

Editorial

Biogeographic Patterns in the Pacific and Australasian Regions

Island systems have fascinated biologists for a long time because of their high percentage of endemic taxa and their isolation and they are often referred to as *natural laboratories* for studying evolutionary processes. Dispersal, establishment and adaptive radiation to/on remote oceanic islands have especially been extensively studied in the past decades. Islands and their role as natural barriers have been used to define phylogeographic areas (e.g., the Wallace Line; Van Welzen et al., 2011). Colonizations to remote islands can be considered very rare events. Successful colonizers must have been able to overcome initial bottlenecks such as inbreeding depression due to a small number of colonizing individuals (Pannell, 2015). Once established on an island, lineages had the chance to adapt to different ecological niches, which often resulted in species-rich adaptive radiations such as Darwin's finches on the Galapagos Islands, Lake Victoria cichlid fishes, the Hawaiian lobelioids or *Aeonium* species (Crassulaceae) on the Canary Islands (Crawford & Archibald, 2017). Several features (e.g., bird-dispersed or salt water tolerant floating diaspores, polyploidy, self-fertility) have been hypothesized to be characteristic for island colonizers (Sakai et al., 1995; de Queiroz, 2005; Linder & Barker, 2014). In turn lineages that have adapted to islands often show a reduced dispersability, e.g., by having an increased fruit size compared to their continental relatives (Carlquist, 1966).

Advances in DNA sequencing since the 1990's have led to a much deeper understanding of organismal lineages on islands. Adaptive radiations on islands are often characterized by a vast morphological diversity that has led to an overestimation of colonization events. Molecular phylogenetic studies have instead revealed that taxa that have been recognized as separate endemic genera within a family often are the result of a single colonization event (e.g., Givnish et al., 2009). Phylogenetic studies have also helped to assure the geographic origin of endemic island lineages as well as dispersal patterns both on large (e.g., across the Pacific ocean) and on regional scales (e.g., within an archipelago). Dispersal patterns across the Pacific Ocean are often quite complex and geographic origins are mainly Asia and Australia, but also the Americas and even African origins have been identified (Keeley & Funk, 2011). Remote archipelagos such as the Hawaiian Islands are often "dead-ends" for dispersal, but with increase in molecular phylogenetic studies exceptions are known becoming increasingly common (Harbaugh & Baldwin, 2007; Harbaugh et al., 2009; Appelhans et al., 2014; Marris, 2014). Dispersal patterns within an island system have been extensively studied on the Hawaiian Islands, which are the result of a moving volcanic hot spot. The islands are

therefore arranged in a West-East sequence from older and more eroded islands to younger islands with active volcanism on which new ecological niches are changing and constantly being formed. In this system, a directional dispersal from older to younger islands can often be observed (progression rule; Wagner & Funk, 1995). Other important advancements concern the estimation of timing and age of dispersal events. Geological studies assured ages of volcanic islands, identified time periods of submergence of islands and improved our knowledge about the complex geotectonic history of Pacific archipelagos (Price & Clague, 2002; Pilon, 2012; Triantis et al., 2016). These geological advancements have been used to calculate divergence times in many molecular dating studies. These studies showed that endemic island lineages are often younger than the islands themselves. Several exceptions of this pattern are known suggesting that lineages evolved on other islands, dispersed to the islands where they are found today and then became extinct on the islands on which they have evolved (Givnish et al., 2009; Appelhans et al., 2018a). This extinction is likely connected to erosion and submergence of the islands.

Next-generation sequencing is again revolutionizing evolutionary studies on islands. Since radiations are often young and species rich, Sanger sequencing did not in most cases produce enough informative sequence information to fully untangle phylogenetic relationships at or below the species level which in turn hampered the establishment of phylogeny-informed classification systems and the identification of biogeographic patterns within an island system. A wide usage of these methods will enable researchers to answer questions regarding speciation, polyploidization, hybridization or introgression of island lineages.

A symposium about Pacific Biogeography was held at the International Botanical Congress in Shenzhen, China in 2017. This special issue includes works presented at this symposium, but also contains studies from the Australasian region, which neighbors the Pacific region and in many cases serves as the source area for Pacific oceanic island colonization. This issue comprises works that aim to reconstruct patterns throughout the entire Pacific (Appelhans et al., 2018b) or that focus on islands groups in the Pacific (Paetzold et al., 2018; Price & Wagner, 2018) or parts of Australasia (Miller et al., 2018; Rutgrink et al., 2018; Zhao et al., 2018).

Appelhans et al. (2018b) studied biogeographic patterns in *Melicope* (Rutaceae), which colonized nearly all major archipelagos in the Pacific Ocean including the remote Austral, Hawaiian and Marquesas islands. The origin of the genus is likely in Australasia and several independent

colonization events resulted in the wide distribution on Pacific islands. Molecular dating revealed that the divergence times match very well with islands ages for most cases, except for the Hawaiian radiation, so that *Melicope* is one of the few examples of organismal lineages known that are older than the current main Hawaiian Islands.

Price & Wagner (2018) and Paetzold et al. (2018) focus on the dispersal patterns of Hawaiian plant groups. Price & Wagner (2018) analyzed the origins of all Hawaiian angiosperm lineages. They reviewed existing literature about phylogenetic studies of Hawaiian plants to evaluate the source areas of Hawaiian lineages and to determine which dispersal modes were predominant and whether different dispersal modes were associated with the different source areas. The authors estimated that the largest proportions of Hawaiian lineages colonized the Islands from Indo-Malayan and widespread ancestors. The percentage of North American origins is considerably higher than that the earlier studies suggested, while that of East Asian ancestors was lower than previously assumed. While bird dispersal is the most important dispersal mode for most lineages and most source areas, an increased number of lineages in the category “widespread” likely arrived by floatation.

Paetzold et al. (2018) review traits characteristic for successful island radiation and evaluate in how far these traits are present in the Hawaiian radiation of *Melicope*. They measured ploidy levels using flow cytometry and concluded that *Melicope* should be considered a paleopolyploid instead of a true polyploid, which has been named as one of the characteristic traits for successful island radiation. The authors characterize the genus *Melicope* as having a high dispersal ability, but did not find any shifts to traits characteristic for successful island radiation in the Hawaiian lineages, which were not also present in the closest extra-Hawaiian relatives of the lineage.

Zhao et al. (2018) and Rutgrink et al. (2018) focus on taxa in Malesia. In their biogeographic analysis of *Prunus* subgenus *Laurocerasus* section *Mesopygeum*, Zhao et al. (2018) found that the Wallace Line is an important line of demarcation for the two major clades within the section. The two clades likely diverged in the Eocene and their geographic origin is in Southeast Asia. The authors conclude that tectonic movements in the Early Oligocene that probably provided pathways for eastward migration from Southeast Asia likely had a large influence on the observed pattern in section *Mesopygeum*.

Rutgrink et al. (2018) look beyond the broad subdivision of Malesia into two (West and East of Wallace’s Line) and three regions (Sunda shelf, Wallacea, Sahul shelf) respectively. They examined the composition of the floras of the north and south Moluccas, which are part of the Sahul shelf. The results of their Species Distribution Modelling, based on the herbarium collection of Naturalis Biodiversity Center in Leiden/Netherlands show that the north and south Moluccas differ greatly in species composition. Continuous dispersal barriers and complex tectonic history of the islands might explain these differences. The authors conclude that the Moluccas as a whole should therefore not be regarded as a single biogeographic unit.

Miller et al. (2018) employ phylogenetic diversity as a tool to measure biodiversity based on a dataset that includes nearly all Australian land plant genera. Instead of counting taxa that occur in a region, phylogenetic diversity is a measurement of branch lengths in a phylogeny. The authors compared

phylogenetic diversity measures with species counts, and found that the two are often not concordant and that most non-angiosperm clades had a higher phylogenetic diversity than expected given the number of genera in the clades. The authors highlight that using phylogenetic diversity as the primary descriptor of biodiversity instead of species counts will be an important step for more quantitative and comparable analyses in biodiversity research.

We hope that the papers from this special issue will stimulate further evolutionary biogeographic studies in the Pacific and the Australasian regions in the coming decade. The Pacific and the Malesian regions have played fundamental roles in serving as models to study evolution and develop biogeography as a science (Wallace, 1860, 1876; Carlquist, 1974, 1996; Wagner & Funk, 1995). Yet studies employing a comprehensive framework to test evolutionary diversification hypotheses for the Australasian and Pacific floras are still largely lacking. Integrative studies utilizing these fascinating island systems clearly need to be emphasized in today’s genomic and informatic era to shed insights into the patterns and processes of plant diversifications across space and through time (also see Wen et al., 2013, 2017; Crawford & Archibald, 2017). Finally, oceanic islands are generally fragile ecosystems with small niches and endemic taxa are often not able to compete with introduced species, and there is an increased likelihood that they become rare or extinct and the introduced species become invasive. Islands are naturally susceptible to climate change and rising sea levels. The Pacific and Australasia present excellent opportunities to explore conservation biology and strategies of island groups/systems.

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References

- Appelhans MS, Reichelt N, Groppo M, Paetzold C, Wen J. 2018a. Phylogeny and biogeography of the pantropical genus *Zanthoxylum* and its closest relatives in the proto-Rutaceae group (Rutaceae). *Molecular Phylogenetics and Evolution* 126: 31–44.
- Appelhans MS, Wen J, Duretto M, Crayn D, Wagner WL. 2018b. Historical biogeography of *Melicope* (Rutaceae) and its close relatives with a special emphasis on Pacific dispersals. *Journal of Systematics and Evolution* 56: 576–599.
- Appelhans MS, Wen J, Wood KR, Allan GJ, Zimmer EA, Wagner WL. 2014. Molecular phylogenetic analysis of Hawaiian Rutaceae (*Melicope*, *Platydesma* and *Zanthoxylum*) and their different colonization patterns. *Botanical Journal of the Linnean Society* 174: 425–228.
- Carlquist S. 1966. The biota of long-distance dispersal. III. Loss of dispersibility in the Hawaiian Flora. *Brittonia* 18: 310–335.
- Carlquist S. 1974. *Island Biology*. New York: Columbia University Press.
- Carlquist S. 1996. Plant dispersal and the origin of Pacific island floras. In: Keast A, Miller SE eds. *The origin and evolution of Pacific island*

- biotas, New Guinea to eastern Polynesia: patterns and processes. Amsterdam: SPB Academic Publishing. 153–164.
- Crawford DJ, Archibald JK. 2017. Island floras as model systems for studies of plant speciation: Prospects and challenges. *Journal of Systematics and Evolution* 55: 1–15.
- De Queiroz A. 2005. The resurrection of oceanic dispersal in historical biogeography. *Trends in Ecology and Evolution* 20: 68–73.
- Givnish TJ, Millam KC, Mast AR, Paterson TB, Theim TJ, Hipp AL, Henss JM, Smith JF, Wood KR, Systma KJ. 2009. Origin, adaptive radiation and diversification of the Hawaiian lobeliads (Asterales: Campanulaceae). *Proceedings of the Royal Society B: Biological Sciences* 276: 407–416.
- Harbaugh DT, Baldwin BG. 2007. Phylogeny and biogeography of the sandalwoods (*Santalum*, Santalaceae): Repeated dispersals throughout the Pacific. *American Journal of Botany* 94: 1028–1040.
- Harbaugh DT, Wagner WL, Allan GJ, Zimmer EA. 2009. The Hawaiian Archipelago is a stepping stone for dispersal in the Pacific: An example from the plant genus *Melicope* (Rutaceae). *Journal of Biogeography* 36: 230–241.
- Keeley SC, Funk VA. 2011. Origin and evolution of Hawaiian endemics: new patterns revealed by molecular phylogenetic studies. In: Bramwell D, Caujape -Castells J eds. *The biology of island floras*. Cambridge: Cambridge University Press. 57–88.
- Linder HP, Barker NP. 2014. Does polyploidy facilitate long-distance dispersal? *Annals of Botany* 113: 1175–1183.
- Marris E. 2014. Tree hitched a ride to island. *Nature* 510: 320–321.
- Miller JT, Jolley-Rogers G, Mishler BD, Thornhill AH. 2018. Phylogenetic diversity is a better measure of biodiversity than taxon counting. *Journal of Systematics and Evolution* 56: 663–667.
- Paetzold C, Kiehn M, Wood KR, Wagner WL, Appelhans MS. 2018. The odd one out or a hidden generalist: Hawaiian *Melicope* (Rutaceae) do not share traits associated with successful island colonization. *Journal of Systematics and Evolution* 56: 621–636.
- Pannell JR. 2015. Evolution of the mating system in colonizing plants. *Molecular Ecology* 24: 2018–2037.
- Price JP, Clague DA. 2002. How old is the Hawaiian biota? Geology and phylogeny suggest recent divergence. *Proceedings of the Royal Society B: Biological Sciences* 269: 2429–2435.
- Pillon Y. 2012. Time and tempo of diversification in the flora of New Caledonia. *Botanical Journal of the Linnean Society* 170: 288–298.
- Price JP, Wagner WL. 2018. Origins of the Hawaiian flora: Phylogenies and biogeography reveal patterns of long-distance dispersal. *Journal of Systematics and Evolution* 56: 600–620.
- Rutgrink ALJ, Visser M, van Welzen PC. 2018. Differences between the floras of the North and South Moluccas (Indonesia). *Journal of Systematics and Evolution* 56: 652–662.
- Sakai AK, Wagner WL, Ferguson DM, Herbst DR. 1995. Origins of dioecy in the Hawaiian flora. *Ecology* 76: 2517–2529.
- Triantis KA, Whittaker RJ, Fernández-Palacios JM, Geist DJ. 2016. Oceanic archipelagos: a perspective on the geodynamics and biogeography of the World's smallest biotic provinces. *Frontiers of Biogeography* 8. 2: e29605.
- Van Welzen PC, Parnell JAN, Ferry Slik JW. 2011. Wallace's Line and plant distributions: two or three phytogeographical areas and where to group Java? *Biological Journal of the Linnean Society* 103: 531–545.
- Wagner WL, Funk VA. 1995. *Hawaiian Biogeography: Evolution on a Hot Spot Archipelago*. Washington, DC: Smithsonian Institution Press.
- Wallace AR. 1860. On the zoological geography of the Malay archipelago. *Zoological Journal of the Linnean Society* 14: 172–184.
- Wallace AR. 1876. *The Geographical Distribution of Animals*, 2 vols. London: MacMillan & Co.
- Wen J, Harris AJ, Icker-Bond SM, Dikow R, Wurdack K, Zimmer EA. 2017. Developing integrative systematics in the informatics and genomic era, and calling for a global Biodiversity Cyberbank. *Journal of Systematics and Evolution* 55: 308–321.
- Wen J, Ree RH, Ickert-Bond S, Nie ZL, Funk VA. 2013. Biogeography: Where do we go from here? *Taxon*: 62: 912–927.
- Zhao L, Potter D, Xu Y, Liu PL, Johnson G, Chang ZY, Wen J. 2018. Phylogeny and spatio-temporal diversification of *Prunus* subgenus *Laurocerasus* section *Mesopygeum* (Rosaceae) in the Malesian region. *Journal of Systematics and Evolution* 56: 637–651.