

## Turban snails as habitat for foliose algae: contrasting geographical patterns in species richness

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**Abstract.** Understanding patterns of species richness is a major goal for ecologists, especially in space-limited habitats where many organisms live on top of others (epibiosis, e.g. by algae growing on gastropods in marine environments). We tested the hypotheses that species richness of epiflora on the gastropod *Turbo torquatus* would not differ between regions with similarly rich algal floras, and that epifloral richness would increase with increasing gastropod size. Macroalgal floras of Hamelin Bay (HB), Marmion (M), Jurien Bay (JB) and Kalbarri (K), Western Australia, ranged from ~20 to 40 species reef<sup>-1</sup> (JB = HB = M ≥ K). Epiflora on small *T. torquatus* (shell area <150 cm<sup>2</sup>) did not differ among regions but epifloral richness increased with increasing basibiont size. Large *T. torquatus* (>150 cm<sup>2</sup>) were only found in Hamelin Bay and Marmion, where epifloral richness differed substantially. Epifloral richness was positively related to basibiont size in Marmion but not in Hamelin Bay. However, densities of patellid limpets on large *T. torquatus* were ~4× higher in Hamelin Bay than in Marmion, implying that limpet grazing suppresses epifloral richness. Epifloral richness on turbinids is not simply associated with regional species pools or gastropod size; rather, biological interactions at the scale of individual basibionts apparently govern broad scale patterns of epibiosis.

**Additional keywords:** epibiosis, grazing, Turbinid snails, *Turbo torquatus*, Western Australia.

### Introduction

Space is often a limiting resource in marine environments, where epibenthic sessile species rely on hard substrata for a significant part of their life cycle. Consequently, hard surfaces are usually rapidly fouled by invertebrates or algae (Wahl 1989). Macroalgae generally dominate on upward-facing surfaces where there is sufficient light and relatively low grazing pressure (Irving and Connell 2002). Where grazing is intense, the substratum is usually devoid of erect vegetation, comprising mainly crusts of coralline algae ('barrens') (Fletcher 1987; Coleman *et al.* 2006).

Shell-producing gastropods are 'islands' of hard substratum, and they often provide habitat to a rich epibiota of algae and sessile animals. More generally, epibiotic associations are defined by a basibiont (the host) that provides habitat for attached or mobile species (the epibionts). Animal basibionts are usually slow-moving or sessile, non-burrowing, long-lived, large and often with a biologically inactive external body surface (Wahl and Mark 1999). With ~80 described host species, Gastropoda is the animal class with the largest number of known

basibionts (Wahl and Mark 1999). However, an abundance of epibiota is also common on many other benthic invertebrates (e.g. Davis and White 1994). Obligate epibionts are rare – the majority of epibionts are facultative (i.e. not host- or substratum-selective), and are usually also found living on other suitable surfaces in the vicinity of their hosts (Wahl and Mark 1999). The ecological significance of epibiosis varies greatly (Wahl 1989); for example, for gastropod basibionts epibiosis has been associated both with positive effects of reducing predation rates (Thornber 2007), and negative effects of increased mortality (Schmitt *et al.* 1983; Warner 1997) and reduced reproductive performance and fitness (Buschbaum and Reise 1999).

Turbinid gastropods (family Turbinidae) are conspicuous elements of intertidal and subtidal habitats in tropical and temperate zones (Fletcher 1987; Foster and Hodgson 2000; Vanderklift and Kendrick 2004). In temperate waters of Australasia, the large *Turbo torquatus* (up to 12 cm shell height) is often the dominant gastropod. In Western Australia, *T. torquatus* is found on most subtidal reefs (5–15 m depth) from Kalbarri (27°S) in the Indian Ocean, and south into the

Southern Ocean (Vanderklift and Kendrick 2004; Wernberg *et al.* 2008). Herbivory is generally not intense on these rocky reefs (Wernberg *et al.* 2008; Vanderklift *et al.* 2009), and a dense cover of macroalgae dominated by the small kelp *Ecklonia radiata* and fuclean algae characterise most sunlit surfaces (Wernberg *et al.* 2003; Smale *et al.* 2010). The south-west coast of Western Australia is one of the most species-rich areas for macroalgae in the world (Bolton 1994). The composition and structure of algal assemblages differ among regions at different latitudes in this region (Wernberg *et al.* 2003; Smale *et al.* 2010), and between reefs of different geology (Harman *et al.* 2003), geomorphology (Toohey *et al.* 2007), and wave exposure (Kendrick *et al.* 1999). However, the taxonomic richness of foliose species with thalli > 0.5 cm in length remains roughly consistent across the region, typically with 15–30 species per 0.25 m<sup>2</sup> (Kendrick *et al.* 1999; Harman *et al.* 2003; Wernberg *et al.* 2003; Toohey *et al.* 2007).

Understanding the mechanisms that drive patterns of species richness is a major research agenda for ecologists (Brown 1995). Many studies have investigated patterns of epibiosis within a location (e.g. between different basibiont taxa: Davis and White 1994), but rarely have patterns among locations been assessed. Because of the facultative nature of epibiosis (Wahl and Mark 1999), the epibiota of basibionts such as *T. torquatus* represent 'samples' of local communities. Patterns of epibiota richness on widespread basibionts may thus be informative of regional and local drivers of community structure more generally, as well as for epibiota specifically. The species richness of local communities depends on the interplay between broad-scale biogeographical and evolutionary processes that determine the regional species pool, and small-scale ecological processes that exclude, or promote, subsets of species through biotic and abiotic interactions (Keddy 1992). Nevertheless, across ecosystems and taxa two general patterns have emerged: strong positive relationships between (a) the richness of regional species pools and that of their local assemblages (Witman *et al.* 2004; Briggs 2007); and (b) the size of a habitat patch and its species richness (MacArthur and Wilson 1967; Whittaker and Fernández-Palacios 2007).

Here, we assess the model that epibiota richness on turbinid gastropods is positively related to the richness of the regional species pool and the size of the basibiont. As the species richness of regional algal floras in our study area are similar, this model predicts that (1) there will be no differences in the species richness of epiflora among different regions, and (2) species richness of the epiflora will increase with increasing size of basibiont.

## Methods

Foliose macroalgae and gastropods were sampled from reefs within four regions (Hamelin Bay, 34°S; Marmion, 32°S; Jurien Bay, 30°S; Kalbarri, 28°S) evenly spaced by ~2° of latitude (~300 km coastline), along the south-west coast of Western Australia. All reefs were similar with respect to depth (10–12 m), kelp canopy cover (60–80%), wave exposure (exposed) and geomorphology (low relief platforms with 1–2 m vertical sections interspersed) (e.g. Tuya *et al.* 2009a). The latitudinal gradient encompassed in this study is characterised by a gradual 2–3°C change in ocean temperature, but there is no

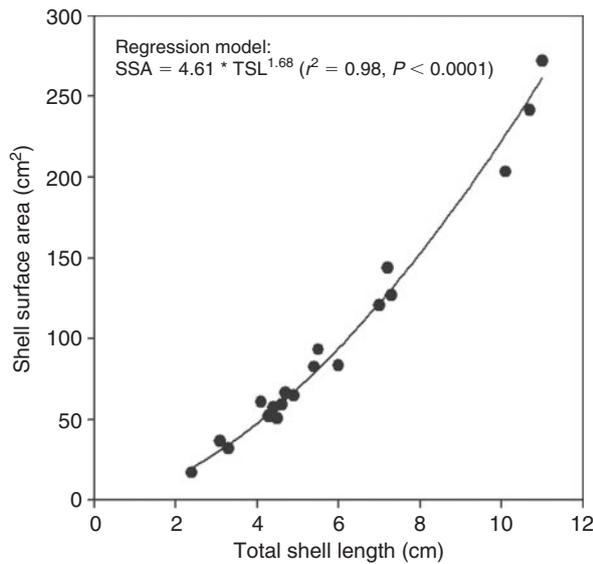
upwelling and water nutrient concentrations are consistently low (Smale and Wernberg 2009).

The species richness of the regional algal floras was assessed by harvesting and identifying all foliose macroalgae > 0.5 cm from 0.25-m<sup>2</sup> quadrats ( $n = 6$  from each reef) from six reefs (>1 km apart) within each region in November 2005. Quadrats were pooled for each reef and the numbers of taxa tallied. One-way ANOVA, followed by *post hoc* Student–Newman–Keuls tests, tested for differences in species richness among regions. Variance homogeneity was assessed by Cochran's *C*-test.

*Turbo torquatus* individuals ( $n = 156$ ) were collected in January–March 2006 (austral summer) from at least three of the six reefs in each region. *T. torquatus* were easily recognisable from other turbinids because of the characteristic 'shoulders' on the shell (a feature peculiar to the West Australian subspecies, *T. torquatus* subspecies *whitleyi*) and their distinctly grooved operculum. Gastropods were collected by SCUBA divers and brought to the boat, where their total shell length was measured with callipers as the distance from the protoconch to the base of the outer lip (Wernberg *et al.* 2008). Epiflora attached to their shells were visually identified, as accurately as possible, before releasing the snails unharmed. Encrusting algae were not included because these were ubiquitous and could not be distinguished on live *T. torquatus* in the field. Although it was often difficult to ascertain the exact identity of each epibiont (many algae require reproductive structures, sectioning and microscopy for proper identification), it was always possible to distinguish the number of different macroscopic species. In addition to foliose algae, we also counted epibiotic gastropod grazers (e.g. small limpets living on top of the turban snails). The number of *T. torquatus* collected varied between reefs, and all gastropods were pooled within their respective region. Consequently, in this study we are not able to assess patterns that might exist among reefs within each region. However, our general observations while working with gastropods on these reefs (e.g. Wernberg *et al.* 2008; Tuya *et al.* 2009b) suggest that such differences are negligible.

The surface area of a gastropod shell cannot easily be determined due to its complex geometry. We used stereophotography to assess the relationship between total shell length, an easily obtainable measure of size, and shell surface area for *T. torquatus* ( $n = 20$  individuals across a range of sizes). Stereo-photography was used to generate a 3-dimensional image of the shell from which surface area could be measured by triangulation between points on the shell surface (Abdo *et al.* 2006). Data were fitted to a power function by non-linear regression.

The relationship between gastropod size (shell surface area) and species richness was explored separately for small (<150 cm<sup>2</sup> shell area, 79.5 mm total shell length) and large (>150 cm<sup>2</sup> shell area) gastropods. The cut-off between small and large gastropods was chosen as the size threshold characterising the latitudinal distribution of *T. torquatus* populations in Western Australia (Wernberg *et al.* 2008); with the exception of one individual from Jurien Bay that was excluded from the analyses, large individuals were only found at the two southern regions, Hamelin Bay ( $n = 40$ ) and Marmion ( $n = 20$ ). Pooling all gastropods within a region, one-way ANOVA tested for differences in epifloral richness among regions for small



**Fig. 1.** Relationship between total shell length (distance from the protoconch to the base of the outer lip) and shell surface area calculated from triangulations based on digital stereo-photography ( $n = 20$ ).

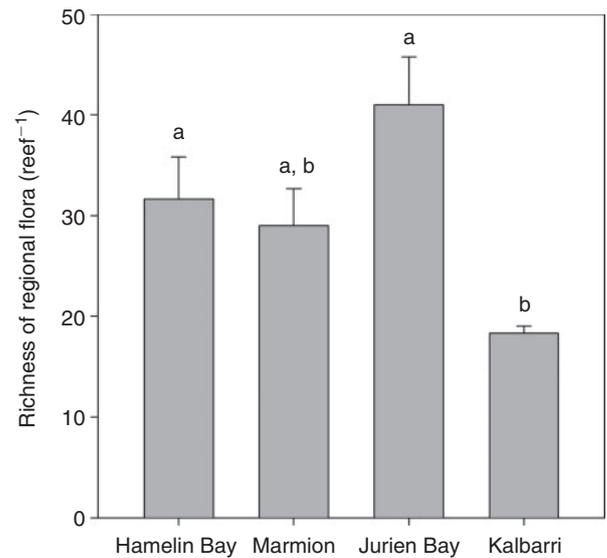
gastropods and  $t$ -tests (uneven variances) tested for differences in basibiont size, epifloral richness and limpet density on large *T. torquatus* between Hamelin Bay and Marmion. Variance homogeneity was assessed by Cochran's  $C$ -test. Pearson product-moment correlation assessed the degree of covariation between basibiont size, epibiotic limpet density, and epifloral richness.

## Results

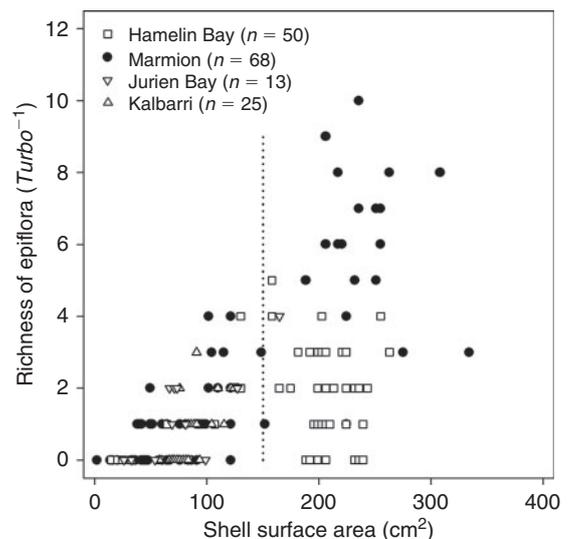
Total shell length was a good predictor of shell surface area ( $r^2 = 0.98$ ,  $P < 0.0001$ ; Fig. 1), and the regression model was used to calculate the shell surface area of all *Turbo torquatus* from field measurements of total shell length.

Mean species richness of regional algal floras ranged from 18.3 to 41.0 species reef<sup>-1</sup>, and there were significant differences among regions ( $F_{3,20} = 6.47$ ,  $P = 0.003$ ), although *post-hoc* SNK tests were unable to establish an unambiguous pattern of differences between regions (Fig. 2; Jurien Bay = Hamelin Bay = Marmion  $\geq$  Kalbarri). Importantly, for the comparison of epifloras on large gastropods, there was no difference in regional species richness between Hamelin Bay and Marmion.

A total of 156 gastropods were sampled across the study area; 95 were small ( $< 150$  cm<sup>2</sup>) and 61 were large ( $> 150$  cm<sup>2</sup>). There were no differences among locations in mean size ( $F_{3,91} = 1.89$ ,  $P = 0.140$ ) or epiflora species richness ( $F_{3,91} = 0.11$ ,  $P = 0.96$ ) for small *T. torquatus*. On average, the size of small gastropods was  $75 \pm 3$  cm<sup>2</sup> and they hosted  $0.91 \pm 0.1$  s.e. ( $n = 95$ ) species of foliose algae. Across all regions, there was a positive relationship between gastropod size and species richness of the epiflora on small *T. torquatus* ( $r = 0.61$ ,  $P < 0.0001$ ,  $n = 95$ ; Fig. 3). Large ( $> 150$  cm<sup>2</sup>) *T. torquatus* were only found in Hamelin Bay and Marmion (Fig. 3). Large individuals from Marmion ( $238 \pm 9$  cm<sup>2</sup>, mean surface area  $\pm$  s.e.,  $n = 20$ ) were significantly larger

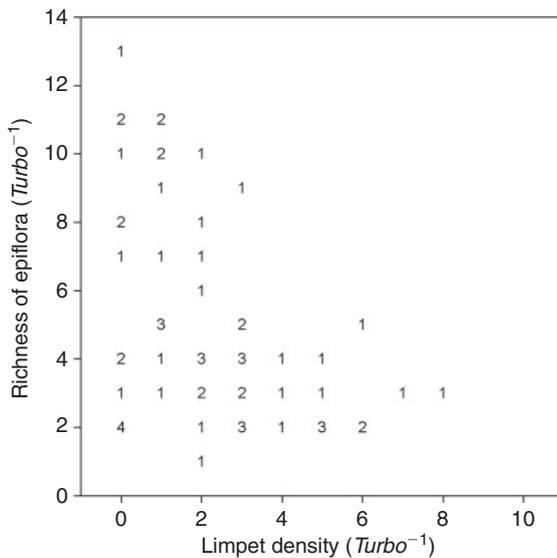


**Fig. 2.** Species richness (mean + s.e.) of foliose macroalgae  $> 0.5$  cm in each region ( $n = 6$  reefs per region). Species richness does not differ among regions sharing a letter above the bar ( $P > 0.05$ , SNK tests).



**Fig. 3.** Species richness of epibiotic foliose algae growing on *Turbo torquatus* sampled from subtidal habitats in four regions (Hamelin Bay, Marmion, Jurien Bay and Kalbarri) across south-western Australia. The dotted line indicates 150 cm<sup>2</sup> (79.5 mm total shell length); the cut-off between small and large gastropods used in the data analyses.

( $\sim 14\%$ ) than those from Hamelin Bay ( $208 \pm 4$  cm<sup>2</sup>,  $n = 40$ ) ( $t_{1,56} = 3.00$ ,  $P = 0.006$ ; Fig. 3). The species richness of epiflora was 2.5 times higher in Marmion ( $8.3 \pm 0.7$  s.e. species *Turbo*<sup>-1</sup>,  $n = 20$ ) than in Hamelin Bay ( $3.4 \pm 0.5$  s.e. species *Turbo*<sup>-1</sup>,  $n = 40$ ), and this was statistically significant ( $t_{1,56} = 6.74$ ,  $P < 0.001$ ). The epiflora in Marmion continued to accumulate species with increasing basibiont size, as we found for small gastropods, which resulted in a positive relationship there between epifloral richness and basibiont size ( $r = 0.13$ ,  $P = 0.590$ ,  $n = 20$ ; Fig. 3). The relatively low value of the



**Fig. 4.** Species richness of epibiotic foliose algae v. epibiotic limpet density for large ( $>150\text{ cm}^2$ ) *Turbo torquatus* from Hamelin Bay ( $n = 40$ ) and Marmion ( $n = 20$ ). Numbers indicate the frequency of overlapping data points.

correlation coefficient was considerably influenced by two individuals with very low species richness (i.e. outliers clearly outside the general pattern); the correlation coefficient increased to  $r = 0.49$  ( $P = 0.044$ ,  $n = 18$ ), when these two samples were omitted. In contrast to Marmion, the richness of the epiflora on large *T. torquatus* did not increase with increasing shell size in Hamelin Bay ( $r = -0.17$ ,  $P = 0.284$ ,  $n = 40$ ).

Epibiotic gastropods were entirely dominated by 10–20-mm patellid limpets (mainly *Patelloida alticostata*), and their average density in Marmion ( $0.7 \pm 0.21$  s.e. limpets  $Turbo^{-1}$ ,  $n = 20$ ) was less than one-quarter of densities in Hamelin Bay ( $3.05 \pm 0.31$  limpets  $Turbo^{-1}$ , s.e.,  $n = 40$ ) ( $t_{1,56} = -6.31$ ,  $P < 0.001$ ). Across all large *T. torquatus*, there was a negative correlation between limpet density and the species richness of foliose epiflora ( $r = -0.44$ ,  $P = 0.0004$ ,  $n = 60$ ; Fig. 4).

## Discussion

*Turbo torquatus* was found to host a rich epiflora comprising up to 13 different species of foliose macroalgae per individual. For small *T. torquatus*, the species richness of the epiflora did not differ between regions and species richness increased with increasing basibiont size. For large *T. torquatus*, there were significantly fewer epifloral species in Hamelin Bay than in Marmion despite no differences in the regional species pools of macroalgae. Moreover, although the species richness of epiflora increased with increasing basibiont size in Marmion, this relationship was not found in Hamelin Bay. Consequently, our data do not support the model that epifloral richness simply reflects the richness of the regional species pool and the size of the basibiont. Substantially higher densities of epibiotic limpets in Hamelin Bay, and a negative relationship on large snails between limpets and algal species richness, suggest that limpets maintain a disproportionately low epifloral species richness in Hamelin Bay compared to that found in Marmion. Thus, our

study indicates that biological interactions between limpets and algae (presumably grazing) modify the expected richness patterns.

No epiflora were found on gastropods smaller than  $49.3\text{ cm}^2$  (41 mm TSL). Assuming an annual growth rate of  $12.9\text{ mm year}^{-1}$  (Joll 1975), this implies that *T. torquatus* are around 3.2 years old before they start to become fouled by macroalgae. The relatively long delay before the onset of fouling suggests that the epibiosis requires some sort of preconditioning of the shell such as damage from failed predation attempts (Schmitt *et al.* 1983), facilitation by earlier colonisers such as serpulid worms (Warner 1997) or encrusting coralline algae (Thornber 2007). Indeed, both serpulids and encrusting corallines were often seen on small shells otherwise devoid of epibionts.

Patterns in species richness of epiflora growing on *T. torquatus* followed the expected patterns for small gastropods and large gastropods in Marmion, but not for large gastropods in Hamelin Bay. Overall, the mean number of epifloral species in Marmion (8.3) was higher than the median epibiota richness (4.8) reported for molluscs as a group (Wahl and Mark 1999). Given that *T. torquatus* individuals are large relative to most other gastropods, this is consistent with an overall positive relationship between basibiont size and epibiont richness. Conversely, the markedly lower epifloral richness in Hamelin Bay (3.4) clearly sets this region apart from the general patterns of epibiosis. Large *T. torquatus* individuals were slightly bigger in Marmion than in Hamelin Bay, but the difference was relatively small (14%), and despite the positive relationship between richness and size in Marmion, size differences seem unlikely to be a significant contributor to the large (~250%) difference in epifloral richness between the two regions. Moreover, size differences do not explain the lack of correlation between size and species richness in Hamelin Bay.

The division between small and large *T. torquatus*, which would be ~6.2 years old assuming  $12.9\text{ mm year}^{-1}$  (Joll 1975), was based on biogeographical patterns of population structure (Wernberg *et al.* 2008). However, this threshold also appears to correspond well to the onset of change in the epifloral richness pattern in Hamelin Bay (cf. Fig. 3). There have been relatively few experimental tests to distinguish between multiple competing models of what drives epifloral assemblages. Abbott and Bergey (2007) found that grazing from other molluscs, not nutrients or chemical defences (antifouling), controlled algal growth on a freshwater snail. Grazing is also a plausible driver of the observed patterns of epifloral species richness on large *T. torquatus*. Limpets and small gastropods have some of the greatest per capita interaction strengths with macroalgae (Sala and Graham 2002), and their ability to control algal communities is well documented (e.g. Fletcher 1987; Coleman *et al.* 2006). The mean density of limpets on large *T. torquatus* in Hamelin Bay (~3 limpets  $Turbo^{-1}$  in  $208\text{ cm}^2$ ) is equivalent to ~140 limpets  $\text{m}^{-2}$ , which is in the same order of magnitude as has been recorded to cause a significant impact on the cover of foliose macroalgae across temperate rocky coasts (Coleman *et al.* 2006). Moreover, a range of invertebrates including limpets, chitons and abalone are known to cue their recruitment to coralline algae (see references in Pearce and Scheibling 1990). If coralline algae have developed

on ~4-year-old *T. torquatus*, then this might attract limpets to recruit onto *T. torquatus* and develop a capacity (density and size) for top-down control as *T. torquatus* approaches the threshold size between small and large, thus explaining the lack of impacts on small *T. torquatus* and the relatively sudden onset of apparent grazing control. The implication is that broad-scale processes that dictate the presence of limpets may indirectly control the patterns of epibiosis on *T. torquatus*. A range of mechanisms could account for regional differences in limpet densities between Hamelin Bay and Marmion. For example, substantial differences across latitudinal gradients, of several hundred kilometres, in adult populations of limpets and other rocky reef invertebrates have been associated with oceanographic control of recruit delivery (Connolly *et al.* 2001) and recruitment and recruit performance (Gilman 2006).

Although the rich epiflora on large gastropods from Marmion can best be described as lush growth, sometimes with attached kelps and fucoids as large as 30–50 cm, the large gastropods from Hamelin Bay resemble ‘mini-barrens’, i.e. hard substratum dominated by encrusting corallines devoid of foliose algae. This classical ‘top-down state’ is interesting because it contrasts with the organisation of subtidal reef assemblages across most of temperate Australia (west of Wilsons Promontory: Connell and Irving 2008), where grazing pressure generally is too low to influence landscape and assemblage structure (Connell and Irving 2008; Wernberg *et al.* 2008; Vanderklift *et al.* 2009).

In conclusion, we found substantial differences in epifloral richness despite similarly rich regional algal floras, and richness did not always increase with increasing basibiont size. As such, the generalisations about species richness did not apply unequivocally to the epiflora on turbinids in Western Australia. We propose that limpets are responsible for the geographical differences in epifloral richness. Our study adds to the mounting evidence that regional differences in biological interactions, perhaps mediated by environmental conditions such as ocean circulation patterns or temperature, is likely to play an important role in influencing broad-scale patterns of biodiversity.

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