my chest. These trees were planted at the same time as the maples in the adjacent monocultural plot, but living with diverse neighbors has clearly made a difference to them. Whereas maples in monoculture tend to be short and

stocky, with little space between leaf buds, maples that are forced to compete for light with faster-growing pine tend to come up long and spindly, with tons of space between each set of leaf buds. And, exposed to a lower level of accumulated leaf litter from other red maples, these trees have a much lower incidence of leaf anthracnose.

These two plots illustrate two extremes of the FAB experiment, which I co-managed while a graduate student at the University of Minnesota. Previously, as a young ecologist, I had devoured the reports of experiments designed to assess the importance of biodiversity coming out of Cedar Creek and applied to a doctoral program at Minnesota in the hopes that I would get to work there. I quickly heard back from Jeannine Cavender-Bares, a plant ecophysiologist and evolutionary ecologist who would become my doctoral advisor. At the time, she and a group of colleagues at Minnesota were in the final stages of planning a tree biodiversity experiment designed to expand on the foundation laid by grassland experiments at Cedar Creek and across Europe. This group was open to bringing in a new graduate student to help with the establishment of the new project and to do some preliminary research. Freshly returned from two years as a Peace Corps volunteer in subtropical Paraguay, I dug out my long underwear and moved to Minneapolis.

### On the Origin of Biodiversity Research

But why go to the trouble of planting thousands of trees in various combinations of species, then take the time to make thousands of minute measurements of their every centimeter of growth and bout with an illness or pest? For me, as for a generation of researchers at Cedar Creek, experiments like FAB have emerged as a powerful approach for asking what role biodiversity, meaning the variety of life in a particular place or across the globe, might play in keeping the natural world working in the way



PHOTOS BY AUTHOR UNLESS NOTED



To understand whether more-biodiverse tree communities are more productive than less-biodiverse communities, Jake Grossman and colleagues at the University of Minnesota designed research plots with different combinations of tree species, including a two-species biculture (top left) and a five-species polyculture (top right). Grossman is pictured within one of the five-year-old polyculture plots.



Over the last thirty years—a time of increasing global concern about the consequences of global diversity loss—ecologists, as well as farmers, foresters, conservationists, economists, and policymakers, have begun to ask how we measure the extrinsic value of biodiversity.

we prefer it to do. To understand these experiments and the findings that come from them, though, we ought to take a step back and consider the history of what I would call the science of biodiversity.

When we speak of the environmental challenges of the current era, we can hardly avoid worrying about the erosion of biodiversity. While considerable disagreement persists over how biodiversity across the earth's diverse landscapes has changed over the last ten thousand years, a period in which humans have exerted a growing influence over the biosphere, a consensus has emerged that, at a global level, our planet has entered into a period of precipitous biodiversity loss (Butchart et al., 2010). A case in point: a recent report from a group of Danish and Swedish authors predicts that the loss of mammal diversity that has taken place since the end of the last Ice Age will take 2.5 billion years—two-thirds of the time during which there has been life on the planet—to be

replenished by natural evolutionary processes (Davis et al., 2018).

Yet such sobering statistics beg a second question: does biodiversity loss really matter? Of course, to many of us—including, I imagine, most readers of *Arnoldia*—the diversity of earth's species represents an irreplaceable gift. We sense a precious value, whether spiritual, emotional, or cultural, inherent to the diversity of life on earth. It is challenging, though, to convince others. And so, those of us who wish to protect biodiversity must ask ourselves whether there is an extrinsic value to diversity and, if so, how we can justify its conservation. The ecosystem services movement has answered this question by, at least to some extent, evaluating biodiversity in terms of dollars and cents. For instance, Canadian scholars Robin Naidoo and Wiktor Adamowicz (2006) estimate that the financial returns from visits by ecotourists to a Ugandan park rich in bird biodiversity far exceed the costs of maintaining the

park. This approach, however, doesn't fully capture a deeper question: does biodiversity support the vast array of ecosystem processes—or functions—that keep our biosphere working and, in doing so, sustain human life? In other words, are more-biodiverse ecosystems stronger and more resilient?

The history of this question is a long one, with origins prior to the formal elaboration of the concepts of biodiversity (by American conservation biologist Raymond F. Dasmann in 1968), of ecosystems (by English botanist Arthur Tansley in 1935), and of ecology itself (by German biologist Ernst Haeckel in 1866). Instead, the question of how biodiversity affects ecosystem function was posed first, at least within Western scientific discourse, by the founding mind of modern biology, Charles Darwin.

While Darwin is known foremost for his role in developing the concept of evolution by natural selection, his works also offer up a clairvoyant catalogue of research questions for contemporary biologists, one that we have yet to plumb fully some 130 years following his death. Through his lifetime, Darwin contributed important insights to the study of insect pollination; plant physiology; soil formation; the genetic origins of animal behavior; and the natural history of barnacles, coral reefs, and carnivorous plants; among other topics. Indeed, if we turn to Darwin's *On The Origin of Species*, first published in 1859, we find a claim that, though peripheral to the broader case for adaptive evolution, constitutes the origin of an important field of biodiversity research: "If a plot of ground be sown with one species of grass, and a similar plot be sown with several distinct genera of grasses, a greater number of plants and a greater weight of dry herbage can thus be raised." In this brief aside, Darwin argues that it was, at the time, well known that more-biodiverse systems—well, grasslands, at least—ought to be more productive than less-diverse ones.

Indeed, indigenous peoples, and especially farmers, have known for millennia that more-diverse ecosystems are more productive. For instance, the "three sisters" technique of growing diverse gardens of corn, beans, and squash developed in pre-Columbian central Mexico

and subsequently radiated throughout the Americas. Contemporary studies have demonstrated that this system of polyculture—or growing multiple crop species together—boosts yield compared to monocultures of constituent species (Zhang et al., 2014). Experimental assessment of traditional Chinese polycultures consisting of varying mixtures of wheat, corn, and soybeans have revealed similar trends (Zhang and Li, 2003). Such traditional techniques have continued to evolve to this day, resulting in, among other practices, the contemporary interest in "companion planting" among home gardeners and farmers. For instance, many gardeners in North America are familiar with the practice of planting African marigolds, mints, and other aromatics in their gardens, both for their own aesthetic or culinary uses and, allegedly, to deter pests. Despite this mountain of traditional knowledge and practical evidence, the empirical reality of the link between biodiversity and ecosystem function went without formal evaluation for over a century before slowly climbing back into the crosshairs of experimental biologists.

### An Ecological Reawakening

For much of the twentieth century, ecologists explored tantalizingly *around* the question of how biodiversity might shape ecosystems, often taking diversity to be a consequence of ecological conditions in a particular place rather than a cause of those same conditions (e.g., Connell and Orias, 1964). Eventually, as ecologists became more attuned to the ecological importance of stability—how much conditions in a forest or grassland might remain constant from season to season or year to year—they began to interrogate its relationship with biodiversity. At the center of this debate was the question of whether increasing the number of species in a community made that community more stable through beneficial effects such as symbiosis (Elton, 1958) or destabilized it by increasing the likelihood of, for instance, local numbers of a critical species crashing due to catastrophic disease (May, 1973).

In their review of the field, American ecologist David Tilman and colleagues (2014) trace a "reawakening" in the study of biodiversity

to incipient awareness of catastrophic global biodiversity loss during the 1980s, which culminated in a 1991 conference of ecologists in Bayreuth, Germany. The papers emerging from this meeting—which were ultimately collected in an edited volume, *Biodiversity and Ecosystem Function*, published in 1994—effectively launched the field of contemporary research on biodiversity-ecosystem functioning, otherwise known as BEF.

The observational findings and theories marshaled in the very early nineties, however, lacked the gold standard of ecological evidence: experimentation. This was not long in coming; two progenitor BEF experiments were already in development at the time of the Bayreuth Conference. At Imperial College London’s Centre for Population Biology, pilot testing of the futuristically named Ecotron facility began in 1991. The Ecotron, still operational today, consists of sixteen isolated rooms, each with its own light, temperature, and atmospheric control systems. Beginning in 1993, these rooms were assigned

to one of three biodiversity treatments. The lowest diversity rooms contained boxes of soil enriched with two common British plant species (e.g., sow thistle), three plant-eating invertebrates (e.g., aphids), one predator (e.g., an aphid predator), and three decomposer species (e.g., earthworms). A second set of rooms contained extra species of each class, and the most diverse rooms contained sixteen plants, five herbivores, two predators, and eight decomposers. Environmental conditions were held constant, and during a two-hundred-day period, an international team of ecologists monitored a variety of ecosystem functions: how much organisms in each room respired, how quickly organic matter decomposed, to what extent nutrients and water ran off, and how productive plants were in each room. In the end, more-diverse communities of plants and animals consumed more carbon dioxide (respired more) and grew more than less-diverse ones (Naeem et al., 1994). Diversity supercharged the functionality of ecosystems with more species.



JACOB MILLER, CEDAR CREEK ECOSYSTEM SCIENCE RESERVE [CC BY-SA 4.0]

Between 1994 and 1995, researchers at the Cedar Creek Ecosystem Science Reserve established the “Big Biodiversity” experiment, which was one of the first field-based experiments to provide empirical evidence about the relationship between biodiversity and ecosystem function.



In a complement to the highly controlled approach of the Ecotron, Tilman and collaborators at Cedar Creek, in Minnesota, were simultaneously figuring out how to ask BEF questions in the field. Based on an observational study in which more-diverse grassland plots showed greater stability in biomass production than less-diverse plots following an extreme drought (Downing and Tilman, 1994), they established what came to be known as Cedar Creek's "Little Biodiversity" experiment. In this seminal experiment, 147 plots, each nine meters square, were denuded of existing vegetation and seeded with one, two, four, six, eight, twelve, or twenty-four species of prairie plants. Echoing findings from the Ecotron, diverse plots (and especially any plot with twelve or twenty-four species) produced far more biomass than less-diverse plots. Furthermore, even after only two summers of growth, more-diverse plant communities in the Little Biodiversity experiment showed lower levels of soil nitrogen, suggesting that their roots more completely and

efficiently utilized available nutrients (Tilman et al., 1996).

These findings have been borne out repeatedly through the expanded "Big Biodiversity" experiment, planted between 1994 and 1995. These plots are larger, more numerous, and contain as many as thirty-two species (Tilman et al., 1997). The assigned diversity levels of most of its original plots are still maintained through diligent weeding by an army of fresh-faced interns hired by Cedar Creek's managers every summer. Now in its twenty-fifth year of growth, the Big Biodiversity experiment still serves as a critical platform for BEF research.

### A FABulous Journey

The Forests and Biodiversity (FAB) project, which I was recruited to work on in 2012, would mimic past grassland experiments insofar as plots were planted with varying species diversity. Yet, in many other ways, the forest project departed from its progenitors. From a logistical standpoint, rather than weighing out



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Researchers have expanded on the "Big Biodiversity" methods to explore the relationship between biodiversity and climate change at additional prairie plots.

and broadcasting consistent quantities of seed, we planted each tree on a grid (sixty-four trees per plot), where each tree was only half a meter from its nearest neighbors. Some plots were monocultures, consisting entirely of one of twelve species native to Minnesota: red (*Pinus resinosa*), jack (*P. banksiana*), or white pine (*P. strobus*); eastern red cedar (*Juniperus virginiana*); paper birch (*Betula papyrifera*); red (*Quercus rubra*), northern pin (*Q. ellipsoidalis*), bur (*Q. macrocarpa*), and white oak (*Q. alba*); basswood (*T. americana*); red maple (*Acer rubrum*); and box elder (*A. negundo*). Other plots (bicultures) contained thirty-two individuals of each of two species. Yet others were planted with five-species polycultures, and we threw the entire kitchen sink at a set of twelve-species plots. We started with two-year-old bareroot seedlings, planted in May of 2013, and over the next three years, we

replanted dead trees and weeded woody invaders so that each plot truly corresponded to its assigned tree-diversity treatment. By the time I finished my doctorate five years later, I could easily conceal myself within their densely interlocking boughs—at least in plots dominated by fast-growing pines and birches.

Beyond logistical considerations, the design of FAB also expanded on past research by making it possible for us to ask which dimensions of biodiversity might be most important to supporting ecological function. For instance, the vaunted boost in productivity associated with higher-diversity plots in the Big Biodiversity grassland study appears not to be entirely due to species richness—the number of species in a plot. Instead, it seems that some of the diversity-related boost really stemmed from functional diversity, the variability in morphological and physiological traits associated with



The Forests and Biodiversity (FAB) plots were established in 2013, with sixty-four seedlings planted in different combinations within each plot—totaling 140 plots and almost nine thousand trees.

species in a community. In particular, it appears that more-diverse plots provided opportunities for nitrogen-fixing legumes and drought-tolerant grasses to interact synergistically, boosting the productivity of their community by sharing resources. Legumes fertilized nearby grasses, which, because they differ in their growth form and resource needs, did not outcompete their beneficial neighbors (Fargione et al., 2007). In this sense, it can sometimes be difficult to determine whether it is more important to have a lot of species present or for those species present to have a diversity of functions.

While functional diversity can be difficult to measure, phylogenetic diversity—corresponding to the evolutionary distance between members of a community—offers a useful proxy. Closely related species tend to share traits and interact with their environment in similar ways, but such similarities are lost as

evolution progresses. Subtly then, FAB was designed so that bicultures—all plots with just two species—varied widely in their functional and phylogenetic diversity. Some two-species pairs, like white oak and bur oak, were both closely related and quite similar in their leaf shape, nutrient consumption, and responses to environmental stresses like drought and shade. Other pairs of relatively closely related species, like red maple and basswood, differed quite a bit in these traits. Yet other pairs, like basswood and eastern red cedar were both distantly related—remember that the split between flowering angiosperms like basswood and non-flowering gymnosperms like pine took place roughly three hundred million years ago—and functionally distinct. And finally, some pairs of distantly related species, like red oak and white pine, had relatively similar functional traits despite considerable evolutionary divergence.



The FAB experiment was designed so that the researchers could determine the role of functional and phylogenetic diversity in bolstering overall productivity. Here, the two-year-old plot in the foreground comprises red oak (*Quercus rubra*) and white pine (*Pinus strobus*).



The researchers wanted to understand the impact of biodiversity on herbivore vulnerability and disease susceptibility. Shown here (clockwise from upper left): red maple (*Acer rubrum*) leaves that have been spotted with anthracnose, an insect gall on a northern pin oak (*Quercus ellipsoidalis*), and insect herbivory on paper birch (*Betula papyrifera*), which Grossman evaluates with a plastic grid.

(This does happen from time to time: consider the functional similarities of bats and insect-eating birds.) The presence of these four types of bicultures in FAB allowed us to tease apart the role of functional and phylogenetic diversity in bolstering the ecological functionality of our newly planted “forest.”

We also wanted to understand whether diversity within a single species—genetic diversity—was as important as diversity among species. Though intraspecific diversity in other species is often invisible to humans, it has been well-documented that some plant traits vary just as much within a species as among related species. And copious evidence from epidemiology to conservation biology has shown that genetically diverse populations are more stable and better poised to cope with environmental stressors than homogenous ones. To assess this question, we designed and planted a second tree-diversity experiment. The eight-hundred-tree Biodiversity in Willows and Poplars (BiWaP) experiment included plots varying not just in species richness but also in genetic diversity. We took advantage of the fact that many species in the willow family (Salicaceae) can be easily propagated by cuttings to grow hundreds of identical clones of several quaking aspens (*Populus tremuloides*), white aspens (*P. alba*), and black willows (*Salix nigra*). We then planted these trees in the field such that some had as neighbors only genetic clones of themselves while others had as neighbors multiple genotypes each of several species. As such, the genetic diversity comprised another dimension of biodiversity whose role in supporting ecosystem function we planned to test.

### The Complex Role of Biodiversity

But what goes into measuring the functionality of an ecosystem—even a highly simplified and orderly biodiversity experiment? At the end of each summer at Cedar Creek, a team of interns—led by me for the first several years of the experiment—measured the stem diameter and height of each tree in FAB. Standardized equations then allowed for easy conversions of these measurements into estimates of trunk biomass. Encouragingly, trunk growth from year to year was higher for trees with more-diverse neighbors compared to those in mono-

culture (Grossman et al., 2017), although we did not see an effect of either species or genetic diversity in the BiWaP experiment (Grossman and Cavender-Bares, 2019). Paralleling findings from Big Biodiversity, Ecotron, and other grassland experiments around the world, our documentation of a productivity boost in more-diverse plots contributed to the growing consensus that this BEF phenomenon is not only confined to grasslands. Indeed, meta-analysis of tree growth data both from global forests (Liang et al., 2016) and managed or experimental systems (Zhang et al., 2012) corroborates our findings. This pattern is perhaps of special note given that monocultural plantations dominate production forestry the world over. Polycultures are harder to maintain and harvest; yet recent experimental findings like ours raise the question of whether increases in yield might compensate for higher costs of maintenance and harvesting.

Going beyond my initial focus on productivity, I wanted to determine how tree biodiversity in these systems related to herbivore vulnerability and disease susceptibility. Since we planted FAB inside a massive fenced enclosure, I knew I would never be able to study, for instance, the role of diversity in preventing deer browsing. But I could measure damage by insects and fungal pathogens, like red maple anthracnose. Over three years, I spent a month each autumn painstakingly measuring leaves of hundreds of plants with a translucent grid: I would estimate the original size of a given leaf and the amount of this tissue that had been chewed up by insects or infected by fungi. I also counted galls (small tumors formed by insect larvae) and leaf mines (burrows in leaves created by other larval feeders). Finally, I surveyed damage across the experiment stemming from two fungal diseases, each specialized to a single species in the FAB and BiWaP experiments.

The story that emerged from these measurements is a complicated one (Grossman and Cavender-Bares, 2019; Grossman et al., 2018). Having diverse neighbors frequently affected how vulnerable a given tree was to insect or disease damage, but the direction and strength of this relationship varied based on the species of tree and type of damage in question. For instance, having diverse neighbors reduced the



Two genetically distinct white aspen (*Populus alba*) are shown in the Biodiversity in Willows and Poplars (BiWaP) experiment in the fall of 2016. These aspen look alike when green, but one has attained fall color before the other.

likelihood that an oak would be attacked by leaf miners but increased the risk of leaf miner attack for birches! And yes, red maples with more conspecific neighbors were more likely to experience intense anthracnose infection. Fascinatingly, it also seemed that very nearby neighbors (within a one-meter radius of a focal tree) had a bigger impact on that tree's risk of pest attack or disease than did farther away neighbors. This spatial scale-dependence of vulnerability to damage was relatively consistent across tree and pest or disease identity. Generally, though, it appears that other factors, like climate, the presence of predators, and chance, might play a role equivalent to or greater than that of diversity in affecting the vulnerability of trees to pests and pathogens.

While pests and diseases constitute the most famous consumers of living plant tissue, an

entire food chain unfolds once leaves and roots are shed and begin to decompose, and I also wanted to know how tree diversity affected this microbial universe. Focusing on the rich, plant-dependent microbial life of rotting leaves and the soil below them, I was interested in using the FAB experiment as a platform to assess whether more-diverse tree communities might beget more active and diverse soil microbial communities. In both cases, we found subtle biodiversity effects. We found that the most important factor shaping the microbial community was the proportion of trees in a plot that were gymnosperms (pines and junipers) versus angiosperms (oaks, maples, birch, and basswood). Interestingly, pines, and especially junipers, created a hostile environment for bacteria, perhaps due to antimicrobial properties exuded by these species. Yet, since I collected

samples after only three years of tree growth, it is important to note that the microbial communities of the FAB experiment have probably not finished responding to the presence of different combinations of tree species. So, this story is only just beginning to unfold.

Across all these projects, I was surprised to find that species richness—long the standard metric of biodiversity for biologists—emerged as a still-critical predictor of ecosystem function. In study after study, the number of tree species in a plot predicted ecosystem function as well as or better than more abstruse dimensions of biodiversity. In some cases, the diversity of particular functional traits within plots emerged as an important predictor of particular functions. But, generally speaking, I saw little evidence that continuing to measure diversity in terms of species richness might obscure important connections between biodiversity and ecosystem function.



To examine the relationship between tree biodiversity and soil microbes, Grossman filled six hundred mesh litterbags with preweighed dried leaves varying in diversity that corresponded with the FAB plots. The weight and chemical composition of the litter provided a measurement of how decomposition had progressed over the course of four seasons.

### From Local to Global to Local

Encouragingly, my findings—or anyone else’s—from the tree-diversity experiments at Cedar Creek don’t have to be the final word on BEF relationships in forests. On establishment, FAB was inducted into TreeDivNet, a network of twenty-five tree-diversity experiments distributed across the globe. The 1.1 million trees making up TreeDivNet have been planted in sites on six continents and range from boreal to Mediterranean and tropical climates. Though the design of these experiments varies from site to site, each includes some experimental manipulation of tree diversity, as in FAB. At most sites, investigators have made periodic measurements of tree survival and growth, and of damage inflicted upon trees by pests and pathogens (Grossman et al., 2018b). This riot of findings has already contributed to our understanding of how changes in tree biodiversity are likely to affect the way that forests function.

And the BEF framework, though developed through experimental work, has now given credence to the idea that biodiversity changes the way ecosystems function. This premise has now been borne out through observational studies of non-experimental (e.g. naturally occurring) ecosystems (van der Plas, 2019).

I argue that this holistic view on the value of biodiversity needs to inform the way that we, as managers and users of natural resources, make local decisions. Though large-scale, systemic change will be required for humans to fully address the current biodiversity crisis, such change can be instigated and incubated on the smallest scales. For urbanites, this might mean turning more and more of our marginal spaces into biodiversity havens. Opportunities of this nature include pollinator-friendly prairie



Based on the initial results of the FAB experiment, Grossman argues that we should work as individuals and communities to promote biodiversity—not simply within designated natural areas but in yards, parks, and through consumer decisions.

yards, urban gardens and food forests, and even no-mow zones such as those currently being put into place at the Arnold Arboretum. Communities can also make choices in our roles as consumers, advocating for less chemically intensive agriculture that protects the incidental biodiversity concomitant with farming prior to the widespread adoption of blanket glyphosate-spraying on row crops.

For me, working mere meters away from the Big Biodiversity plots and playing my own part in the establishment of new biodiversity experiments has also highlighted the importance of humility. Empirical evidence shows us that biodiversity plays critical, complex roles in mediating the way ecosystems function. Yet we are often not nor, I would argue, will we ever be able to fully understand and thus manage these BEF dynamics. Instead of assuming that we can figure out how to optimize global biodiversity to provide for the ecosystem functions that we

want, it might make more sense to take a precautionary approach. In doing so, we should be highly conservative in both senses of the word, protecting biodiversity far more stringently than we think is necessary to sustain critical ecological functioning, especially in the face of ongoing challenges such as climate change. We would be foolish, I believe, to fail to conserve global biodiversity, which BEF research has shown us to be valuable beyond measure.

#### Acknowledgements

The author wishes to acknowledge his doctoral advisor, Jeannine Cavender-Bares, as well as the other co-PIs of the Forests and Biodiversity (FAB) experiment: Sarah Hobbie, Rebecca Montgomery, and Peter Reich. Work described here also stems from collaborations with Peter Kennedy, Jess Gutknecht, and several undergraduate collaborators and interns. Susan Barrott offered helpful feedback on an early draft of this article. Finally, the author is incredibly grateful for the opportunity to work at the Cedar Creek LTER site and to collaborate with TreeDivNet partners.



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Jake J. Grossman is a Putnam Fellow at the Arnold Arboretum.

## A Medlar by Any Other Name

*Tiffany Enzenbacher*

This is an account of a meddling medlar that placed an inquisitive thorn in the side of Jane Ellenbogen Stern, an environmentalist from Pine Bluff, Arkansas. In 1969, Stern was leading a bird-monitoring project at a small remnant of tallgrass prairie and bottomland woods about fifty miles northeast of her home—a natural area now preserved within an expanse of rice fields and aquaculture ponds. She noticed an unusual plant that resembled a hawthorn (*Crataegus*), only shrubbier, which was covered in white flowers. She collected a branch sample and notified regional biologists, including Edwin Burnell Smith, the curator of the University of Arkansas Herbarium. Stern's discovery triggered the interest of an entourage of plant professionals, who spent nearly a half century attempting to provide a proper identification and name. The plant is now recognized as an unusual naturally occurring hybrid and is known as Stern's medlar ( $\times$ *Crataemespilus canescens*).

In October 2018, Plant Growth Facilities Manager Kea Woodruff and I eagerly followed Stern's trail to gather propagules from her rare find, during our Arnold Arboretum plant collecting expedition to Arkansas and Oklahoma, which we nicknamed the A-OK expedition. The expedition was part of the Arboretum's Campaign for the Living Collections, a ten-year initiative to collect nearly four hundred taxa from around the globe. We reached out to staff at the Arkansas Natural Heritage Commission in the summer of 2018 to prepare for our upcoming expedition. Theo Witsell, a botanist and ecologist at the commission, explained that Stern's medlar is protected, and as such, we would not be permitted to harvest propagules from the only known wild population growing at the Konecny Grove Natural Area, located in Prairie County. Witsell, however, connected us to his friend Tom Frothingham, a former commission staff member, now of

the Little Rock Zoo. Frothingham had obtained a Stern's medlar from the Natural Resources Conservation Service's Plant Materials Center in Booneville, Arkansas, a decade prior. That plant, in turn, had been propagated from the Konecny Grove. Frothingham wrote to Woodruff that, in addition to having a large specimen growing in his yard, he had already potted up a division. "You'd be welcome to it," he wrote, and he also volunteered that we could dig additional divisions.

Woodruff and I planned to be near Little Rock during the initial two days of our nine-day expedition, so we arranged to visit Frothingham directly after our six-hour flight (with layover) on October 1. We obtained our rental car and drove forty-five minutes in the unanticipated afternoon heat, starting in the bustling city of Little Rock and continuing through the serene and rural landscapes northwest of the city. We then zeroed in on his address and proceeded to the end of the wooded side road. "Mine is the second driveway, with the mailboxes," Frothingham had instructed. We found our spot.

### An Unexpected Discovery

Born in Little Rock, in 1918, Jane Ellenbogen Stern moved to the suburb of Pine Bluff at about age thirty, with her husband, Howard Stern, and their two children, Arthur and Ellen. Stern developed a long-standing love of the outdoors through birdwatching, which she became passionate about while Arthur was obtaining his Boy Scout nature badge. As her hobby advanced, she became a charter member of the Jefferson County Audubon Society. Coincidentally, Stern was searching for a small bird, the Traill's flycatcher (*Empidonax traillii*), when she first encountered the medlar. The Traill's flycatcher is now more commonly known as the willow flycatcher. It had been previously documented in the low, moist tallgrass prairies of eastern Arkansas, and Stern was directed to



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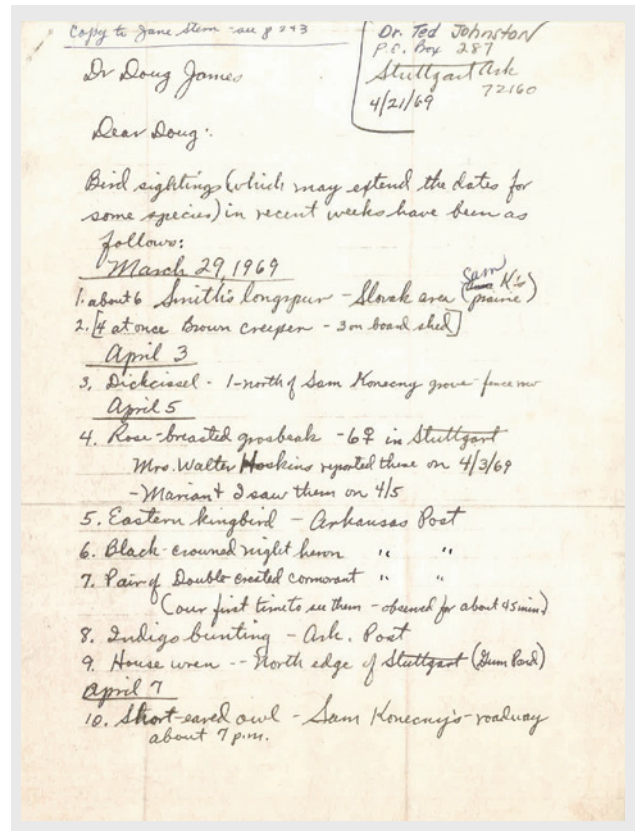


In 1969, Jane Ellenbogen Stern observed an enigmatic shrub in an Arkansas woodland where she was searching for the Traill's flycatcher (*Empidonax traillii*). Her curiosity about the shrub aroused longstanding taxonomic research. The shrub is now known as Stern's medlar (*×Crataepilus canescens*).

the Konecny Prairie and Grove—then unnamed and unprotected—which was one of the few remnant prairies remaining in the region. In 1951, a nesting study had documented flycatchers at the site and found that out of the fifteen nests that were discovered, thirteen were in presumed hawthorn trees. One can speculate that the “hawthorns” may have been an initial sighting of Stern’s medlar.

In the summer of 1968, Stern first visited the property, searching for the flycatcher with Raymond McMaster, the manager of the White River National Wildlife Refuge, and Thomas Foti, who would later be appointed senior ecologist for the Arkansas Natural Heritage Commission. Sam Konecny, the owner of the property, showed them around. “We piled into Mr. Konecny’s new car and roared off, helter skelter, across the farm, stopping occasionally to leap out and pull a ‘weed’ while battling off mosquitos and sweltering in the heat,” Foti later wrote in the *Ozark Society Bulletin*. The remnant landscape was divided into two sections— a seventy-one-acre rectangle of tall-grass prairie, which had been preserved as a hayfield (Konecny Prairie), and a twenty-two-acre grove of swampy woods (Konecny Grove), known as *slash timber*, which included over-story species like persimmon (*Diospyros virginiana*), green ash (*Fraxinus pennsylvanica*), and honey locust (*Gleditsia triacanthos*). Along the edge of this woodland were the hawthorn-like thickets in which the flycatchers nested.

The following winter, Stern was contacted by Douglas James, a professor of zoology at the University of Arkansas, who asked her to organize an effort to determine when the Traill’s flycatcher arrived at the grove. The reason for the effort was due to uncertainty about flycatcher taxonomy. Ornithologists increasingly believed the Traill’s flycatcher should be treated as two species, rather than one, but they were uncertain which species deserved the original scientific name, which was based on a bird John James Audubon had observed in Arkansas. The song is considered the best way of distinguishing between the two species. The population that was already known to breed in Arkansas sang “fitz-bew,” but the popula-



Stern organized a group of volunteer bird-watchers in the spring of 1969. The volunteers visited the Konecny Prairie and Grove Natural Area—then unofficially named—to monitor the arrival of the Traill’s flycatcher.

tion that sang “wee-be-o” had previously not been reported to nest in the state. Due to Stern’s experience and proximity to the site, she was the ideal individual to lead the effort. She was eager for the challenge. “We will do our best to cover the Konecny place,” she wrote to James on February 26, 1969. “If the fiz-bew one hollers as loud as the spit-chee and che-bek and wee-bee-o, I don’t see how anyone could miss him.”

Several months later, the “Traill’s Flycatcher Vigil” commenced. Stern assembled twenty-seven birdwatchers to take turns observing the grove daily, beginning March 29, to determine when the flycatchers arrived to roost. On May 6, Stern was on the lookout with Jewel Herring, another birder from Pine Bluff, when they heard one of the flycatchers singing, and the song was “fitz-bew.” On July 7, Foti and Stern returned and found an empty nest, assumed to



"Originally he had it perched on a honey locust twig," zoologist Douglas James wrote to Stern, describing an illustration of the Traill's flycatcher. "I returned it saying good grief it's the hawthorn that determines the bird's presence on the Grand Prairie." James, however, was uncertain whether the illustration matched the unusual hawthorn-like shrub Stern had observed, and he requested her confirmation.

be a Traill's flycatcher's, burrowed in a branch of a hawthorn-like shrub. Stern observed that the plant did not appear like other hawthorn species in the grove, and so she sent a sample to Edwin Burnell Smith, the curator of the University of Arkansas Herbarium. Stern would ignite a decades long process of pursuing an accurate name for the plant, even while the confusion around the flycatcher taxonomy was resolved. The "wee-be-o" species, commonly known as the alder flycatcher, was given the official name of *Empidonax alnorum* in 1973.

### The Search for a Name

On July 10, 1969, Smith wrote to Stern with an initial classification of the mystery plant. "I must say, [this is one] of the most difficult plants I've received for identification," Smith wrote. "The small tree is a type of *Crataegus*,

'Hawthorn,' in the Rose Family. The genus *Crataegus* is cursed with a very complex taxonomy which makes the individual species quite difficult to identify. The one you sent in is probably (and I emphasize probably) *Crataegus engelmannii*." As Smith was unsure of his initial naming, he solicited an additional sample and offered another stab—hillside hawthorn (*C. collina*). Smith even mailed a herbarium sheet to the Arnold Arboretum for assistance, likely due to the reputation of Charles Sprague Sargent, the Arboretum's founding director, as an expert on hawthorn taxonomy. Director Richard Howard responded to Smith on October 23 with a complicated assessment: it appeared to be a "mixed collection." The flowering stems looked like red chokeberry (*Aronia arbutifolia*), and Howard agreed that the fruiting stems (obtained that fall) resembled *C. collina*. "Unhappily,"

Howard wrote, “the specimens lack the young leaves and flowers which are equally critical for accurate determination.”

Correct identification was proving to be exceedingly difficult, and the only sense that could be made was that Stern was harvesting samples from multiple plants. However, in a letter to Stern on June 8, 1970, Smith suggested an alternate explanation for the “enigmatic ‘Haw’”—the possibility of “a strange hybrid of some kind.” But then, after studying additional collections, Smith was relieved to finally provide the name of dotted hawthorn (*Crataegus punctata*). Dotted hawthorn is very similar to *C. collina*, and is occasionally considered the same species. “Well, finally (!) I am able to report to you with great relief that I have been able to determine the frustrating ‘haw,’ at least to my satisfaction,” Smith wrote to Stern on October 15. “It turns out that the plants are not a new species or a hybrid, which is kind of sad after all the trouble we have both gone to.”

Later, upon reexamination of specimens for the *Vascular Flora of the Southeastern United States* in the 1980s, taxonomists rejected Stern’s medlar as a hawthorn. Although the flower and fruit characteristics are similar to hawthorns, as is the overall plant height, hawthorn leaves are shallowly to deeply lobed, unlike the simple, subentire leaves of Stern’s medlar. Also, hawthorns typically grow as small trees with one large stem, occasionally producing suckers, while Stern’s medlar is a large shrub with equal-diameter shoots. Taxonomist James B. Phipps, of the University of Western Ontario, was intrigued by the anomalous specimens, and contacted Smith in 1988. Phipps had been researching hawthorn taxonomy since the 1970s, and years later, he would author the hawthorn section of the *Flora of North America*. Smith relayed the news to Marie Locke of Pine Bluff in a letter dated July 13, 1988. “I recently heard some interesting news from a botanist in Canada: He plans to name a new species (and new genus, for Arkansas) in the Rose family from collections made several years ago by Jane Stern,” Smith wrote. “I think that this is the plant I had such difficulty identifying—remember it? It had two strikingly different kinds of leaves on it.”

Stern was later in contact with Phipps herself. She agreed to collect additional herbarium specimens in mid-September, when the fruit would be ripe, and she also promised to arrange for Phipps to visit the Konecny property himself. On October 21, a group of Arkansans, including Stern, escorted Phipps to the coveted shrubs. Phipps ultimately published a new name for the plant in 1990: *Mespilus canescens*. He recognized that although Stern’s plants resembled hawthorns, other characteristics uniquely resembled common medlar (*Mespilus germanica*), the singular species within that genus, which is native to southeastern Europe and Iran. Among other things, it shared a multi-stemmed habit; distinctive leaf venation, with secondary veins curving toward the margins; and fine, white (canescent) hairs on the inflorescence. While even this comparison didn’t match completely—the common medlar, for instance, produces larger brown fruit, unlike the red fruit of Stern’s discovery—Phipps suggested that a hybrid origin seemed unlikely, given the lack of suitable parent species. “The most likely explanation of the status of *M. canescens* is that it is an ancient relic,” Phipps wrote. “One should always be cautious in describing a new species from such limited material (all the cited collections come from the same locality), but *M. canescens* is so distinct from all other native American Maloideae that there can be no doubt that it is not a previously described North American member of this subfamily.” In the same paper, the shrub was aptly given the common name of Stern’s medlar.

But the story was not over. Almost twenty years later, Eugenia Y. Y. Lo and colleagues further investigated the relationship of Stern’s medlar to the common Eurasian medlar. Through DNA amplification and phylogenetic analyses of over ninety Rosaceous species, including hawthorn, chokeberry, crabapple (*Malus*), medlar, and serviceberry (*Amelanchier*), they concluded that although Stern’s medlar shares a common ancestor with the Eurasian medlar, it is more closely related to blueberry hawthorn (*Crataegus brachyacantha*)—a species whose range is centered in Louisiana, eastern Texas, and southern Arkansas. Their analyses, published in 2007, suggested a hybrid origin of Stern’s med-



THE FAYETTEVILLE HILTON

Phone:  
(501) 534-8281

2404 West 47th Avenue  
Pine Bluff, Arkansas 71603  
16 August 1988

Dear Dr. Phipps:

I am attending a meeting in Fayetteville and had the opportunity to visit with Dr. Ed Smith this morning. We discussed your study of the trees in the Konecny Grove which first attracted my attention in 1969.

The enclosed slides are duplicates of originals made by my husband. One was taken from the relic Konecny Prairie, looking across a wet field toward the grove (April 1969); the other is a photograph of one of the trees in bloom (May 1970).

The Konecny Grove is the last known nesting site of Traylor's Flycatcher in Arkansas. This is a "special bird" in our state, because Audubon first collected, named, and painted this flycatcher on the Grand Prairie in Arkansas. The bird is not known to be nesting in the state now.

The Arkansas Natural Heritage Commission, a state agency, purchased a perpetual easement on 25 acres of the prairie and the 18-acre grove from Mr. and Mrs. Sam Konecny several years ago. Thus, the grove is preserved.

70 North East Street • Fayetteville, Arkansas 72701 • 501/442-5555



as from: Dept. of Rand Sci  
University of Western Ontario  
LONDON, Ontario  
N6A 5B7.  
24-x-1988

Mr. Thomas L. Felt,  
Arkansas Natural Heritage Commission,  
LITTLE ROCK,  
Ark. 72201

Dear Tom.

It was good meeting you

Bert, Jane and Marie last Friday. What an exciting day!

I would much appreciate it if you could center certain notes by return since my article describing the new species is ready to go apart from that aspect.

Points to note.

exact locality coordinates

exact altitude.

Your views on where the *Mespilus* spot is the lowest in the locality.

a paragraph or so explaining your general view of the ecology of Grand Prairie.

I shall, of course, properly acknowledge their contribute.

Best wishes,

Sincerely,

Jim Phipps

HOLIDAY INN/ST. JOSEPH  
100 Main Street • St. Joseph, Michigan 49085 • 616/663-7541



The UNIVERSITY of WESTERN ONTARIO

Department of Plant Sciences

July 12, 1989

Mrs. Jane E. Stern  
2404 West 47th Ave.  
Pine Bluff, Arkansas 71603  
U.S.A.

Dear Mrs. Stern:

This is a circular letter to my friends and colleagues involved in the discovery of a new species of *Mespilus* in Arkansas. A manuscript describing and discussing the new species has been accepted for publication in *Systematic Bot.*, probably the first issue of 1990.

Meanwhile, I would very much appreciate it if you do not give any circulation to the suggested specific name prior to publication. It is, however, alright to call the plant a new species of *Mespilus*.

With best wishes.

Yours sincerely,

Jim Phipps  
J. B. Phipps  
Professor

JBP/st

Biological-Geological Sciences Building • 1151 Richmond Street N. • London, Ontario, Canada • N6A 5B7  
Telephone: (519) 673-2111 • Fax: (519) 961-3292



ARKANSAS NATURAL HERITAGE COMMISSION

THE HERITAGE CENTER, SUITE 200  
225 EAST MARKHAM  
LITTLE ROCK, ARKANSAS 72201  
Phone: (501) 371-1706

Harold K. Grimmatt  
Director



Bill Clinton  
Governor

May 31, 1989

COPY

Dr. James Phipps  
Department of Plant Sciences  
University of Western Ontario  
London, Ontario N6A 5B7  
CANADA

Dear Dr. Phipps:

Though I have not yet had an opportunity to meet you, I have followed with great interest the reports from Jane Stern and from members of my staff concerning your determination of plant specimens that she and others collected years ago from Konecny Grove. Developments following that determination have heightened my interest further, and I am grateful to you for making sense of a problem that had confounded others. (You even relocated the plant when no one else could find it, and we are grateful for that too!) Accordingly, I was pleased to ask Tom Felt and Bert Pittman to accompany you on your visit to Konecny Grove last fall and to have Mina Marsh and Bill Shepherd accompany you in your most recent visit.

Members of the Natural Heritage Commission staff hold permits for collecting scientific specimens in areas under the Commission's management. All others wishing to collect specimens for study from such an area also must have permits issued by me in the Commission's name. The presence and supervision of members of my staff during each of your visits to Konecny Grove thus far have meant that the specimens you took with you after those visits were removed from the preserve under the personal permits of staff members and therefore in accordance with Arkansas law and agency regulations.

It is my understanding that either you or Mr. O'Kennon may wish to visit Konecny Grove again later this year. For this reason I am enclosing a form for applying for a collecting permit with the suggestion that you fill the permit out and submit it in advance of your next visit. If you know of others who may wish to collect material from Konecny Grove, please advise them also that permits are required and that permit applications are

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In 1988, taxonomist James B. Phipps visited Konecny Grove with Stern and other local environmentalists. Archival correspondence revealed the back-and-forth excitement, with a letter from Stern to Phipps (top left), coordinating Phipps's visit, and a letter from Harold Grimmatt, the director of the Arkansas Natural Heritage Commission (bottom right), providing a collecting permit for a follow-up visit. Phipps proposed that the plant was a new species of medlar, which he named *Mespilus canescens*.

lar, with blueberry hawthorn as the maternal parent. Because the fruit of blueberry hawthorn is fittingly blue, however, the authors acknowledged that another native red-fruited hawthorn (or even an ancient, now extinct medlar species) may have been involved in past hybridization.

The authors surmised that common medlar and blueberry hawthorn may have hybridized if they were cultivated within range of one another. Hawthorns are known to hybridize, and the authors pointed to literature confirming that common medlar was, indeed, cultivated in an agricultural station in Louisiana as far back as 1893. Furthermore, Slovak, the small town two miles north of Konecny Prairie and Grove, was home to at least fifty families of Eastern European heritage by 1909. Immigration to Arkansas in the mid- to late-nineteenth century was encouraged by advertising, legisla-

tion, and aid from government agencies, private land corporations, and the railroad industry. Perhaps the families in Slovak had brought along plants or seeds of a favorite fruit? Common medlar has been cultivated as far back as the ancient Romans.

Phipps accounted for these new conclusions, and in 2017, he reclassified Stern's medlar as *×Crataemespilus canescens*. The *×Crataemespilus* nothogenus was created in 1899 to accommodate an assumed hybrid, *×C. grandiflora*, originating from midland hawthorn (*Crataegus laevigata*) and common medlar, that was also initially described as medlar. In 1914, a second hybrid was discovered: *×C. gillottii*, an intermediate between English hawthorn (*Crataegus monogyna*) and common medlar. Now Stern's medlar has joined the ranks as the third member of this hybrid genus.

WONDERLANE, CC BY 2.0



Common medlar (*Mespilus germanica*) is harvested while unripe and allowed to blet (soften). After storing in a cool dark place until squishy and aromatic, the fruits are ready for direct consumption or for use in jellies or wine.





Through genetic analyses, researchers have now determined that Stern's medlar ( $\times$ *Crataemespilus canescens*, right) is a hybrid between the common medlar and the blueberry hawthorn (*Crataegus brachyacantha*).

### An Unconventional Collection

The taxonomic and conservation status of the Stern's medlar initially placed this plant on the radar of the A-OK expedition. When Woodruff and I pulled into the driveway at Tom Frothingham's property, northwest of Little Rock, we were greeted by him and two colleagues, Lauren Goldstein and Connor Livingston. Woodruff and I could hardly contain ourselves as Frothingham led us from the driveway to where the specimen was planted, out in full sun, between the shed and house. The shrub was vigorous—it was nearly fifteen feet tall—and I thought its habit resembled that of a serviceberry or large rose (*Rosa*)—upright with slightly cascading branches. After months preparing for the A-OK expedition and a day's worth of travel, it was surreal that our target was in plain sight. To add to our excitement, the medlar was fruiting!

Frothingham and I alternated ascending the ladder to gather the cherry-sized pomes, which were relatively sparse. After we collected a handful, Frothingham insisted that the whole group sample one, to which we all curiously obliged. The shiny red fruit was surprisingly sweet, and Woodruff and I saved all the seed from the consumed fruit to send back to the Arboretum's Dana Greenhouse for propaga-

tion. I then slowly walked around the specimen and found an appropriate division to dig. Frothingham lent me a trowel for the job. After the division was successfully dug and bagged, Frothingham then led us to the promised potted plant, harvested as a division several years prior, at the front of his house. We chatted about seed propagation and the rich history of the plant for a while, before Woodruff and I loaded up our bounty. We repeatedly thanked our collaborator for his generosity, and we backed out of his driveway, delighted about how successful the first day of the expedition had been.

### Preserving an Unusual Hybrid

Not only is Stern's medlar a rare hybrid but it is visually appealing to boot. In September 1989, Stern wrote to Harold Grimmett, then the director of the Arkansas Natural Heritage Commission, urging him to request that Phipps withhold the location of the Stern's medlar in his 1990 paper. "The plant is extremely attractive in appearance and can be expected to be aggressively sought by the horticultural trade," Stern wrote. Phipps, in response, suggested that the commercial threat seemed "highly unlikely" and noted that the location was already well-documented with herbarium spec-



The author harvests a division from the Stern's medlar (*Crataegospilus canescens*) at Tom Frothingham's property on the outskirts of Little Rock, Arkansas. The division was bagged and mailed for next-day delivery to the Arnold Arboretum's Dana Greenhouse.

imens. Nonetheless, Phipps agreed with Stern's assessment of the plant's beauty. In his book *Hawthorns and Medlars*, published in 2003, Phipps states that "Stern's medlar is arguably the most exquisite ornamental treated in this book." Its exfoliating bark has hues of cream and olive, and he describes the plants as "a fountain of white flowers." I personally like to imagine that this attractive nature is the reason that Stern initially took such keen interest in the plant—launching a pursuit that continued well beyond the Traill's flycatcher.

In fact, the medlar has proved to be a conservation boon for Konecny Prairie and Grove. From the beginning, Stern recognized the significance of this site as the only remaining Traill's flycatcher's nesting habitat in eastern Arkansas and as one of the few tallgrass prairie remnants that escaped plowing in the region. Stern awakened a movement to preserve the prairie and grove, and in February 1976, the grove became the first conservation easement purchased by the Arkansas Natural Heritage Commission. This was a victory for so many, and on May 14, 1977, a gathering was held on the Konecny land to celebrate, which coincided with the Traill's flycatcher arrival. A decade later, however, the

flycatcher migrated elsewhere to nest, and the landowner told Stern that he was interested in reclaiming the property. "So many things connect with the Konecny prairie, the grove, the bird, and the Tree," Stern wrote to Phipps on April 24, 1989. "Bless the bird for hanging on long enough for the Commission to purchase the easement on the grove ... He would have plowed some or all of it ... but you and The Tree have put an end to that idea."

Stern's medlar is now graded as critically endangered, which means it has an extremely high risk of extinction in the wild. Only twenty-four individuals are known to exist, and because Stern's medlar is triploid

(having three sets of chromosomes), it is likely sterile. This means the seeds we collected from Frothingham's specimen will be difficult (if not impossible) to germinate. As hawthorns have been found to produce seed through apomixis (asexual seed formation), however, hope for potential seedlings is well-founded. Regardless, the clonal division that we harvested, as well as the potted plant that Frothingham provided, are thriving at the Dana Greenhouse production facility. In two to three years, they will be added to the Arboretum's living collections to join the other 179 taxa in our landscape that are of conservation concern. I am proud to have brought Stern's medlar to the Arboretum with Woodruff, to have the opportunity to learn of Stern's tireless conservation efforts, and to have experienced, first-hand, what Phipps devoted his entire career to—the complicated identification of hawthorns, medlars, and their hybrids.

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All archival correspondence and images were provided courtesy of the Jane E. Stern Collection, University of Central Arkansas Archives (M90-02, Series II, Sub-Series IV, Box 1, Files 12–17), Torreyson Library, University of Central Arkansas, Conway, Arkansas.



TIFFANY ENZENBACHER

**Tom Frothingham (at left) encouraged the collectors to sample fruit of the Stern's medlar (*×Crataemespilus canescens*). His colleagues Lauren Goldstein and Connor Livingston are pictured, along with Kea Woodruff (right).**

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## A Botanist in Borneo: Understanding Patterns in the Forested Landscape

*Peter Ashton*

When I began as a field researcher on the island of Borneo, in 1957, little was known about the distribution of the inland rainforests. The forests are incredibly diverse and are dominated by large overstory trees in the dipterocarp family (Dipterocarpaceae), which often tower more than two hundred feet above the forest floor. While variation in the forests was evident, it appeared as chaotic and random as the colored specks in a children's kaleidoscope. Odoardo Beccari, a Florentine botanist who spent two years in northern Borneo in the 1860s, had provided the first confirmation that specialized lowland habitats, including peat swamps and sandy exposures, bear distinct forest types, but neither he nor his successors until my time had recognized any correlation between habitat characteristics and forest structure on the yellow-to-red tropical soils that characterize much of the inlands.

Yet as I tramped along Bukit Biang—a long ridge in eastern Brunei—I was surprised to see dipterocarp species I had come to know on the sandy coastal hills of western Brunei, and I began to sense that these forests were divided into two distinct communities—one on sandy soils, the other on loams. These communities would reappear in different localities as I extended my explorations throughout Brunei. I came to anticipate the flora by the distinctive sounds of the cicadas that inhabited each and by the smells of the forest, which I later recognized all over Borneo and even Peninsular Malaysia—the mellow fruitfulness and fermentation from the loams or the resinous aroma from the peaty humus covering the sandy soils. Those forest smells returned to me decades later, after I had assumed the directorship of the Arnold Arboretum and first trekked into the loamy bottomlands in the Connecticut River Valley and the sandy pine barrens of New Jersey and Cape Cod. It was only then that I came to understand that these habitat patterns in the forested land-

scapes of mild, moist climates are universal. Yet, in Brunei, I began to sense that individual species within these rainforest communities were often more highly habitat specific than I had ever seen in temperate forests.

After twenty-eight intensive months of fieldwork, camping, and longhouse life in Brunei, I made the case that differentiating between these inland forest types—known collectively as mixed dipterocarp forests (or MDFs)—could have important implications for timber inventories and silviculture. At that time, timber was only cut for local use in northwestern Borneo, although research towards sustainable harvesting was advanced in Peninsular Malaysia. Even there, as elsewhere in the tropics, distinct types of lowland MDFs had yet to be defined. The forestry department gave me clearance and funding to lay out sets of plots to test my hypothesis. For foresters, understanding the distribution of these tree communities could guide sustainable harvesting practices. But knowledge of tree species preferences and distributions would also provide the means of mapping biodiversity, locating centers of richness and endemism, and identifying and demarcating priorities for conservation—a first for the tropics.

Work on the research plots commenced in 1959. But first, I briefly returned to England for my own wedding. My wife, Mary, was to become the perfect companion for a life of jungle exploration. She had been born and spent her first years in Sri Lanka, where her family had been in trade and tea for over a century. She would join my hectic field life at once, and we only had a few days in town before departing for a long stay in the *hulu* (or upriver country). I wanted to document and compare the two main forms of MDFs that I had recognized in my explorations. I decided to compare two seemingly contrasting sites—one on the sandy coastal hills of Andulau, in western Brunei, and the other on



ALL PHOTOS BY AUTHOR FROM ARNOLD ARBORETUM ARCHIVES



MAP BY PETER ASHTON, ARNOLD ARBORETUM, AND GIS COMMUNITY

Peter Ashton's research identified distribution patterns in the hyperdiverse inland rainforests of northern Borneo, collectively known as mixed dipterocarp forests (MDFs). His research ranged between sites like the Andulau hills, in western Brunei, where forests occur on sandy soils (above left), and Carapa Pila, in central Sarawak, which supports large trees like *Shorea mujongensis* (above right) on loam soils. Ashton's research sites are mapped, along with his primary expedition routes (green) and his shorter secondary routes (blue) between 1963 and 1966.



After their marriage in 1959, Mary Ashton joined Peter in the field. Here, Mary is shown with longtime field assistant Asah anak Unyong at Kuala Belalong, a research site on loam soils in eastern Brunei. Asah collects Borneo fiddleheads (*Diplazium esculentum*) for supper at the same site (below), while another collector poses a flowering branch of *Dillenia excelsa* (Dilleniaceae), a large tree observed on the sandier soils of the Andulau hills.

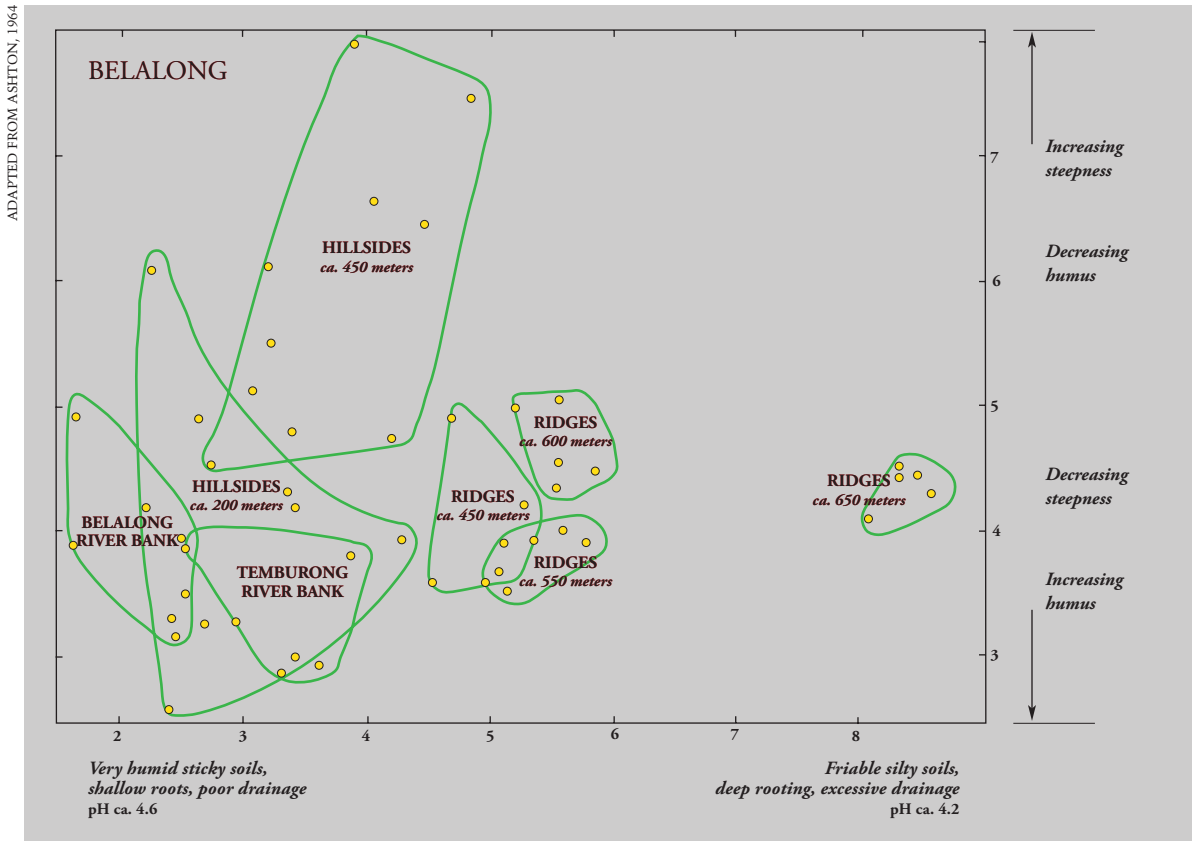
steep clay-loam ridges near Kuala Belalong, in eastern Brunei. I sensed that topography was an important feature, causing local variation in the form, composition, and possibly growth rates of the forests, so at each site, I planned for fifty one-acre plots that covered the complete topographic spectrum (including ridgetops, slopes, valley bottoms, and riverbanks). Each one-acre plot represented a homogeneous topography, and the number and size of the plots were visually estimated to be representative of the forest variation at each site. This method had already become a standard procedure for ecologists studying temperate grasslands, but it was a first for biodiverse tropical forests and, indeed, for any forests known to me. All trees above one-foot circumference were to be documented. We measured the trunk girth and estimated the height for each. We also identified each as morphologically different species by means of fallen leaves and local Iban names. But I rarely knew the scientific name for these visually distinct trees.

Life eventually settled down to calm and peace at our first location, Kuala Belalong. It was one of the most beautiful places in which we ever camped, with the rush of water over the rapids in our ears as we lived and slept. While I scrambled daily up the muddy slopes, locating plot positions, surveying, and initiating documentation with the teams, Mary would take her typewriter to the shingle beach, preparing herbarium labels and editing field notes. She saw the wildlife that I rarely or never experienced: a pair of small-clawed otters (*Aonyx cinerea*) that came to join her, squeaking and gamboling in the shallow water nearby; the extraordinary and terrifying pack of Bornean bearded pigs (*Sus barbatus*), thundering headlong down the steep hillside opposite, then splashing across a rapid upriver, on migration in search of fruiting trees; and a macaque (*Macaca fascicularis*) who discovered our food store and made off with some delicacies.

Our work in Andulau began the following year, in 1960, and was carried out smoothly, given our growing experience and the gentle landscape. I continued to conduct multi-week collecting expeditions until I was satisfied that the diversity of landscapes and forests in Brunei had been examined.

When we returned to the University of Cambridge, after the 1960 field season, I brought back two suitcases of fallen leaves and twenty notebooks—all needed to complete my doctoral dissertation. I had presorted the leaves into nearly eight hundred morphospecies, which were recognizable entities that were mostly (dipterocarps excepted) lacking a formal scientific name and therefore named using indigenous nomenclature. They were to be named with the help of taxonomists at the University of Leiden and the Royal Botanic Gardens, Kew, supported wherever possible by our herbarium-quality specimens in flower or fruit. This groundwork provided the basis for a *Checklist of Brunei Trees*, which I co-authored with Hasan bin Pukul, the ascendant curator of the Brunei Herbarium, who had been a mentor on tree identification from the time he joined our team. He was an experienced informant on traditional plant uses and became a good friend who involved Mary and me in his family activities, including marriages and births (and he even got us invited to a royal circumcision).

Our combined efforts eventually provided accurate names to support the baseline data from our one hundred plots: some twenty-five thousand individuals representing nearly seven hundred species. I had no idea how I could sort and compare the plots using this elephantine data set! But luck came my way, for a few months after my arrival in Cambridge, the annual meeting of the British Ecological Society was convened there. I attended, where I was recommended to confess my rash achievements to Peter Greig-Smith, a professor at the University College of North Wales, Bangor, who was one of the leaders of a new science known as quantitative plant community ecology. Greig-Smith, a modest if somewhat austere academic, asked whether I had seen the recent paper, published in *Ecological Monographs*, on the woodlands bordering the tallgrass prairies of northern Wisconsin. Authors Roger Bray and John Curtis of the University of Wisconsin were to save my career. They had devised a method of relating their forests to one another, and to their climate and soils, by comparing plots according to the presence and abundance of each species



Ashton used a statistical method known as a Bray-Curtis ordination to visualize the relationships between habitat characteristics and the tree communities for two research sites in Brunei. Here, fifty plots from Kuala Belalong have been organized into groups using this method.

present. This general method is known as ordination, and elements of their novel approach are still used today.

Examination of the data from Brunei indicated that the tree flora at Belalong was markedly different from that at Andulau, with only a third of species common to both sets of plots, so I decided to ordinate the two sets separately. I set to work, entering the plot data and calculating the matrix of similarity indices. I toiled night and day, for more than three weeks, using a bulky hand calculator, the Swedish *Facit*. The day of reckoning arrived when I started to place the plots, as dots, using a simple geometric technique for ordination, in two dimensions so that the distance between them related to their floristic similarity. To my amazement, a recognizable pattern gradually emerged for the fifty plots at each site, much like, in those days, how a photographic print would emerge

on paper set in *hypo* solution. The patterns confirmed intuitions gained from field experience, with the tree flora tied intimately with geology and topography.

Although we hadn't recensused the plots to show change over time, the initial results were clear. The species composition indicated that the dipterocarp species on clay loams, and particularly the lower slopes and undulating land, were predominantly light hardwoods that grow relatively fast. These species might yield a timber crop within a half century. But the sandy soils of Andulau, and also the shallow loams along the sharp Belalong ridges, were dominated by heavy dipterocarps and other hardwoods whose growth rates were known from other research to be much slower, implying that more complex management would be needed to sustain selective felling, with growth cycles exceeding a century.





The Ashtons returned to Borneo in 1962. Here, Mark Ashton, at age four, carries a macaque (*Macaca fascicularis*) named Mr. Nips. Mark currently professes silviculture at Yale, where he also directs the Yale School Forests. Peter Ashton's research sites ranged from coastal locations like Bako National Park (top) and mountainous inland locations like Carapa Pila (bottom).

The ordinations demonstrated, for the first time, that hyperdiverse tropical lowland forests were as floristically variable and habitat-specific as temperate broadleaf forests; indeed, the individual species showed a degree of habitat specificity only found in temperate forests in specialized habitats such as limestone crags. It is the tree species, through their chemical and physical interactions with other forms of life, that directly or indirectly mediate all biodiversity. This knowledge provided a breakthrough, and I knew that the work needed to be

expanded—both geographically, to see whether the same trends would be observed elsewhere on Borneo, and temporally, to observe changes in the forest structure over time.

Mary and I, now with a young family, returned to Borneo in 1962. I resumed my explorations, this time as forest botanist in the adjacent state of Sarawak (which became part of Malaysia in 1963), where we eventually spent five years. It was a perfect place to bring up our three children. Soon we were taking them to the woods where

we, looking up into the canopy for signs of flowering, would be nudged by them, looking down with a detail to be observed from their stature alone, alerting us to a nest of giant ants, or a huge millipede, or a leech swaying encouragingly.

Sarawak is slightly larger than New York State and therefore twenty times the area of Brunei. This presented both a challenge and an opportunity. I adopted a plan whereby, as in Brunei, I would undertake one major botanical exploration each year, while making periodic short forays when time allowed. Although Sarawak and Brunei share a dominant sedimentary geology of sandstones, shales, and clays, Sarawak also supports tantalizing habitats on isolated pockets of limestone karst and volcanic rocks. I further suspected that the major waterways—the Baram, Rajang and Lupar Rivers—could provide evidence of separate diversification, even speciation, in the lowland forests isolated on either side of their extensive floodplains. The major expeditions provided opportunities to set up plot clusters in a diverse

set of habitats and geographical locations. As in Brunei, plot results would add to knowledge needed to understand patterns of timber supply and quality. We would also have opportunities to initiate recensusing of permanent plots, conducted on five-year intervals. This would allow us to test predictions of growth rates and management protocols inferred from the static data gathered in Brunei.

Our first year of plot surveys started with a crisis: The December-to-February northeast monsoon came in with a fury not matched in recent history. Kuching, in the west, where we all lived, received continuous rain rattling on our roofs for more than two weeks at a time. Over one-third of the state was underwater, but miraculously, no lives were lost thanks to the army with their inflatable rivercraft. But it also provided an opportunity to establish permanent plots on landslide locations, uniquely allowing us to monitor forest regeneration from scratch.

Afterwards, these journeys became routine, socially as well as botanically. For the first



Upriver travel occasionally proved dangerous and taxing. Here, one of Ashton's boats approaches the head of a rapid, Ulu Mujong, in central Sarawak.

few hours upriver, travelling in a dugout canoe known as a *prahu*, we would pass through mangrove forests to the first Malay fisherman's town where we would check in at the government office, buy food, and learn whether our advance party had succeeded in attracting local Dayaks—the indigenous people of Borneo—who were familiar with the terrain and who would also provide boats. We would then proceed to the forest, often spending nights in riverside longhouses along the way. Each longhouse is essentially a village of wooden rowhouses, on stilts and under one roof, entered by ascending a notched log (like a ladder) at either end. The shared roof shelters a gallery on whose floor all social activities flourished.

These stayovers were always hilarious, if somewhat raucous, experiences. As the chosen house approached, our team of local field assistants would begin combing and oiling their hair, smartening up and adding perfume; when we turned the corner and saw the longhouse for the first time, as often as not there would be a

group of young women, having heard the noise of our outboards, who would have descended to the landing to wave and shout encouragement. Conversations on these boat rides were always alive with joking and good-natured braggadocio.

At first, the riverside vegetation would consist of a mix of cultivated trees—indigenous mango and durian species, rambutans, coconut palms, and native and Cavendish bananas—and the indigenous species of the floodplains. But things would change as soon as the current quickened and the first rocky banks were exposed. A distinct flora appeared below the flood line: miniature palms, aroids, ferns, and a diversity of shrubs and coarse herbs, known as rheophytes, which are adapted to periodic immersion and sweeping floodwaters—a community rich in rare species awaiting collection. Overhead, trees that had gained traction on the rocks leaned precariously over the narrowing water, their branches dripping with epiphytic ferns, orchids, and even rhododendrons (*Rhododendron* sect. *Vireya*). We



Supplies were carried in woven rattan packs known as *selabits*, shown with field assistants at Ulu Mujong (left). The work resulted in massive amounts of specimens. A field assistant, Brain, arranges and prepares specimens near the coastal town of Bintulu.



Ashton's research ultimately documented around twenty-five hundred tree species at research plots in Sarawak and Brunei. Clockwise from top left: *Scyphostegia borneensis* (willow family, Salicaceae), *Dysoxylum* sp. (mahogany family, Meliaceae), *Melanorrhoea inappendiculata* (cashew family, Anacardiaceae), *Ixora* sp. (coffee family, Rubiaceae), *Didesmandra aspera* (Dilleniaceae), and *Sterculia megistophylla* (mallow family, Malvaceae).

observed trees like *Dipterocarpus oblongifolius*, which produces bright-pink winged fruit that hang like Christmas decorations, and the fragrant babai (*Saraca declinata*), a leguminous species, which produces decorative yellowish-orange flowers on its trunk.

At this point in the upriver journey, those with boating skill came to the fore, led by the outboard operator and the individual stationed on the prow with a long *suar*—a fending pole—who was known as the *jagar luan* (or prow-guard). The most crucial moment was always at the head of a rapid when the prahu, lifted during its ascent, would drop onto the calm water as we entered a lagoon. The stern would lift, and with it the propeller. All hands took to the poles for, if we failed to heave the baggage-filled prahu across, we could lose control, fall back headlong, probably sideways, and lose everything to the torrent. I experienced this seven times, but thanks to willing and experienced hands, we never lost our precious specimens, notebooks, or soil samples, although a camera could get a dousing. I would watch and admire the skill shown. But upriver travel was punishing to the outboard motor: what would start as a shiny new Evinrude with fancy hood would, on occasion, end up as an unprotected swirling stick, topped with a greasy bareboned engine—still miraculously spinning!

We aimed to establish plots representing the full range of yellow-red tropical soils and the MDFs that dominate the lowland Bornean landscape. In addition to recording representative forest profiles along transects, at sites of uniform geology, I had suspected that much of the floristic variation was influenced by soil fertility, perhaps individual nutrient ions, as in temperate forest communities. Soil analytical laboratories hadn't been available in Brunei, but in Sarawak, facilities were available. So, this time around, we sampled soils: at the surface, where organic duff was concentrated, and at a standard depth of 30 inches (75 centimeters), where tropical soils would be mineral alone, bereft of visible humus. But bringing back these heavy samples was a nightmare, not least because it had to be done without delay, before microbial activity influenced decay rates and the release of nitrogen and other salts into

solution. Everything—everything—had to be kept waterproof, in camp and in transit, and this required commissioning special durable waterproof backpacks.

This work became my ecological specialty. We ended up with 105 plots, each 1.5 acres (increased from the Brunei experience), at thirteen sites in eleven localities. The work at each site, following establishment, which I personally undertook, was carried out by my team of climbers, some of whom had rejoined me when they heard of my return, and was led by an experienced Sarawak Malay forester. Among these foresters, I most remember Ilias bin Pa'ie, keeper of the Sarawak herbarium, who was a close friend and mentor, ever cautious and gentle, who tragically died from a heart attack when overseeing the 1975 recensusing at Lambir, a hilly site in the northeastern corner of the state. While this was some years after my departure, the loss was profound.

Otherwise, in those initial years, camp life during surveys became routine, with little of excitement to report. One exception was the accident our team experienced on the upper basalt slopes of Bukit Mersing, a mountain in central Sarawak where thirty plots were eventually installed, four of which became permanent for periodic recensusing. The Bornean climate is almost windless, except for the squalls that foreshadow the frequent afternoon thunderstorms. Occasionally, these take the form of violent cold-air downdrafts, flattening the forest in a patch of fifty acres or more. Our camp found itself in one when a giant emergent tree toppled nearby. The team hid beneath its cylindrical trunk, while the camp itself, including the tent frame and its tarpaulin, were trashed. But nothing was lost, and the work could continue.

And there were the occasional culinary surprises. We discovered, to our amazement, that civets at some camps would bite into the cans of tinned mackerel and suck out their contents. How did they know what was within? We deduced that a smell, or dry juice, had been left outside during the canning process. And, then again, there was the *jaoung*: Bornean forests have few canopy palm species, and most



While the mixed dipterocarp forests of Borneo had long been viewed as a random assortment of species, discernible and predictable patterns emerged through Ashton's research. Here, a tree climber collects fruits from *Sterculia megistophylla* (mallow family, Malvaceae) within a research plot at Ulu Mujong.

are scattered or local. This one is a *Pholidocarpus*, which locally formed small groves in damp valleys. It would be felled on discovery and cut open to reveal the massive starchy pith with the portly grubs of a large beetle nestled inside. The trick was to pick these up by the head and bite off the wriggling body, which resembled a greasy polythene tube full of shortening. Then, you had to swallow fast while the three pairs of scratchy legs tickled past your uvula. For me, once was enough!

We ultimately conducted four recensuses on five-year intervals, but the work still continues as I write. Different rainforest species achieve trunk-diameter growth rates from ten millimeters to less than two millimeters per annum,

which is similar to a stand of regenerating red oaks (*Quercus rubra*) in a Massachusetts forest. The majority of individuals in any mature MDF, however, are losing to competitors and in slow decline. It required twenty years to gain sufficient data to start comparing the dynamic performance of forests on contrasting rock and soils, and then infer potential lengths of felling cycles and means of sustainable management for timber. By that time, I had spent twelve years on the biology faculty of the University of Aberdeen, where tropical forest research of another kind was occurring, and the work continued after I joined the Arnold Arboretum in 1978. It would take longer still before Harvard graduate student Matthew Potts was to use our data in his doctoral dissertation and

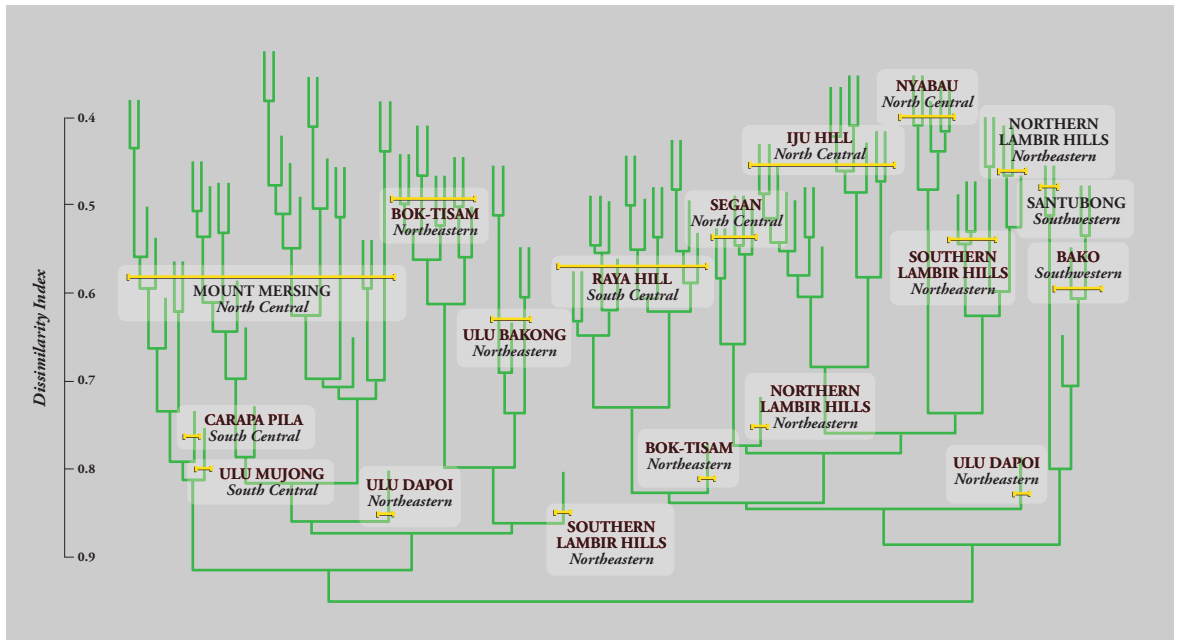
devise the most informative methods to analyze patterns and correlations.

But even the first results were impressive. Our 105 plots covered 157 acres and included just under two hundred dipterocarp species exceeding one-foot girth. This amounted to four-fifths of all dipterocarps known from Sarawak and Brunei, even though our plots only included MDFs and therefore excluded the characteristic species of the peat swamp forest and other specialized communities. We even captured 70 percent of approximately thirty-five hundred known tree species in all families. This is tribute to our careful selection of sites representative of the full range of predicted species-specific habitats.

These initial results were amplified by Matthew, who devised an elegant method of visually depicting the similarities (or dissimilarities) between the plots. The model, known as a dendrogram, resembles a family tree, with the twigs and branches grouping plots according to their similarities. His analysis revealed several patterns of importance. First, the plots were grouped into two major branches, confirming the original observations and ordinations from Brunei: Fifty-seven Sarawak plots,

primarily at eight sites, occurred on sandy soils, characterized by higher acidity, lower nutrient levels, and a distinct surface layer of slow-decomposing raw organic matter. The other forty-eight plots, mainly at the other five sites, occupied the more widespread fertile loams, with a higher capacity to retain water thanks to their open lattice of clay molecules. These major groups were consistent, regardless of the underlying bedrock (sedimentary or igneous).

Based on Matthew's dendrogram, it could be argued that the reason why two-thirds of the species differed in our original Bruneian plots was simply because the distance between the two sites—sixty miles—is sufficient for the random turnover that might be expected over time from their restricted seed dispersal distances. But the plot sites from Sarawak correlated with soil properties, irrespective of their location, indicating that the selective influence of the physical habitat dominates the random effect of seed dispersal over time in structuring the tree communities. This is particularly evident for isolated plots, where the soil type differs from the surrounding forest, supporting a floristic island of tree species that differ from the surrounding habitat sea. Immediately, I real-



ADAPTED FROM POTTS ET AL., 2002.

Taxonomists create phylogenetic trees to show the relatedness between organisms. Ashton, Potts, and colleagues used a similar visualization to classify 105 forest plots in Sarawak. This dendrogram groups the plots according to nine physical habitat characteristics (including altitude, steepness, and soil chemistry). The major branch on the left includes forty-eight plots on fertile loams; the branch on the right includes fifty-seven plots on sandy soils.



Ashton's research had important implications for sustainable forestry, as well as conservation. Similajau National Park, in northeastern Sarawak, received national protection in 1976.

ized that the limited dispersal of pollen and seeds results in tropical tree species evolving more-restricted, habitat-defined spaces through competitive speciation. These floristic islands form the ecological equivalent of terrestrial archipelagoes. Other organisms such as symbiotic fungi or insects whose larvae specifically depend on those trees will be similarly confined. The implications for conservation planning are obvious.

But although the plots within a particular site occupied distinct terminal branches of the dendrogram (no plots were identical), plots from

a particular site generally remained within a single subsection of the dendrogram. This was even true for neighboring sites like the Bok-Tisam Forest Reserve and Ulu Bakong, which are located about twenty miles apart in northeastern Sarawak. Even though these sites share geology and soil characteristics (both primarily occur on yellow-brown loam), their forest compositions could be distinguished from one another. This provided strong evidence that, whereas soil properties dominate at broad landscape scales, the effects of dispersal are dominant over shorter distances, provided the



soils are uniform. Within a single site, we also found that the floristic composition of the plots correlated with topography, as well as nutrient concentrations in the soil. Topography and nutrient concentrations were themselves inter-related, but we were eventually able, by clever analysis, to find that nutrient influences are generally stronger.

This research ultimately provided the basis for sustainable management of Bornean MDFs for timber production. Foresters in Peninsular Malaysia have never conducted plot surveys aimed at defining floristically distinct forest types, but they had, over many decades, developed a means of sustainably harvesting timber from MDFs by simulating natural succession: The forest is clearcut in patches hardly larger than large windthrows, after first checking to confirm that there was sufficient natural regeneration that would survive the logging process. Felling cycles of fifty to seventy years were envisaged. Our recensuses confirmed that Bornean forests on loam soils could be managed using the same method.

But foresters from Peninsular Malaysia are still finding it difficult to develop sustainable management systems for their high-hill and coastal dipterocarp forests, which floristically resemble the Bornean MDFs of low-nutrient sandy soils. Our findings have suggested a more sophisticated management system is necessary for these forests. Our forest structure measurements and recorded growth rates on these indicated that species attaining timber diameters were slow growing and in lower numbers, although there was an adequate cohort of young trees, rather than seedlings, for successive crops. Sustainable management would, therefore, require foresters return to the same stand at shorter intervals to selectively harvest individual trees, given that it might take a century for a seedling to mature to timber size. For this method, a more experienced workforce would be essential.

Our research also supported a new protocol for identifying the locations—to be tested by field censuses—of areas with potentially outstanding species diversity or concentration of endemics, meriting strict conservation. In

this way, previously unexplored areas of conservation importance can be identified due to their surface geology. Up to then, conservationists were unable to make such extrapolations. Three national parks in Sarawak had already been legislated in the 1960s. I proposed five more, aimed at comprehensive representation of the flora. These were successfully passed into legislation by the new government of an independent Sarawakian state within Malaysia, in the 1970s, long after our departure from those raucous longhouse days and our entrance into the aethereal realm of academia.

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Peter Ashton is Harvard University Bullard Professor Emeritus and was director of the Arnold Arboretum from 1978 to 1987. Among many career honors, his research on tropical forests was recognized with the prestigious Japan Prize in 2007. He and his wife, Mary, live in Chiswick, London.

The map in this article was created using Esri, HERE, Garmin, (c) OpenStreetMap contributors, Sources: Esri, USGS, NGA, NASA, CGIAR, N Robinson, NCEAS, NLS, OS, NMA, Geodatastyrelsen, Rijkswaterstaat, GSA, Geoland, FEMA, Intermap and the GIS user community.

## Leaning into Legend: *Acer mono*

*Jon Hetman*

Ambling over nearly every acre of the Arnold Arboretum over the past two decades has made many of its pathways and collections special to me, but perhaps my favorite journey of all is the one I take nearly every day from the Forest Hills Gate to the Hunnewell Building—the lion’s share of my morning commute. My great fortune in walking the short mile from home to work in a city recently named the nation’s worst for rush-hour traffic\* is certainly not lost on me—nor is the fact that it is always a journey of beauty and discovery as the seasons ebb and flow. One tree I never tire of admiring along my way is a superb accession of painted maple (*Acer mono*, accession 5358\*A) leaning somewhat languorously toward the road and welcoming visitors to our national collection of maples.

Walking in either direction down Meadow Road, the tree is nearly impossible to miss and even harder to ignore. Though not extremely tall—*Acer mono* typically tops out at a moderate thirty to forty feet at maturity—it has a beautifully low, broad, and symmetrical crown that suggests the kind of idealized form that bonsai artists pursue. In spring, yellow-green flowers appear in tandem with the pale green foliage, which in autumn may turn a yellow-orange or apricot. Come winter, the tree’s graceful architecture shines through its bare canopy, and the sight of sparkling snow twisting across its branches never fails to send me running for my camera. And then there’s the soft twist and southward tilt of the trunk, subtended by a thick knot of exposed roots seemingly coiled like a snake at its base. These thickly layered roots spread out in the opposite direction of the lean, illustrating how tree structure leverages the dynamics of tension and compression (like a suspension bridge) to mitigate the gravitational forces that might otherwise topple them over.

While the case can be made that this individual represents its species rather well, the taxonomy of *Acer mono* remains largely unresolved. Although the Arboretum recognizes *A. mono* as the correct name, authorities have been mixed on both the name and identity of

this widespread maple, often placing it within *A. pictum*, among other taxa. Seed for 5358\*A was received in 1902 from the Imperial Botanic Garden in Tokyo, an institution that has shared material with the Arnold Arboretum since Charles Sprague Sargent made his pioneering expedition to Japan in 1892. Painted maple inhabits the forests of Japan, and it can also be found in China, Korea, Mongolia, and eastern Russia. The Arboretum’s wild-collected holdings of the taxon include material collected on several North America-China Plant Exploration Consortium expeditions, including the 2018 expedition to western Hubei Province.

Nevertheless, this particular tree has attained a level of celebrity at the Arboretum. Its position at the head of the maple collection, contrasting handsomely with the texture and seasonal hues of the showy Japanese (*Acer palmatum*) and Korean (*A. pseudosieboldianum*) maples nearby, contributes to its appeal. As such, the tree and its neighbors receive attention in many of the Arboretum’s public tours each growing season. When famed horticulturist Michael Dirr published the 1983 edition of his seminal *Manual of Woody Landscape Plants*, following his tenure as a Mercer Fellow at the Arboretum in 1979, he heralded this painted maple as “one of the most beautiful trees in the Arnold Arboretum.” And this praise has unwaveringly remained in subsequent editions.

This individual may, in fact, be the most famous and recognizable painted maple in the world: as of this writing, a photograph of it adorns the entry for the species on *Wikipedia*. Its status as a botanical treasure and museum object, one perhaps endangered by an overabundance of public attention, has been acknowledged more definitively of late by the Arboretum as well. Like other eminent accessions across the Arboretum, the tree has been roped off to preserve the health and integrity of its root system from soil compaction. Hopefully this additional protection will contribute to its well-being for years to come and allow this noble maple to be admired as a masterpiece for as long as nature wills.

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\* INRIX 2018 GLOBAL TRAFFIC SCORECARD





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