SYMPOSIUM

The Ancient Lakes of Indonesia: Towards Integrated Research on Speciation

James J. Vaillant,[1] G. Douglas Haffner and Melania E. Cristescu

Great Lakes Institute for Environmental Research, University of Windsor, Windsor, ON, N9B 3P4, Canada

[1]E-mail: vaillanj@uwindsor.ca

Synopsis Ancient lakes have provided considerable insights into the drivers of speciation and adaptive radiation in aquatic organisms. Most studies of species-flocks, however, focus only on a single group of organisms, and few have attempted to integrate geological, limnological, ecological, and genetic drivers of speciation on multiple species-flocks at various trophic levels. As such, there is a need for a comprehensive model system for research on speciation in aquatic environments where multiple radiations are investigated at various levels of biological organization (e.g., individual, population, and ecosystem) and placed in light of geographical and geological setting. The ancient Malili Lakes of Sulawesi, Indonesia, are ideal candidates for such a model, and represent the only hydrologically connected ancient lakes in the world. These lakes are characterized by ultra-oligotrophy and unique physicochemical conditions that govern the composition and production of planktonic communities. At higher trophic levels, there are three recurring trends: (1) low taxonomic richness and simple community structures, (2) adaptive radiations with trophic specialization, and (3) remarkably high endemism with evolutionary innovations throughout the lakes and species-flocks. Furthermore, the restricted geographic distributions of species-flocks within the Malili Lakes indicate that each lake constitutes a unique environment, and dispersal among lakes is limited, despite close contemporary connectivity. These observations suggest that ecological and evolutionary processes are regulated from the bottom up, and speciation is primarily facilitated by interspecific and intraspecific competition for limited resources. The Malili Lakes represent an outstanding natural model for integrative research into speciation as they offer the opportunity to explore the roles of geography, dispersal, and selection in the radiation of aquatic organisms.

Introduction

Ancient lakes as research models

Ranging from 1 to about 30 million years in age, the earth's oldest extant lakes are regarded as the aquatic equivalents of islands, and typically harbor very high levels of endemic fauna (Brooks 1950; Martens 1997; Cristescu et al. 2010). These ancient lakes have revealed many rapid, adaptive, and nonadaptive radiation events and have provided considerable insights into the major driving forces of speciation; they serve as natural model systems for research into evolution and speciation (Schön and Martens 2004; Seehausen 2006). Their prolonged existence, isolation from ecologically similar habitats, and wide diversity of intralacustrine environments are thought to have accelerated an array of speciation processes (Schön and

Martens 2004). Consequently, there is strong empirical evidence for the various theoretical frameworks that have arisen from studies of these systems (Martens 1997; Cristescu et al. 2010). For example, the use of cichlid species-flocks in the East African Rift lakes as model systems has led to advancements in modeling of speciation processes (Danley and Kocher 2001; Gavrilets and Losos 2009). This model system revealed the relative importance of various drivers of adaptive radiation, including ecological opportunity, introgressive hybridization, and sexual selection (Salzburger et al. 2002; Smith et al. 2003; Kocher 2004; Seehausen 2004, 2006; Joyce et al. 2011). Additionally, detailed phylogeographic studies of the cichlid species-flocks have emphasized the importance of habitat fragmentation and allopatry in
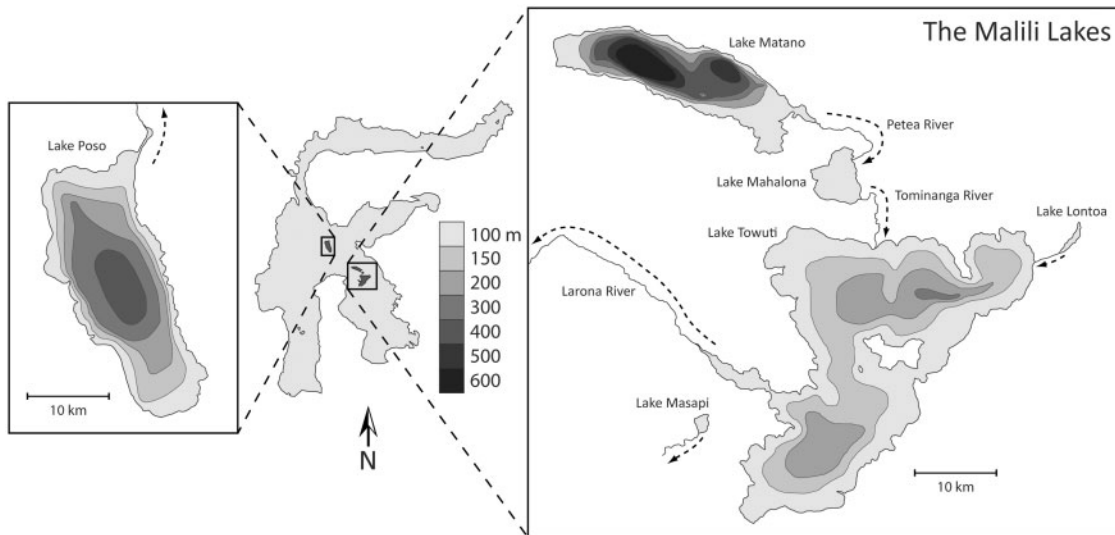
Fig. 1 The ancient Malili Lakes and nearby Lake Poso of Sulawesi, Indonesia. Dashed arrows represent the direction of water flow. Shaded regions indicate water depth in meters.

generating species diversity (e.g., Rico and Turner 2002; Allender et al. 2003; Genner et al. 2010).

Comparisons among different ancient lakes and their species-flocks have also been useful in identifying specific extrinsic and intrinsic factors responsible for driving radiation events (Fryer 1991; Martens and Schön 1999). Extrinsic factors that are often cited include the long, continuous existence of the lake, topology, depth and fragmentation of littoral habitats, as well as historical fluctuations in climate, temperature regimes, and water levels. Intrinsic factors include specific life-history characteristics such as brooding and philopatry, as well as developmental or genetic constraints such as the modification of the pharyngeal jaw apparatus of cichlid fishes or communication signals in sexually selective species (Fryer 1991; Allender et al. 2003; Schön and Martens 2004).

Classical examples of adaptive radiation and speciation in ancient lakes come mainly from studies on the endemic fauna of the African Great Lakes, Lake Baikal, and the Caspian lakes. Many smaller ancient lakes of the world, such as Lakes Titicaca, Biwa, Ohrid, and the Malili Lakes have received relatively little attention. Some of these systems stand out as remarkable settings of adaptive radiation. Our particular interest is the biota of the ancient Malili Lakes of Sulawesi, Indonesia, which is characterized by extremely high levels of endemism and an unusual lack of major taxonomic groups in phytoplanktonic, zooplanktonic, and fish assemblages (Kottelat 1990a; Haffner et al. 2001; Herder et al. 2006b; Bramburger et al. 2008; Sabo et al. 2008). Here, we discuss the unusual bio-geo-chemical

nature of these lakes which leaves them not only geographically but also ecologically isolated from surrounding aquatic ecosystems. We present recent findings of evolutionary and ecological studies across various species-flocks, and discuss emerging evolutionary trends and potential drivers for these speciation processes. Finally, we outline the overall importance of this study system for future research on speciation, especially of planktonic and crustacean taxa.

The ancient Malili Lakes

The Malili Lakes, situated in the central eastern part of the island of Sulawesi, are composed of three major lakes, Matano, Mahalona, and Towuti, and two smaller satellite lakes, Lontoa (or Wawantoa) and Masapi (Fig. 1); these represent the only hydrologically connected ancient lake system in the world (Brooks 1950). Lake Matano lies within the Matano fault line, and as such might well be the oldest lake in the system (2- to 4-million years old; based on fault-line displacements), whereas the other lakes are in areas of complex faulting and currently are estimated to be <1-million years old (based on sedimentary characteristics). Lake Poso is located in a separate drainage system northwest of the central Malili Lakes, and therefore represents a disconnected, yet ecologically and geographically proximal ecosystem.

Lake Matano, the best-studied lake of the system, forms the head of the drainage basin. It is a large (164 km^2) and exceptionally deep (590 m), steep-sided graben lake (Brooks 1950). The lake is contained in a

ferruginous basin with the highest iron concentration of any freshwater lake on earth at 2 µmol l^{-1} in the epilimnion and as much as 140 µmol l^{-1} at greater depths (Crowe et al. 2008a, 2008b). The lake is permanently stratified in both temperature and total dissolved solids at about 100 m depth where there is a sharp transition between the warm oxygenated epilimnion, and the cool anoxic metalimnion (Sabo et al. 2008; Crowe et al. 2011). Furthermore, Lake Matano is characterized by low, possibly limiting, levels of dissolved phosphorus (<0.2 µmol l^{-1}) and nitrogen (<5 µmol l^{-1}) (Sabo et al. 2008), and potentially toxic concentrations of chromium (180 nmol l^{-1}; Crowe et al. 2008b). These low levels of nutrients and potential long-term toxicity may have considerable implications for the evolution of the biological community of the lake, and it is very likely that the diatom assemblages are controlled by high metal concentrations (P. B. Hamilton, personal communication). Restricted vertical mixing results in the depletion of nutrients from the epilimnion through sedimentation, and the relatively high concentrations of iron are thought to limit the bioavailability of phosphorus in upper waters (Sabo et al. 2008). Therefore, it is not surprising that Matano has the lowest standing crops of phytoplankton among tropical and temperate ancient lakes with a peak biomass of about 0.013 mg l^{-1}, and harbors a rather simple faunal assemblage (Sabo et al. 2008). Lake Matano discharges into the Petea River, a shallow, fast-flowing river that drops 72 m in elevation before reaching Lake Mahalona.

Lake Mahalona is a much smaller (25 km^2) and shallower (62 m) lake than Matano. It is thought to be more recent in its formation than either Matano or Towuti, although there are no reliable estimates of its age. It is slightly more productive than Matano with respect to supporting subsistence fisheries, and has higher numbers of endemic shrimp and gastropod species, but lower richness of diatom taxa (Brooks 1950; Bramburger et al. 2004; von Rintelen et al., in press). Mahalona flows out through the Tominanga River, where the water gradually descends 17 m before joining the third major lake of the system, Lake Towuti.

Towuti is the largest of the Malili Lakes with an area of 560 km^2 and a maximum depth of 200 m. Although the age of the lake is uncertain, it is estimated to be at least 600,000 years old. It is also remarkably oligotrophic and unproductive (Tierney and Russell 2009); however, it contains the largest number of total species, with at least 13 species of shrimp, 10 species of molluscs, 10 species of fish, and 154 taxa of diatoms, 39 of which are endemic (Brooks 1950; Kottelat 1990b; Bramburger et al.

2004; Herder et al. 2006b; von Rintelen et al., in press). Lake Towuti drains through the Larona River and finally discharges at sea into the Gulf of Boni. Nearby, there are also two small satellite lakes, Lontoa (or Wawantoa) and Masapi, which are considerably more isolated and taxonomically impoverished.

Finally, Lake Poso is located about 80 km northwest of the central Malili Lakes in the central metamorphic belt of Sulawesi. It is a large (323 km^2; 450 m deep), oligo-mesotrophic lake that lies in a separate drainage basin from the Malili Lakes, and drains northward via the Poso River into the Gulf of Tomini. The lake was likely formed during the collision between the eastern and western plates composing the island, but there is still much uncertainty surrounding the timing of accretion in this region (Audley-Charles 1987; Wilson and Moss 1999). Like the Malili Lakes, the antiquity of Lake Poso is reflected in its biota, as it harbors a number of endemic species-flocks, including aytid shrimps, gastropods, bivalves, and crabs (von Rintelen et al. 2004; von Rintelen and Glaubrecht 2006; von Rintelen et al. 2007; Schubart and Ng 2008; von Rintelen et al., in press).

Evolutionary trends in the Malili species-flocks

Adaptive radiation

Adaptive radiations result in the diversification of species through the evolution of morphological or physiological traits that exploit an array of types of resources (Futuyma 1986; Schluter 1996). During rapid diversification, trophic specialization is frequently (although not always) a key feature that characterizes sister species (Fryer 1991; Schön and Martens 2004). Both theoretical modeling and empirical data indicate that ecologically important morphological features are the first to differentiate during radiation (reviewed by Streelman and Danley 2003; Gavrilets and Losos 2009). This has been observed in the fauna of the Malili Lakes, where nearly all of the species' radiations described (e.g., telmatherinid fish, gastropods, aytid shrimps, crabs) show trophic specialization, suggesting an exceptionally important role of habitat and resource partitioning in these lakes (von Rintelen et al. 2004; Roy et al. 2007b; Schubart and Ng 2008; von Rintelen et al. 2010).

The best-studied intralacustrine adaptive radiation is that of the endemic sailfin silverside fish *Telmatherina* of Lake Matano. The sailfins comprise two endemic radiations within Lake Matano, the

"sharpfins" with seven morphospecies and "roundfins" with three (Kottelat 1991; Herder et al. 2006; 2008; Pfaender et al. 2010). These species differ in several morphological traits associated with different food sources, including length of the snout, position of the mouth, height of gape, and number of gill rakers (Roy et al. 2004; Pfaender et al. 2010). Further examination of jaw structure and diet (i.e. stomach contents and stable isotope ratios) revealed that each of the morphotypes utilize different feeding strategies that are reflected in their trophic morphologies (Roy et al. 2007b; Pfaender et al. 2010). There are also polymorphisms in coloration of males within each of the lineages, and it is likely that sexual selection is of importance in maintaining these color patterns across varying lake habitats (Gray et al. 2008). However, it is difficult to interpret the historical and contemporary role of color polymorphism in these species as AFLP (Herder et al. 2008), microsatellite (Walter et al. 2009a), and mitochondrial (Roy et al. 2007a) data indicate that color is not correlated with population structure. Furthermore, different morphospecies show sympatric distribution at fine scales (Herder et al. 2008), and are likely to disperse around the lake (Walter et al. 2009b), implicating the importance of habitat isolation through resource partitioning for the coexistence of these closely related lineages of fish.

Striking cases of adaptive radiation that involve the parallel evolution of adaptive traits have also been observed in the Malili Lakes. Parallel evolution, or the appearance of the same trait in independent lineages, is regarded as a signature of natural selection, as genetic drift is unlikely to produce environmentally correlated changes multiple times (Schluter and Nagel 1995; Rundle et al. 2000). The observation of this phenomenon is usually an indication of adaptation to similar environmental pressures. For example, each of the Malili Lakes and Lake Poso harbors endemic crab species characterized by three different ecotypes: a generalist, a molluscivore, and a detritivore (Schubart and Ng 2008; von Rintelen et al., in press). While representatives from each of these types are always present in any given lake, examination of phylogenetic relationships between lake populations suggests that these ecotypes evolved independently at least twice (Schubart and Ng 2008; Schubart et al. 2008), thereby lending support to the primary role of natural selection and specialization in feeding preferences.

One of the most notable cases of parallelism is that of the remarkable variation in trophic specialization in the endemic freshwater gastropods of the genus *Tylomelania*. While the morphology of the

gastropods' radula is generally considered a conserved character at the species level, nine different morphologies were found in the *Tylomelania* complex of the Malili Lakes, with nearly identical types occurring in different populations from different lakes. Furthermore, the molecular phylogeny reveals that in three of the four major lineages, these characters evolved in parallel following colonization of the lakes. This strongly suggests functionality of these traits and a principal role of ecological divergence in the intralacustrine speciation process (von Rintelen et al. 2004; von Rintelen et al., in press).

Pronounced trophic specialization has also been found in the aytid shrimps of Lake Poso and the Malili Lakes. This is the largest known radiation in the genus *Caridina*, with 14 different species characterized by seven ecotypes (von Rintelen and Cai 2009). Within this species complex, morphological features likely associated with substrate preference were found to be very strong predictors of habitat type, and several of these specializations have evolved more than once in different lineages (von Rintelen et al. 2007, 2010). With most of these species endemic to single lakes, habitat specialization has been suggested as the primary driver of the radiation (von Rintelen and Cai 2009).

Several authors have proposed that the initial stage of the radiation process in ancient lakes is driven by divergence in habitat preference, closely followed by morphological differentiation attributed to trophic specialization (Danley and Kocher 2001; Streelman and Danley 2003; Kocher 2004). The Malili Lakes represent an ideal system to test this model, as the members of a given species-flock are frequently found occupying distinct microhabitats and display adaptive trophic morphologies, and several radiations exhibit the characteristics of early speciation (e.g., shallow divergence between sister species, lack of intraspecific genetic structure, relatively small number of species within the flocks). This constant theme undoubtedly points toward selection due to limited resource availability as the principal driver of divergence.

Evolutionary novelty

Considering the prolonged isolation of ancient lakes, it is not surprising that endemic species possess highly specialized or distinctive characters. The Malili Lakes are exceptional in that they harbor several species that display novel morphological and behavioral traits that are unique to their taxonomic grouping. Here, the species-flock of the limpet snail *Protancylus,* endemic to Lake Poso and the Malili

Lakes, exhibits a novel type of brood care. This behavior is not found in any other known limnetic pulmonate snails and consists of ovipositing eggs on the hard shell as a substrate, followed by development of the embryos under the mantle of the female's shell (Albrecht and Glaubrecht 2006). Interestingly, the use of the shell as a substrate for oviposition is also seen in the pulmonate snails of the ancient Lake Baikal, suggesting that similar selective pressures may have played a role in the development of this behavior (Albrecht and Glaubrecht 2006).

Lake Poso and the Malili Lakes harbor several corbiculid bivalve species. One species, endemic to Lake Poso, is the only sessile (i.e. cementing) species of the lakes and was long thought to have evolved independently. However, a molecular phylogeny reveals that this lineage is very closely related to one of the nonsessile lineages of the lake, and is quite divergent from the other lake species, suggesting rapid evolution of this behavior within its lineage and highlighting the importance of developmental plasticity in adaptation (von Rintelen and Glaubrecht 2006). Furthermore, the molluscivorous crabs of the Malili Lakes possess large molariform chelar teeth, a morphological characteristic known only from marine crabs and, interestingly, those of the ancient Lake Tanganyika (Schubart and Ng 2008). The crabs are closely related to other species from Sulawesi, making this morphological feature unique within the family Gecarcinucidae. Overall, these innovations and their similarity to marine and other ancient-lake systems suggest that these lakes maintain certain characteristics, such as long-term stability or unusual selection regimes, that promote differentiation, although it is still unclear which forces are responsible for the appearance of such a high degree of specialization.

Hybridization and speciation

The role of introgressive hybridization as an important evolutionary force for speciation in animals has been debated for many years (Barton 2001; Mallet 2007). Traditionally, hybridization between distinct populations has been regarded as either a transient process of little evolutionary significance as populations diverge, or in direct opposition to divergence through the continuous exchanging of genes (Barton 2001). More recently, however, hybridization has been gaining support as a process that actually promotes speciation, primarily because it can result in increased variation in quantitative or mating traits, genome rearrangements, or transgressive segregation,

with the appearance of "extreme" phenotypes (Rieseberg et al. 1999; Seehausen 2004; Mallet 2007). Indeed, this concept has been supported by studies of several species-flocks from ancient lakes (e.g. Baikalian sculpins, African cichlids) (Salzburger et al. 2002; Kontula et al. 2003; Smith et al. 2003; Seehausen 2004; Seehausen 2006), including the *Telmatherina* of the Malili Lakes (Herder et al. 2006a; Herder and Schliewen 2010).

Speciation with introgressive hybridization has been demonstrated in the atheriniform fishes of the Malili Lakes, and represents one of the most convincing cases of hybridization in a radiation event. Within Lake Matano, there are two major morphological telmatherinid species-flocks, the "roundfins" and the "sharpfins", while the surrounding streams harbor another species. Nuclear AFLPs support monophyly of the "roundfins" and "sharpfins" (Herder et al. 2006a). However, the "sharpfins" possess two mitochondrial lineages. One lineage is sister to the "roundfins," corroborating common ancestry of both Matano species-flocks, while the other lineage is closely related to the *Telmatherina* from streams, indicating mitochondrial introgression from the stream telmatherinids into the lacustrine "sharpfin" population (Herder et al. 2006a; Schwarzer et al. 2008). This introgressed population also exhibits substantially higher morphological diversity, suggesting that hybridization may facilitate the evolution of novel phenotypes (Herder and Schliewen 2010). Additionally, at least three other major hybridization events have been shown between other lake and stream *Telmatherina* populations of the Malili Lakes, leaving open the possibility that reticulate speciation has had a significant role in their diversification as well (Herder et al. 2006a). Hybridization is also highly suspected in the *Tylomelania* flock of the Malili Lakes, as there is little species-level resolution in their mitochondrial phylogeny and several major morphological features (e.g., shell ribbing) conflict with their placement within mitochondrial phylogenies (Glaubrecht and von Rintelen 2008). Further investigation, including the use of nuclear markers, is needed to confirm this.

As multilocus genetics studies become more widely available, hybridization continues to emerge as an important driver of speciation in many animal taxa (Dowling and Secor 1997; Seehausen 2004). Although it appears that reticulate speciation is more common in fish, this is likely a biased conclusion as very few invertebrate taxa have received the same level of attention. It remains possible that hybridization between moderately divergent lineages is a major creative force in the evolutionary process

and is far more common in nature than traditionally considered. Additionally, while it has been suggested that the same habitats promote both hybridization and adaptive radiation (i.e., novel or perturbed environments) (Seehausen 2004), the specific conditions under which hybridization is likely to generate new species are still unclear. More studies across many different taxonomic groupings are still necessary to better understand these processes.

Speciation patterns in the Malili Lakes

Overall, the common themes from each of these studies, including low taxonomic richness, high endemism, and restricted geographic distributions of species within the Malili Lakes, suggest that each of these lakes is characterized by unique and intense physical, chemical, and ecological selection regimes. Furthermore, each of the species-flocks examined thus far display signatures of adaptive radiation, especially in trophic morphologies, implying that the system is regulated from the bottom up, and that availability of resources is the critical factor governing speciation. Many authors have commented on the simple community structures of the Malili lakes (Haffner et al. 2001; Roy et al. 2004; Bramburger et al. 2008; Sabo et al. 2008). Within the planktonic community, there is a notable lack of entire classes of phytoplankton and centric diatoms, which are typically found in other taxonomically impoverished ancient lakes (Bramburger et al. 2008; Sabo et al. 2008). The zooplankton assemblages of the Malili Lakes are also very simple, composed of single calanoid and cyclopoid lineages, and at least in Matano, a single reported rotifer (Sabo et al. 2008; personal observation). Furthermore, the radiation of telmatherinids into fifteen different species within several intermediate-sized lakes and a number of river and stream ecosystems that present a wide range of heterogeneous habitats can also be considered limited when compared to the extensive radiations of fish in other ancient lakes, including the 33 species of Baikalian cottoids (Kontula et al. 2003) and hundreds of species of African cichlids within single lakes (Seehausen 2006). The absence of cosmopolitan species and simple community structures characterizing the Malili Lakes suggests that there is a low susceptibility to new colonizations, perhaps due to limited availability of niche space for new migrants and the peculiar geo-chemistry that involves potential chromium-induced toxicity.

Endemism is clearly one of the defining features of the Malili Lakes. Much of this endemism may be attributed to Sulawesi's isolation and prolonged existence within Wallacea. This explains the absence of "primary" freshwater fishes as well as cosmopolitan phytoplankton and zooplankton species (e.g., centric diatoms, cladocerans) (Bramburger et al. 2004, 2008; Sabo et al. 2008). Indeed, almost all members of zooplanktonic, molluscan, shrimp, crab, and fish species-flocks are endemic to the Malili Lakes and tributaries (Brooks 1950; Roy et al. 2004; Herder et al. 2006b; von Rintelen et al. 2007; Schubart and Ng 2008). This high level of endemism supports long-term geographic and ecological isolation of the lakes and limited potential for new colonizations (Roy et al. 2004). While the Malili Lakes are considered a hotspot for biodiversity, it appears that the majority of this diversity is contained within a handful of endemic species-flocks which have radiated within the lakes.

Many species involved in radiation in the Malili Lakes are confined to single lakes. In the phytoplanktonic assemblage, 32% of the diatom flora is endemic to single lakes (Bramburger et al. 2004). New evidence shows that a major genetic split exists for the calanoid fauna between lakes Mahalona and Towuti (unpublished data). This is especially surprising, as planktonic species are expected to disperse passively throughout the lake system. The restricted distributions of some species also indicate that despite being interconnected, each lake contains distinct biotic communities. Lake Matano harbors ten species of *Telmatherina*, while Mahalona and Towuti share at least five different species from *Telmatherina* and the closely related genera *Tominanga* and *Paratherina* (Herder et al. 2006a). Although there is some support for gene flow between closely related species of lakes Matano and Mahalona through introgression and backcrossing with riverine populations (Schwarzer et al. 2008), the lacustrine telmatherinids of Lake Matano are not found in the Petea River, which links the two lakes. The Petea River also marks a distinct distributional barrier for freshwater crabs. Of the two independent colonizations by crabs in the Malili Lakes, one lineage has radiated into two distinct genetic clades, one shared between Mahalona and Towuti, and the other harbored solely by Matano (Schubart et al. 2008; Schubart and Ng 2008). Once again, a similar pattern is found in the shrimps. The Malili Lakes have been colonized twice by representatives of the genus *Caridina* (von Rintelen et al. 2010). One colonization resulted in the radiation of *C. lanceolata*, in which a major genetic divergence exists between the population of Matano and that of Mahalona/Towuti (Roy et al. 2006; von Rintelen et al. 2010) and the second colonization resulted in a larger radiation of

13 species, 11 of which are present in only one or two lakes (von Rintelen et al. 2010). There have also been three independent colonizations of the Malili Lakes by members of the gastropod genus *Tylomelania*. Two of these colonizing lineages are still primarily confined to lakes Mahalona and Towuti. The third contains species distributed throughout the Malili Lakes, with several restricted to single lakes, mainly Matano (von Rintelen et al. 2004). The interconnectedness of the Malili Lakes suggests that most taxa should be able to disperse both upstream and downstream throughout the system (Brooks 1950). The restriction of so many species to single lakes, despite hydrological connectivity, is curious and suggests the prevalence of ecological (biotic or abiotic) obstacles to contemporary dispersal and colonization.

Within the diatom assemblage, taxonomic richness at the generic level varies greatly among lakes, suggesting differential success of various species in each lake. The ultra-oligotrophy and unique physical, chemical, and limnological conditions of each these lakes are most likely responsible for limiting the success of different taxa of diatoms (Bramburger et al. 2008; Sabo et al. 2008). The specialized feeding morphologies of the gastropod and shrimp species-flocks likely reflect this scarcity in phytoplankton and periphyton crops (von Rintelen et al. 2004; von Rintelen et al. 2010). The telmatherinid fish of Lake Matano also display variation in feeding morphologies and preferences indicative of resource partitioning (Roy et al. 2007b; Pfaender et al. 2010). Hence, it is likely that such extreme resource limitation has strongly promoted specialization at each trophic level, and speciation based on resource partitioning has reduced intraspecific competition for resources. Furthermore, local adaptation of resident species may enhance priority effects and reduce the success of establishment of new colonists (De Meester et al. 2002). This effect would be even more pronounced in the resource-limited Malili Lakes, as locally adapted populations would retain an exceptional advantage over migrants from neighboring lakes; this would explain the limited geographic distributions of many species to single lakes and the absence of perhaps less specialized cosmopolitan species. Thus, we conclude that intralacustrine radiations within the Malili Lakes are primarily driven by limited primary production ultimately resulting from the unique physical, chemical, and limnological conditions of each lake, while competition for, and specialization to, lake-specific food sources are responsible for the lack of interlacustrine dispersal and colonization of many species.

Alternatively, it is possible that geography and allopatric processes are also partly responsible for the distributions of species-flocks in the Malili Lakes. There is some evidence of fluctuation in water level from acoustic and seismic surveys (J. M. Russell, unpublished data), such as submerged river valleys, in lakes Matano and Towuti that may have caused changes in habitat or periods of isolation between different lakes. It is likely that these periods of isolation may have generated diversity among lakes and facilitated local adaptation within lakes. This corroborates many of the large genetic splits between species of different lakes. However, these processes do not explain the maintenance of restricted distributions following rejoining of the lakes or the presence of multiple intralacustrine radiations with parallel evolution of adaptive traits. While it remains likely that the complex radiations of species-flocks in this system are the result of sympatric and parapatric processes, the potential role of allopatry cannot be discounted. Such stochastic natural events, including sudden geological or limnological changes and recent extinctions, may have played an important role in determining the community composition and the distribution of species-flocks in the lakes (Whitten et al. 1987).

Towards integrated research on speciation

Overall, when the biotic and abiotic characteristics of the Malili Lakes are considered, we are presented with a unique opportunity to study speciation processes. The low taxonomic richness and simple community structures within these lakes facilitate the study of the specific forces driving radiations in the system by limiting the total number of abiotic and biotic interactions to consider. In such a system, a comprehensive characterization of the physicochemical conditions and the entire food web of the lakes will allow for the quantification of physical and biological interactions. Moreover, ecological-genomics studies in the system can link the direct genomic effects of environmental factors (e.g., metal toxicity, nutrient availability) to genotypes and infer population-level responses and speciation events. Detailed characterization of biotic interactions, such as bioenergetics and food-web dynamics, may then lead to the prediction of community-level changes. Furthermore, the interconnectedness of the lakes offers an ideal arena to observe passive dispersal and speciation patterns of planktonic species in the differing environments of each lake. The inclusion of Lake Poso as a proximal but segregated system

would also reveal much about the role of geography and dispersal ability in the evolution of various study taxa. As more advanced geological studies are conducted on the lake basins, it will become possible to add timelines to various radiations. This may include correlating physical conditions of the lakes with the occurrence of speciation events, the age and rate of radiations events, and using fossils to calibrate molecular clocks in many taxa. It appears that the radiations of shrimp, fish and possibly gastropods may be in their early stages, as there is a lack of genetic structure at the intra-specific level and divergences of mitochondrial sequences between sister species are still very small (von Rintelen et al. 2007; von Rintelen et al. 2010; Herder and Schliewen 2010). Indeed, the utility of this system for studying radiations has already been highlighted by several authors, as the small size and intermediate complexity of the radiations opens a rare opportunity to observe and follow the early stages of a radiation and investigate the principal drivers of this process (Herder et al. 2006a; Herder and Schliewen 2010).

Perhaps even more noteworthy is the potential utility of the Malili Lakes for studying crustacean radiations, particularly because of their young ages and intermediate sizes. While many other remarkable crustacean radiations have occurred within ancient lakes, including the amphipods of Lakes Ohrid, Titicaca, and Baikal (in which there are over 300 species) (Kamaltynov 1992), over 200 species of ostracods in both Lake Tanganyika and Baikal of which 90% are endemic (Martens 1994), many of these radiations are old and extensive. Although large-scale comparisons between these radiations have been helpful in revealing the relative importance of certain factors responsible for speciation (e.g., brooding, trophic specialization, sexual selection), the extremely old age of these radiations and the large numbers of species have proven difficult in demonstrating common drivers of diversification (Martens and Schön 1999). While the Malili Lakes still possess very high crustacean endemicity, the number of species within these young radiations is relatively small. Thus, they may provide a key step in linking crustacean diversity to specific evolutionary forces.

The Indonesian ancient lakes represent a remarkable system for evolutionary study. Their unusual physical conditions and varying degrees of isolation and interconnectedness promotes them as an ideal natural model for research on speciation. The use of an integrated approach involving geological, limnological, ecological, and genomics will certainly provide valuable insights into the mechanisms of speciation in aquatic taxa. Important conservation issues can also be addressed as increasing anthropogenic activity surrounding the lakes threatens endemic fauna (Whitten et al. 1987; Sabo et al. 2008). The Malili Lakes will unquestionably continue to reveal much about radiation and may potentially lead to comprehensive understanding of speciation processes in natural systems.

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