# The puzzle of sympatry

Recent evidence supports the notion of sympatric speciation—the rise of new species in the same location—but the reasons for this phenomenon remain elusive

*Howard Wolinsky*

For centuries, the greatest puzzle in biology was how to account for the sheer variety of life. In his 1859 landmark book, *On the Origin of Species*, Charles Darwin (1809–1882) finally supplied an answer: his grand theory of evolution explained how the process of natural selection, acting on the substrate of genetic mutations, could gradually produce new organisms that are better adapted to their environment. It is easy to see how adaptation to a given environment can differentiate organisms that are geographically separated; different environmental conditions exert different selective pressures on organisms and, over time, the selection of mutations creates different species—a process that is known as allopatric speciation.

It is more difficult to explain how new and different species can arise within the same environment. Although Darwin never used the term sympatric speciation for this process, he did describe the formation of new species in the absence of geographical separation. "I can bring a considerable catalogue of facts," he argued, "showing that within the same area, varieties of the same animal can long remain distinct, from haunting different stations, from breeding at slightly different seasons, or from varieties of the same kind preferring to pair together" (Darwin, 1859).

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In the 1920s and 1930s, however, allopatric speciation and the role of geographical isolation became the focus of speciation research. Among those leading the charge was Ernst Mayr (1904–2005), a young evolutionary biologist, who would go on to influence generations of biologists with his later work in the field. William Baker, head of palm research at the Royal Botanic Gardens, Kew in Richmond, UK, described Mayr as "one of the key figures to crush sympatric speciation." Frank Sulloway, a Darwin Scholar at the Institute of Personality and Social Research at the University of California, Berkeley, USA, similarly asserted that Mayr's scepticism about sympatry was central to his career.

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Since Mayr's death in 2005, however, several publications have challenged the notion that sympatric speciation is a rare exception to the rule of allopatry. These papers describe examples of both plants and animals that have undergone speciation in the same location, with no apparent geographical barriers to explain their separation. In these instances, a single ancestral population has diverged to the extent that the two new species cannot produce viable offspring, despite the fact that their ranges overlap. The debate about sympatric and allopatric speciation has livened up since Mayr's death, as Mayr's influence over the field has waned and as new tools and technologies in molecular biology have become available.

Sulloway, who studied with Mayr at Harvard University, in the late 1960s and early 1970s, notes that Mayr's background in natural history and years of fieldwork in New Guinea and the Solomon Islands contributed to his perception that the bulk of the data supported allopatry. "Ernst's early career was in many ways built around that argument. It wasn't the only important idea he had, but he was one of the strong proponents of it. When an intellectual stance exists where most people seem to have gotten it wrong, there is a tendency to sort of lay down the law," Sulloway said.

Sulloway also explained that Mayr "felt that botanists had basically led Darwin astray because there is so much evidence of polyploidy in plants and Darwin turned in large part to the study of botany and geographical distribution in drawing evidence in *The Origin*." Indeed, polyploidization is common in plants and can lead to 'instantaneous' speciation without geographical barriers.

In February 2006, the journal *Nature* simultaneously published two papers that described sympatric speciation in animals and plants, reopening the debate. Axel Meyer, a zoologist and evolutionary biologist at the University of Konstanz, Germany, demonstrated with his colleagues that sympatric speciation has occurred in cichlid fish in Lake Apoyo, Nicaragua (Barluenga *et al*, 2006). The researchers claimed that the ancestral fish only seeded the crater lake once; from this, new species have evolved that are distinct and reproductively isolated. Meyer's paper was broadly supported, even by critics of sympatric speciation, perhaps because Mayr himself endorsed sympatric speciation among the cichlids in his 2001 book *What Evolution Is*. "[Mayr] told me that in the case of our crater lake cichlids, the onus of showing that it's not sympatric speciation lies with the people who strongly believe in only allopatric speciation," Meyer said.

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The other paper in *Nature*—by Vincent Savolainen, a molecular systematist at Imperial College, London, UK, and colleagues—described the sympatric speciation of Howea palms on Lord Howe Island (Fig 1), a minute Pacific island paradise (Savolainen *et al*, 2006a). Savolainen's research had originally focused on plant diversity in the gesneriad family—the best known example of which is the African violet—while he was in Brazil for the Geneva Botanical Garden, Switzerland. However, he realized that he would never be able prove the occurrence of sympatry within a continent. "It might happen on a continent," he explained, "but people will always argue that maybe they were separated and got together after. […] I had to go to an isolated

 

**Fig 1** | Lord Howe Island. Photo: Ian Hutton.

piece of the world and that's why I started to look at islands."

He eventually heard about Lord Howe Island, which is situated just off the east coast of Australia, has an area of 56 km² and is known for its abundance of endemic palms (Sidebar A). The palms, Savolainen said, were an ideal focus for sympatric research: "Palms are not the most diverse group of plants in the world, so we could make a phylogeny of all the related species of palms in the Indian Ocean, southeast Asia and so on."

> **…the next challenges will be to determine which genes are responsible for speciation, and whether sympatric speciation is common**

Yet, in Savolainen's opinion, Mayr's influential views made it difficult to obtain research funding. "Mayr was a powerful figure and he dismissed sympatric speciation in textbooks. People were not too keen to put money on this," Savolainen explained. Eventually, the Leverhulme Trust (London, UK) gave Savolainen and Baker £70,000 between 2003–2005 to get the research moving. "It was enough to do the basic genetics and to send a research assistant for six months to the island to do a lot of natural history work," Savolainen said. Once the initial results had been processed, the project received a further £337,000 from the British Natural Environment Research Council in 2008, and €2.5 million from the European Research Council in 2009.

From the data collected on Lord Howe Island, Savolainen and his team constructed a dated phylogenetic tree showing that the two endemic species of the palm *Howea* (Arecaceae; Fig 2) are sister taxa. From their tree, the researchers were able to establish that the two species—one with a thatch of leaves and one with curly leaves—diverged long after the island was formed 6.9 million years ago. Even where they are found in close proximity, the two species cannot interbreed as they flower at different times.

According to the researchers, the palm speciation probably occurred owing to the different soil types in which the plants grow. Baker explained that there are two soil types on Lord Howe—the older volcanic soil and the younger calcareous soils. The Kentia palm grows in both, whereas the curly variety is restricted to the volcanic soil. These soil types are closely intercalated—fingers and lenses of calcareous soils intrude into the volcanic soils in lowland Lord Howe Island. "You can step over a geological boundary and the palms in the forest can change completely, but they remain extremely close to each other," Baker said. "What's more, the palms are wind-pollinated, producing vast amounts of pollen that blows all over the place during the flowering season—people even get pollen allergies there because there is so much of the stuff." According to Savolainen, that the two species have different flowering times is a "way of having isolation so that they don't reproduce with each other […] this is a mechanism that evolved to allow other species to diverge *in situ* on a few square kilometres."

According to Baker, the absence of a causative link has not been demonstrated between the different soils and the altered flowering times, "but we have suggested that at the time of speciation, perhaps when calcareous soils first appeared, an environmental effect may have altered the flowering time of palms colonising the new soil, potentially causing non-random mating and kicking off speciation. This is just a hypothesis—we need to do a lot more fieldwork to get to the bottom of this," he said. What is clear is that this is not allopatric speciation, as "the micro-scale differentiation in geology and soil type cannot create geographical isolation", said Baker.

> **…although molecular data will add to the debate, it will not settle it alone**

The results of the palm research caused something of a splash in evolutionary biology, although the study was not without its critics. Tod Stuessy, Chair of the Department of Systematic and Evolutionary Botany at the University of Vienna, Austria, has dealt with similar issues of divergence on Chile's Juan Fernández Islands—also known as the Robinson Crusoe Islands—in the South Pacific. From his research, he points out that on old islands, large ecological areas that once separated species—and caused allopatric speciation—could have since disappeared, diluting the argument for sympatry. "There are a lot of cases [in the Juan Fernández Islands] where you have closely related species occurring in the same place on an island, even in the same valley. We never considered that they had sympatric origins because we were always impressed by how much the island had been modified through time," Stuessy said. "What [the Lord Howe researchers] really didn't consider was that Lord Howe Island could have changed a lot over time since the

**Sidebar A** | Research in paradise

Alex Papadopulos and Ian Hutton doing fieldwork on a very precarious ridge on top of Mt. Gower. Photo: William Baker, Royal Botanical Gardens, Kew, Richmond, UK.

Alexander Papadopulos is no Tarzan of the Apes, but he has spent a couple months over the past two years aloft in palm trees hugging rugged mountainsides on Lord Howe Island, a Pacific island paradise and UNESCO World Heritage site.

Papadopulos—who is finishing his doctorate at Imperial College London, UK—said the views are breathtaking, but the work is hard and a bit treacherous as he moves from branch to branch. "At times, it can be quite hairy. Often you're looking over a 600-, 700-metre drop without a huge amount to hold onto," he said. "There's such dense vegetation on most of the steep parts of the island. You're actually climbing between trees. There are times when you're completely unsupported."

Papadopulos typically spends around 10 hours a day in the field, carrying a backpack and utility belt with a digital camera, a trowel to collect soil samples, a first-aid kit, a field notebook, food and water, specimen bags, tags to label specimens, a GPS device and more. After several days in the field, he spends a day working in a well-equipped field lab and sleeping in the quarters that were built by the Lord Howe governing board to accommodate the scientists who visit the island on various projects. Papadopulos is studying Lord Howe's flora, which includes more than 200 plant species, about half of which are indigenous.

Vincent Savolainen said it takes a lot of planning to get materials to Lord Howe: the two-hour flight from Sydney is on a small plane, with only about a dozen passengers on board and limited space for equipment. Extra gear—from gardening equipment to silica gel and wood for boxes in which to dry wet specimens—arrives via other flights or by boat, to serve the needs of the various scientists on the team, including botanists, evolutionary biologists and ecologists.

Savolainen praised the well-stocked researcher station for visiting scientists. It is run by the island board and situated near the palm nursery. It includes one room for the lab and another with bunks. "There is electricity and even email," he said. Papadoupulos said only in the past year has the internet service been adequate to accommodate video calls back home.

Ian Hutton, a Lord Howe-based naturalist and author, who has lived on the island since 1980, said the island authorities set limits on not only the number of residents—350—but also the number of visitors at one time—400—as well as banning cats, to protect birds such as the flightless wood hen. He praised the Imperial/Kew group: "They're world leaders in their field. And they're what I call 'Gentlemen Botanists'. They're very nice people, they engage the locals here. Sometimes researchers might come here, and they're just interested in what they're doing and they don't want to share what they're doing. Not so with these people. Savolainen said his research helps the locals: "The genetics that we do on the island are not only useful to understand big questions about evolution, but we also always provide feedback to help in its conservation efforts."

origins of the species in question." It has also been argued that one of the palm species on Lord Howe Island might have evolved allopatrically on a now-sunken island in the same oceanic region.

In their response to a letter from Stuessy, Savolainen and colleagues argued that erosion on the island has been mainly coastal and equal from all sides. "Consequently, Quaternary calcarenite deposits, which created divergent ecological selection pressures conducive to *Howea* species divergence, have formed evenly around the island; these are so closely intercalated with volcanic rocks that allopatric speciation due to ecogeographic isolation, as Stuessy proposes, is unrealistic" (Savolainen *et al*, 2006b). Their rebuttal has found support in the field. Evolutionary biologist Loren Rieseberg at the University of British Columbia in Vancouver, Canada, said: "Basically, you have two sister species found on a very small island in the middle of the ocean. It's hard to see how one could argue anything other than they evolved there. To me, it would be hard to come up with a better case."

Whatever the reality, several scientists involved in the debate think that molecular biology could help to eventually resolve the issue. Savolainen said that the next challenges will be to determine which genes are responsible for speciation, and whether sympatric speciation is common. New sequencing techniques should enable the team to obtain a complete genomic sequence for the palms. Savolainen said that next-generation sequencing is "a total revolution." By using sequencing, he explained that the team, "want to basically dissect exactly what genes are involved and what has happened […] Is it very special on Lord Howe and for this palm, or is [sympatric speciation] a more general phenomenon? This is a big question now. I think now we've found places like Lord Howe and [have] tools like the next-gen sequencing, we can actually get the answer."

Determining whether sympatric speciation occurs in animal species will prove equally challenging, according to Meyer. His own lab, among others, is already looking for 'speciation genes', but this remains a tricky challenge. "Genetic models […] argue that two traits (one for ecological specialisation and another for mate choice, based on those ecological differences) need to become tightly linked on one chromosome (so that they don't get separated, often by segregation or crossing over). The problem is that the genetic basis for most ecologically relevant traits are not known, so it would be very hard to look for them," Meyer explained. "But, that is about to change […] because of next-generation sequencing and genomics more generally."

**Many researchers who knew Mayr personally think he would have enjoyed the challenge to his views**

Others are more cautious. "In some situations, such as on isolated oceanic islands, or in crater lakes, molecular phylogenetic information can provide strong evidence of sympatric speciation. It also is possible, in theory, to use molecular data to estimate the timing of gene flow, which could help settle the debate," Rieseberg said. However, he


**Fig 2** | The two species of Howea palm. (**A**) *Howea fosteriana* (Kentia palm). (**B**) *Howea belmoreana*. Photos: William Baker, Royal Botanical Gardens, Kew, Richmond, UK.

cautioned that although molecular data will add to the debate, it will not settle it alone. "We will still need information from historical biogeography, natural history, phylogeny, and theory, etc. to move things forward."

Many researchers who knew Mayr personally think he would have enjoyed the challenge to his views. "I can only imagine that it would've been great fun to engage directly with him [on sympatry on Lord Howe]," Baker said. "It's a shame that he wasn't alive to comment on [our paper]." In fact, Mayr was not really as opposed to sympatric speciation as some think. "If one is of the opinion that Mayr opposed all forms of sympatric speciation, well then this looks like a big swing back the other way," Sulloway commented. "But if one reads Mayr carefully, one sees that he was actually interested in potential exceptions and, as best he could, chronicled which ones he thought were the best candidates."

Mayr's opinions aside, many biologists today have stronger feelings against sympatric speciation than he did himself in his later years, Meyer added. "I think that Ernst was more open to the idea of sympatric speciation later in his life. He got 'softer' on this during the last two of his ten decades of life that I knew him. I was close to him personally and I think that he was much less dogmatic than he is often made out to be [...] So, I don't think that he is spinning in his grave." Mayr once told Sulloway that he liked to take strong stances, precisely so that other researchers would be motivated to try to prove him wrong. "If they eventually succeeded in doing so, Mayr felt that science was all the better for it."

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