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Biogeographic conundrum: Why so few stream nerite species (Gastropoda: Neritidae) in Australia?

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Abstract

Nerites (Gastropoda: Neritidae) are prominent members of tropical marine and freshwater gastropod faunas and rich assemblages can be found in many streams of islands in the Indo-Pacific. For example, the streams of Fiji and New Guinea each support at least 23 species of freshwater neritimorphs, with representatives in the genera: Clithon, Neripteron, Neritilia, Neritina, Neritona, Neritodryas, Septaria, and Vittina. The striking diversity of this group in the small coastal streams of Pacific Islands contrast with a paucity of taxa in tropical Australia, despite northern Australia occupying a similar latitude. Just four taxa have been reported from Australia and only two can be considered common. These patterns are in marked contrast to the wide distribution of many marine nerites in the Pacific and conflicts with Island Biogeography Theory. Strikingly, many of these stream taxa have adopted an amphidromous lifestyle; adult gastropods feed and reproduce in freshwater, whereas larvae are swept to the ocean and undergo a marine dispersive phase before settling near the entrance to creeks and re-entering these freshwater systems as crawling juveniles. Rapid transit of larvae to the ocean via short, steep, fast-flowing streams may offer an explanation for this biogeographic conundrum. Larvae that do not reach the ocean within a few days may starve or exhibit poor survival. Hence, the disruption of stream-ocean connectivity may explain the low diversity of these taxa in northern Australia. Sea level rise in northern Australia in the current interglacial has further weakened stream-ocean connectivity with the development of vast flood plains and slow-moving rivers. We contend that: (1) poor stream-ocean connectivity is not conducive to the maintenance of populations of nerites in northern Australia; and (2) new records of freshwater nerites may be revealed by surveys in short, steep coastal streams of northern Australia.

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Biogeographic conundrum: why so few stream nerite species (Gastropoda: Neritidae) in Australia?

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Summary

1. Nerites (Gastropoda: Neritidae) are prominent members of tropical marine and freshwater gastropod faunas and rich assemblages can be found in many streams of islands in the Indo-Pacific. For example, the streams of Fiji and New Guinea each support at least 23 species of freshwater neritimorphs, with representatives in the genera: *Clithon*, *Neripteron, Neritilia*, *Neritina*, *Neritona, Neritodryas, Septaria and Vittina*.

2. The striking diversity of this group in the small coastal streams of Pacific Islands contrast with a paucity of taxa in tropical Australia, despite northern Australia occupying a similar latitude. Just four taxa have been reported from Australia and only two can be considered common. These patterns are in marked contrast to the wide distribution of many marine nerites in the Pacific and conflicts with Island Biogeography Theory.

3. Strikingly, many of these stream taxa have adopted an amphidromous lifestyle; adult gastropods feed and reproduce in freshwater, whereas larvae are swept to the ocean and undergo a marine dispersive phase before settling near the entrance to creeks and re-entering these freshwater systems as crawling juveniles.

4. Rapid transit of larvae to the ocean via short, steep, fast flowing streams may offer an explanation for this biogeographic conundrum. Larvae that don’t reach the ocean within a few days may starve or exhibit poor survival. Hence the disruption of stream-ocean connectivity may explain the low diversity of these taxa in northern Australia. Sea level rise in northern Australia in the current interglacial has further weakened stream-ocean connectivity with the development of vast flood plains and slow-moving rivers.

5. We contend that (i) poor stream-ocean connectivity is not conducive to the maintenance of populations of nerites in northern Australia and (ii) new records of freshwater nerites may be revealed by surveys in short, steep coastal streams of northern Australia.

1. The conundrum

The Neritimorpha are a group of gastropods totalling several hundred taxa in marine brackish and freshwater habitats, particularly in tropical regions (Scott & Kenny 1998, Fukumori & Kano 2014). The marine members of this group often dominate tropical shores. Streams on many Pacific Islands also support a rich fauna with around 33 species of Neritidae drawn from eight genera in the Indo-Pacific region (Haynes 1988†). More than 20 species of stream nerites can be found in Fiji as well as New Guinea, closely followed by the islands of New Caledonia, Samoa, the Solomon Islands and Vanuatu with species numbering in the high teens (Table 1). Even modest-sized creeks in this region can possess an impressive range of taxa, often in large numbers (Kano et al. 2011, Fig. 1).

The diversity that occurs in the modest sized creeks of these Pacific Island nations contrasts with the paucity of this stream fauna observed in tropical and subtropical Australia. Just four taxa, drawn from four genera, are recorded in the Atlas of Living Australia for Australian streams (Table 2)‡. Even the Islands of Hawaii support as many taxa, despite their remoteness (Table 1). The small number of taxa in Australia runs counter to Island Biogeography theory (MacArthur & Wilson 1967). Species-Area relationships alone suggest northern Australia should support many more taxa than have been observed (Mcguinness 1984). Here we seek to highlight this apparent biogeographic conundrum and offer an explanation.

2. Amphidromy: the key to understanding nerite biogeography?

Streams on Pacific Islands are usually short, steep and reliant on very small catchments. Consequently, they experience extremes in climatic and hydrological variation. In turn, these streams carry a high likelihood of faunal extirpation and have selected for an unusual mode of development - amphidromy (McDowall, 2007, 2010, Abdou et al. 2015). Adult gastropods feed and reproduce in freshwater, while their larvae are swept to the ocean and may undergo an extended marine dispersive phase before resuming a freshwater existence.

† Haynes originally noted the presence of five genera, but this has subsequently expanded to eight as listed in the World Register of Marine Species (WoRMS).

‡ We note though that the recent monograph by Eichhorst (2016) records the genus *Septaria* and several additional taxa in the genera *Clithon, Neritina* and *Vittina* from Australian streams.

Following recruitment at the entrance of creeks and streams, upstream movements by crawling snails have been observed, sometimes *en masse* following significant river discharge (Schneider & Frost 1986, Blanco & Scatena 2005).

The important role of amphidromy in the biogeography of insular lotic fauna of islands has been recognised for some time (Smith et al. 2003). Amphidromy has evolved in a range of disparate taxa including decapod crustaceans (Cook et al. 2012, Castelin et al. 2013) and at least nine families of stream-dwelling fishes, particularly representatives of the Eleotridae and Gobiidae (McDowall 1988, Keith & Lord 2011). Among gastropods, amphidromy is also observed for a few Thiaridae (e.g., Hidaka & Kano 2014) and the neritimorph families Neritiliidae (Kano & Kase 2003) and neritids (Abdou et al. 2015, Eichhorst 2016). These taxa possess small larvae which may reduce their risk of being swept from their natal estuaries (Fukumori & Kano 2014), however all studied amphidromous taxa have extended Pelagic Larval Duration (PLD) with their planktotrophic larvae capable of dispersing for weeks and even months (Myers et al. 2000, Crandall et al. 2010, Alda et al. 2016 and references therein). It has been hypothesised that these larvae are capable of delayed metamorphosis (Pechenik 1990) resulting in the possibility of extremely long-distance dispersal events (Crandall et al. 2012).

The high dispersal potential of amphidromous nerites is reflected in the distribution of this group among Indo-Pacific islands; these islands share many taxa in common. If we ignore the four taxa restricted to Hawaii, then 27 of the remaining 29 species are shared among three or more Island nations, as well as Southeast Asia (see Table 1 in Haynes 1988). Furthermore, three of the four taxa in Australia are widespread across the Pacific (Table 2). Genetic evidence lends support to the high dispersive potential of amphidromous species; they show little evidence of population structuring in the Caribbean (Page et al. 2013) and the Pacific (Myers et al. 2000, Crandall et al. 2010). The high dispersal potential of these taxa adds further to our biogeographic conundrum; amphidromous species should be capable of reaching Australian streams, so why don't they?

It is now widely accepted that the amphidromous mode of development is a response to unstable habitats where expiration through flood or drought is highly likely (Thuesen et al. 2011, Abdou et al. 2015). But, not only are these habitats unstable over ecological time frames; islands erode and no longer induce orographic rainfall. Consequently, oceanic islands are relatively short-lived and represent unstable habitats over evolutionary and geological time scales (Smith et al. 2003, Whittaker et al. 2008). Changes in the suitability of habitat as island chains 'evolve' may explain the apparent preference of the amphidromous nerite, *Neritona* (*Neritina) granosa*, for younger Islands in the Hawaiian chain (Alda et al. 2015).

3. The importance of stream-ocean connectivity

Amphidromy is most prevalent on small oceanic islands and is co-incident with steep, short coastal streams with small catchments (McDowall 2010, Thuesen et al. 2011). These conditions provide strong connectivity between stream and ocean, ensuring the rapid transit of larvae to the ocean. Rapid transit appears to be important, at least for amphidromous fish larvae, as delays induce starvation and increase mortality among early life stages (Iguchi & Mizuno 1999). Data for nerites are scant, but there is an unpublished report of high mortality associating with holding nerite larvae in freshwater for several days (Ford 1979 - cited in Abdou et al. 2015). Consistent with the notion of rapid transit Resh et al. (1992) observed five-fold more nerite egg cases deposited on stones in fast-moving sections of creeks in French Polynesia compared with pools.

Surveys of short, steep streams in Northern Australia have revealed a poorly characterised fish assemblage and added 10 new records (8 of them gobies) to the Australian freshwater fish fauna (Thuesen et al. 2011). Most of these streams were fed from tiny catchments <6 km^2. Amphidromous fishes dominated this fauna and these streams were faunistically more similar to high islands of the Pacific than to nearby continental river systems. McDowall (2010) has also observed the low incidence of amphidromy on continents, noting that coastal streams of central America are the exception, but are characterised by small steep streams derived from small catchments (McDowall 2010).

Changes wrought by sea level rise since the last glacial may have further compromised stream-ocean connectivity (Thuesen et al. 2011). Northern Australia is now dominated by extensive flood plains with relatively slow-moving rivers. Larvae released from the headwaters of streams will take some time to reach the ocean, disrupting stream-ocean connectivity. We are not aware of any studies on the development of amphidromous nerite larvae, including their growth and survivorship in freshwater environments, but these hypotheses are clearly testable.

Australia's increasing aridity (White 1994) and variability in hydrological flows (Unmack 2001, Kennard et al. 2010) will no doubt see the extinction of established freshwater taxa. Yet the recent documenting of a freshwater fish fauna in very small streams in Australia's wet tropics, dominated by amphidromous taxa (Thuesen et al. 2011) is instructive. It argues that the dispersive abilities of fishes with amphidromous development allows their reinvasion and persistence in unstable habitats.

We conclude that hydrological conditions on continental northern Australia are currently not conducive to the maintenance of amphidromous gastropods. We also predict that searches in small coastal northern Australian streams may generate new records of nerites for Australia, and given the dispersal abilities of amphidromous species it seems unlikely that endemic taxa will be found.

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Data availability statement

All data presented in this opinion piece are from published sources and have been cited.

Conflict of interest statement

The authors have no conflicts of interest to declare.

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Table 1: Indo-Pacific stream neritid gastropods taxa by nation or region. Numbers of species and genera are drawn from two sources: 1 Smith (1992); 2 Haynes (1988) with taxon counts updated using WoRMS (World Register of Marine Species)

Location	species	genera	source
Australia	4	4	1[†]
SE Asia	20	7	2
New Guinea	23	7	2
Palau	5	4	2
Guam	7	4	2
Caroline Is. Truk & Ponepe	9	6	2
Hawaii	4	2	2[‡]
Solomon Is.	16	7	2
Vanuatu	14	7	2[§]
New Caledonia	18	6	2
Fiji	23	8	2
Samoa	16	7	2[¶]
Tahiti	12	6	2

† Eichhorst (2016) lists an additional genus and several additional species (see text for details), but only those taxa listed Table 2 are recorded in the Atlas of Living Australia

‡ Cowie et al. 1995 conservatively listed 2 species in a single genus

§ Kano et al. 2011 suggested that "approximately" 40 species occur on the Island of Santo, Vanuatu

¶ Cowie et al. 1998 listed 26 species in 5 genera, although 3 subgenera are now elevated to the level of genus

Table 2: Numbers of Australian Records (Atlas of Living Australia, ALA) for freshwater Neritidae in Australia. Distribution in the Pacific is drawn from Table 1 of Haynes (1988) and the WoRMS database; data are the number of nations or Island States in which a taxon has been recorded from a maximum of 12.

Taxon	ALA records in Australia	Distribution in the Pacific
Clithon oualaniense (Lesson, 1831)	186	8/12
Neritina pulligera (Linnaeus, 1767)	56	9/12
Vittina variegata (Lesson, 1831)	30	11/12
Neripteron violaceum (Gmelin, 1791)	128	3/12

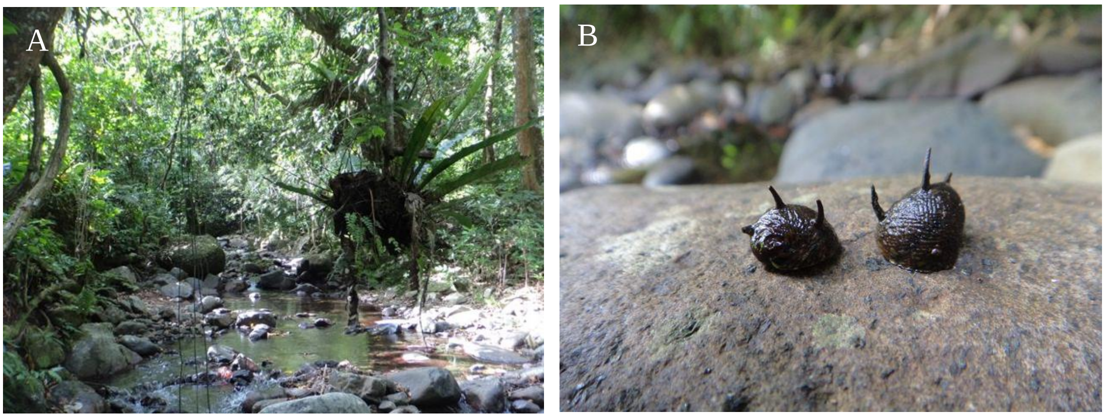

Figure 1. Typical modest-sized Pacific high island creek containing 15 species of nerites; Rukuruku Creek, Island of Ovalua, Fiji. A, creek ≈1.5km above the entrance. B, *Clithon pritchardi* (spinose form).