Glossary

Arbuscular mycorrhizae: Also known as vesicular-arbuscular mycorrhizae (VAM). Most widespread type of mycorrhizae, fungi penetrates the plant root cell walls.
Arbuscules: Finely branched fungal hyphae that are the site of exchange of materials between plant and fungus in arbuscular mycorrhizae.
Bryophytes: Informal name for mosses (phylum Bryophyta) and other non vascular plants such as liverworts and hornworts.
Ectomycorrhizae: Second most widespread type of mycorrhizae where the fungus forms a sheath around the outside of the root and spreads between (not into) the plant cells.
Glomus: Important genera of arbuscular mycorrhizal fungi.
Mycorrhizae: Intimate association between fungi and plant roots, usually mutualistic.

provides net benefits to each partner'[12]. However, it should be noted that, in the ectomycorrhizal case, the transitions appear to have been between mutualists and free-living forms, rather than between mutualists and parasites.

In discussing their results, Hibbett *et al.* point out that several factors are often cited as promoting stability in mutualisms. These include vertical transmission of symbionts and one-to-one correspondence of host and symbiont. As neither of these are found in mycorrhizal associations, Hibbett *et al.* concluded that 'the apparent instability of ectomycorrhizae is not surprising'[3]. This raises the question; how can these mutualisms ever persist? There are several possible answers[13], including retaliation against exploitation by the partners, local dispersal of symbionts (pseudovertical transmission[13]) or partner choice where there is a biological market[15] for compatible symbionts. The evolution of mutualism appears to be a more complex and dynamic process than many textbooks suggest. These two recent studies provide important data to inform theoretical speculation that, in turn, will hopefully identify new questions for observational and experimental study.

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David M. Wilkinson
Biological and Earth Sciences, Liverpool John Moores University, Byrom Street, Liverpool, UK L3 3AF.
e-mail: D.M.Wilkinson@livjm.ac.uk

Scatter-hoarding rodents and marsupials: convergent evolution on diverging continents

Pierre-Michel Forget and Stephen B. Vander Wall

Neotropical rainforests host a rich community of fruit-eating animals, among them neotropical scatter-hoarding rodents that bury seeds in soil. These animals perform an important community-building process because the seeds germinate and establish seedlings away from the parent plant. In three recent studies, researchers have demonstrated a comparable role for paleotropical rodents in southeast Asia. With the discovery that a frugivorous kangaroo behaves similarly to its neotropical rodent counterpart, a new level has been reached in our understanding of the evolution of tropical forests.

The role of scatter-hoarding animals in plant dispersal has been well established in the temperate regions for many years[1], but studies in tropical rainforests are still attempting to determine the extent of food-hoarding behavior and to measure the consequences of the behavior for plant biology. Despite the early description of scatter-hoarding behavior among neotropical rodents[2,3] the influence of this behavior on seed dispersal and plant establishment was not documented until the early 1990s[4,5]. Since then, we have found scatter-hoarding neotropical rodents to be very effective agents of secondary dispersal, as they gather seeds initially scattered by gravity or frugivores and move them to cache sites[6,7]. Three recent studies[8–10] on food hoarding in Malaysia and Australia have caused us to reassess the role of rodents and marsupials as seed dispersers in paleotropical rainforests, which have been even more neglected than forests in the neotropics.

Despite clear, unambiguous reports of scatter hoarding of nuts of *Panda oleosa* (Pandaceae) trees by the large ground squirrel (*Epixerus ebii wilsoni*) in Makokou, Gabon[11], and the presence of numerous species of nut-producing Fagaceae (i.e. *Quercus*, *Lithocarpus* and *Castanopsis*) in tropical southeast Asia, almost no one has determined the implications of scatter-hoarding behavior for tree recruitment in these regions. Rodents from other paleotropical forests from Africa to Australia have suffered from the same disinterest, the focus of study being either primates, birds, bats or wind-dispersal, such as in the large family Dipterocarpaceae. Using fruit of the

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introduced oil palm species (*Elaeis guineensis*), Masatoshi Yasuda *et al.*[9] have now revealed that scatter hoarding was practiced by several rodent species at Pasoh Forest Reserve, Peninsular Malaysia. Yasuda *et al.* followed the fate of individual fruits removed by animals by attaching a thread and plastic tag with serial number to each fruit. Rodents often cached the fruits but often the string and serial number remained exposed on the ground surface. The animals were often observed from a feeding platform and visits were recorded with an automatic camera system. This photographic evidence not only catches the agent of secondary dispersal or predation in the act, but also provides interesting insights into the behavior of foraging animals that is otherwise seldom seen. Visiting animals that removed the fruit with a certain tag could be easily identified to species. Yasuda *et al.* found that the nocturnal long-tailed giant rat (*Leopoldamys sabanus*) accounted for nearly 50% of fruits removed, whereas the diurnal three-striped ground squirrel (*Lariscus insignis*) removed 20%. Each rodent species hid fruits in soil and plant litter an average of 16 m and 15 m and a maximum of 29.4 m and 32.7 m away, respectively. This is the first evidence for scatter hoarding by terrestrial rodents in Malaysian rainforests.

In an Australian rainforest, following earlier observations by Harrington *et al.*[10], Tad Theimer (Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ, USA)[10] successively observed removal and determined the fate of large seeds of *Beilschmedia bancroftii* (Lauraceae). Theimer used *B. bancroftii* seeds marked with a small bobbin of thread glued to the endocarp, and the free end of the thread tied to a metal stake near the base of the tree. Seeds were taken and cached an average of 13 m and up to 55 m from the parent tree by the scansorial white-tailed rat (*Uromys caudimaculatus*), a large murid rodent inhabiting the rainforests of Queensland (Australia) and New Guinea. Differences among the initial distribution of cached seeds, secondary caches and the final locations of seedlings of *B. bancroftii* suggest a recurrent, multistep seed dispersal process. Therefore, the leptokurtic curve of seed dispersal distances appears less skewed towards the adult tree, leading to a much lower concentration of fruits around the

Fig. 1. The agouti, *Dasyprocta punctata. Photograph, reproduced with permission, from Pierre-Michel Forget.*

source tree than previously thought. Although such 'ricochet' seed dispersal patterns have been recently described[12] for a temperate tree species, the relationship between initial cache sites and final seedling establishment has not been clear in tropical forests, leading to underestimates of the role of rodents as long-distance dispersal agents. The two recent important contributions of Yasuda *et al.*[9] and Theimer[11] highlight the key role of these little-studied rodents on forest processes on both sides of Wallace's line between the Oriental and Australian regions.

Another equally important recent discovery is that of Andrew Dennis (CSIRO, Tropical Forest Research Centre, Atherton, Australia)[13], who found that a diurnal, terrestrial and frugivorous marsupial, the musky rat-kangaroo (*Hypsiprymnodon moschatus*)[14], also scatter-hoards fruits and seeds in Queensland, Australia, but in different rainforest areas than its competitor, the white-tailed rat. Musky rat-kangaroos, only the second marsupial known to store food, behave similarly to neotropical rodents. A spool-and-line device[15] was used for an artificial fruit that was made of a wrapped cotton bobbin (the 'seed') placed inside a Chinese date (the 'pulp'), therefore simulating the indigenous walnut *Entiandra sankeyana* (Lauraceae). Using this technique, Dennis was able to show that the 'fruits' can be taken, on average, at least 17 m, and as far as 68 m, from the parent tree to cache sites. Other tree species, such as *Fontainea picrosperma* (Euphorbiaceae) and *Baileyoxylon lanceolatum* (Flacourtiaceae), appear to be dependent on scatter hoarding for successful regeneration because none of their seeds and nuts are likely to survive if seeds are not protected from fungal pathogens and from predation by rats under the parent tree. And the list of plant species is far from being complete as up to 11 species with large fruits ranging from 14 to 60 mm in length have already been observed to be dispersed by this marsupial.

The important finding that seed-hoarding rodents and marsupials appear to be critical to the survival of Australian rainforest trees leads us to reassess the history and evolution of certain forms of animal-mediated plant dispersal on the southern continents, and to propose a new scenario for the evolution of seed-dispersal interactions initially involving marsupials but later including rodents in tropical rainforests. Marsupials are thought to have migrated from South America into Australia via Antarctica well before rodents colonized Australia 10 Mya. Some of these marsupials might have developed scatter-hoarding behavior similar to that exhibited today by Dasyproctidae, Heteromyidae and Echimyidae in America, Sciuridae in central Africa and southeast Asia, and Muridae and *Hypsiprymnodon* in northern Australia. In all of these regions, fallen fruits can be ingested and dispersed by large frugivores such as tapirs in South America and southeast Asia, elephants in Africa and southeast Asia, and cassowaries in Australia. Just as agoutis (*Dasyprocta* spp.; Fig. 1) and acouchies (*Myoprocta* spp.) redistribute tapir-dispersed seeds in Amazonia and Central America, ancestral scatter-hoarding marsupials might have effected secondary dispersal of seeds and nuts processed by frugivores in Gondwanaland.

More recently, the role of seed disperser through scatter hoarding appears to have been taken over by rodents, although future studies might reveal other seed-caching marsupials. These recent studies in paleotropical rainforests have provided a clearer picture of the often complicated pathway from seed to seedling. Much remains to be discovered about the intricate relationships between plants and animals in tropical rainforests. The new findings of Yasuda *et al.*[9], Theimer[11] and Dennis[13] have shed light on the dark undergrowth of the tropical rainforest, allowing us to see more clearly the critical role that tropical rodents and marsupials, which independently evolved the same scatter-hoarding behavior, play in the evolution of tropical forests.

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Pierre-Michel Forget*
Museum National d'Histoire Naturelle, Laboratoire d'Ecologie Générale, UMR 8571 CNRS-MNHN, 4 avenue du Petit Château, F-91800 Brunoy, France.
*e-mail: forget@mnhn.fr

Stephen B. Vander Wall
Dept of Biology and the Program in Ecology, Evolution and Conservation Biology, University of Nevada, Reno, NV 89557, USA.

Meeting Report

Marine macroecology

Evie Wieters

The Workshop on Marine Macroecology and Conservation was held in Viña del Mar, Chile, from 23 to 25 June 2000.

Human impacts on nearshore marine environments have reached a global scale. With growing recognition that past, primarily single-species approaches have failed to capture the dynamics of marine ecosystems, there is now a pressing need to adopt multi-species, large-scale approaches. An important step in expanding our knowledge of nearshore systems has been taken in Chile by a varied team of researchers under the umbrella of a FONDAP (Fondo de Investigacion Avanzada en Areas Prioritarias) grant. Such research efforts, driven by the urgent need to generate databases for large-scale, biogeographic studies to identify priority areas for conservation, led to the first Workshop on Marine Macroecology and Conservation. This workshop, organized by Sergio Navarrete, Miriam Fernandez and Pablo Marquet [PUC (Pontificía Universidad Católica de Chile), Santiago, Chile], brought a diverse group of ecologists together to discuss the state of marine macroecology and assess the type and quality of data available. The meeting provided the first opportunity to compare the macroecological patterns of the two hemispheres and to contrast these with well-studied terrestrial systems.

Macro-scale biogeographic patterns

The continental scale

Latitude has long been identified as an important factor influencing the richness, distributional range and size of species. Kevin Gaston (University of Sheffield, Sheffield, UK) pointed out that the strength of these patterns, which often explain only 40% of variation, lies in their repeatability over different scales and varying habitats and taxa. Although many hypotheses have been proposed to explain maintenance of latitudinal gradients, empirical testing is scarce.

It is the possibility of testing explanatory models for latitudinal patterns that makes the new developments in marine ecosystems so exciting. Kaustuv Roy (University of California–San Diego, La Jolla, CA, USA) compared distributional patterns of mollusks inhabiting eastern Pacific and western Atlantic continental shelves, which differ in geography, biotic histories and location of biogeographic provinces. Roy found that species richness along both coasts peaked in the tropics and sharply decreased towards the poles, mirroring patterns in many taxa of terrestrial flora and fauna[1]. This pattern of diversity could not be explained by Rapoport's Rule or area effects, but instead appeared to correlate with mean sea surface temperature (SST). These results agree with the energy hypothesis[2,3], which proposes that species richness is controlled by the quantity of solar enery available in the area.

However, correlation with SST does not seem to explain mollusk species richness along the southeastern Pacific coast. Claudio Valdovinos (Centro EULA, Universidad de Concepción, Concepción, Chile), Navarrete and Marquet showed that mollusk diversity remained relatively low and constant between 10°S and 42°S, and dramatically increased south of 42°S. Thus, whereas SST plays a controlling

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