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Running head: Parasite diversity increases with latitude

Parasite species richness and intensity of interspecific interactions increase with latitude in two  
wide-ranging hosts

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1 **Abstract**

2           Although the latitudinal diversity gradient is a well-known and general pattern, the  
 3 mechanisms structuring it remain elusive. Two key issues limit differentiating these. First,  
 4 habitat type usually varies with latitude, precluding a standardized evaluation of species richness.  
 5 Second, broad-scale and local factors hypothesized to shape diversity patterns co-vary with one  
 6 another, making it difficult to tease apart independent effects. Examining communities of  
 7 parasites in widely distributed hosts can eliminate some of these confounding factors. We  
 8 quantified diversity and interspecific interactions for trematode parasites infecting two similar  
 9 snail species across 27 degrees of latitude from 43 locations in tropical and temperate oceans.  
 10 Counter to typical patterns, we found that species richness, levels of parasitism, and intensity of  
 11 intraguild predation increased with latitude. Because speciation rates are precluded from driving  
 12 diversity gradients in this particular system, the reversed gradients are likely due to local  
 13 ecological factors, specifically, increased productivity and stability. We highlight how this  
 14 system may serve as a useful tool to provide insight into what processes drive diversity gradients  
 15 in general.

16  
 17 **Keywords:** diversity patterns, latitudinal gradients, species richness, rarefaction, dispersal,  
 18 trematodes, parasites, intraguild predation, biotic interactions

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1 **INTRODUCTION**

2           Perhaps the greatest challenge to understanding why there are more species in the tropics  
 3 compared to temperate regions has been that many of the proposed mechanisms for the well-  
 4 known latitudinal diversity gradient (LDG) co-vary with one another and are likely not mutually  
 5 exclusive (Rohde 1992, Willig et al. 2003, Mittelbach et al. 2007). It would therefore be helpful  
 6 to examine the LDG for systems that, by their nature, preclude some groups of proposed  
 7 mechanisms from possibly driving diversity patterns. Similar to a gene knockout experiment, the  
 8 results of such a study would provide insight into the forces that underlie the LDG, no matter the  
 9 results. For instance, if an LDG was not observed, this would suggest that the excluded  
 10 mechanisms are important in driving the general LDG. Alternatively, if an LDG was still  
 11 observed, it would provide evidence against the importance of the excluded mechanisms, and a  
 12 smaller pool of potential mechanisms would remain to be considered. Here, we examine the  
 13 diversity of parasites that infect widespread host species that span tropical and temperate  
 14 latitudes in the Pacific and Atlantic Oceans. We posit that this system can serve as a tool for  
 15 elucidating general principles concerning the LDG because it precludes the operation of several  
 16 explanatory factors.

17           Most functional explanations for the latitudinal diversity gradient can be at least crudely  
 18 placed into two different categories (Huston 1999, Harrison and Cornell 2008). First, there are  
 19 mechanisms that involve evolutionary or historical processes that operate at relatively large  
 20 temporal and spatial scales. Examples of large-scale mechanisms include greater rates of  
 21 speciation (e.g., given higher temperature and insolation (Rohde 1992) and lower rates of  
 22 extinction at lower latitudes (reviewed by Mittelbach et al. 2007). Secondly, there are ecological  
 23 mechanisms that can operate at both relatively large and small spatial and temporal scales. For

1 example, the “species-energy” hypothesis (also known as the “productivity” or “more  
 2 individuals” hypotheses, Brown 1981, Wright 1983, Currie et al. 2004) proposes that tropical  
 3 ecosystems have more species because greater tropical productivity supports a larger aggregate-  
 4 pool of individuals. This larger group of individuals can be partitioned into a greater number of  
 5 species that can maintain viable population sizes. A major challenge with testing various  
 6 hypotheses is that many proposed mechanisms are not mutually exclusive and that they  
 7 frequently co-vary with each other and with latitude. Hence, if it were possible to examine  
 8 systems that preclude the functioning of some groups of proposed mechanisms, we could  
 9 perhaps more clearly determine the mechanisms underlying the LDG.

10 Another difficulty with determining the patterns and mechanisms underlying the LDG is  
 11 the variability in the types of habitat and resources across latitudes. In fact, it has long been  
 12 hypothesized that a substantial part of the LDG may be driven by the tropics having a greater  
 13 variety of habitats or resources (MacArthur 1965, Brown 1981). If we were to control for habitat  
 14 and resource variability, would we still observe the LDG? Although work documenting the LDG  
 15 at local scales (alpha richness) does provide some control of habitat and resource variability,  
 16 there is still uncertainty concerning the importance of heterogeneity. Experimental manipulation  
 17 using artificial habitat patches (e.g., Freestone and Osman 2011, Freestone et al. 2011) is one  
 18 way to control for this. Another way to control both habitat and resource variation is to examine  
 19 widespread host species infected with specific parasites because of the natural standardization  
 20 they can provide.

21 Hosts provide naturally replicated, standardized habitat and resource units for  
 22 communities of parasites (Holmes and Price 1986, Price 1990, Hechinger 2013). Therefore, a  
 23 widely distributed host species could provide a high degree of standardization of habitat and

1 resource type across latitudes. Additionally, for some hosts it is feasible to sample numerous  
 2 populations, providing high replication of local parasite communities throughout the latitudinal  
 3 range. Hence, the feasibility of rigorous sampling and habitat/resource standardization provided  
 4 by communities of parasites specialized on broadly distributed hosts suggests that they can  
 5 provide powerful systems for understanding latitudinal diversity gradients. Despite this, we are  
 6 aware of no previous studies examining parasite diversity in a single species spanning the  
 7 temperate zone to the tropics (other than humans, see discussion).

8         Diverse communities of trematode parasites infect and castrate the Pacific horn snail,  
 9 *Cerithideopsis californica* (= *Cerithidea californica*, see Reid and McClaremont 2014) and the  
 10 Atlantic horn snail, *Cerithideopsis pliculosa* (= *Cerithidea pliculosa*)(Martin 1972, Wardle 1974,  
 11 McNeff 1978, Hechinger et al. 2007, this study). These snails are sister species that diverged  
 12 from one another following the formation of the Isthmus of Panama (Miura et al. 2010). Each  
 13 snail species is broadly distributed in their respective oceans, from the tropics to the temperate  
 14 zone (Keen 1971, Warmke and Abbott 1975, Miura et al. 2012). The snails are common and  
 15 often very abundant in intertidal mangrove and mudflat habitats. These habitats are major  
 16 foraging areas for migratory shorebirds, which serve as final hosts for the trematodes and  
 17 disperse them widely along their flyways (e.g., Miura et al. 2006). Thus, these trematode  
 18 parasites have several useful attributes for examining latitudinal diversity gradients. First, the  
 19 broadly distributed snail hosts serve as a standardized habitat and resource-type across latitudes.  
 20 Second, the use of widely ranging migratory birds as final hosts permits the rapid dispersal of  
 21 trematodes over thousands of kilometers to different snail populations across latitudes (Miura et  
 22 al. 2006). This rapid and wide dispersal of species among latitudes should remove the signature  
 23 of regional-scale processes, such as oceanic current dispersal boundaries, latitudinal variation in

1 the composition of species pools, or latitudinal variation in speciation rates. Supporting this idea,  
 2 the known geographic ranges of most of these trematode species span the ranges of their hosts,  
 3 from tropical to temperate latitudes in both Pacific and Atlantic Oceans (Fig. 1). Combined,  
 4 these attributes permit focus on how local (versus broad-scale) ecological factors contribute to  
 5 latitudinal diversity gradients.

6 In addition to species richness, current, albeit limited, evidence suggests that the intensity  
 7 of interspecific interactions also increases towards the tropics (see review by Schemske et al.  
 8 2009, and Freestone et al. 2011). Indeed, the biotic interactions hypothesis proposes that strong  
 9 species interactions in the tropics increase diversification rates, leading to high diversity at low  
 10 latitudes (Dobzhansky 1950, Mittelbach et al. 2007, Schemske et al. 2009). Additionally, higher  
 11 diversity could lead to increased opportunities for interspecific interactions to occur. While  
 12 measuring interspecific interactions in free-living species presents several challenges, trematode  
 13 parasitic castrators enable straightforward examination of the intensity of interspecific  
 14 interactions, and do so in two different ways. Most simply, we can directly measure the level of  
 15 parasitism in host populations across latitudes (e.g., proportion of snails infected and castrated by  
 16 trematodes). However, we can also examine interactions between the parasite species  
 17 themselves. These trematodes strongly interact through a form of intraguild predation that  
 18 follows a well-defined dominance hierarchy (Kuris 1990, Sousa 1993, Lafferty et al. 1994,  
 19 Hechinger 2010). When two trematode species encounter each other in the same host, the  
 20 dominant species predictably kills (excludes) the subordinate species, most often by eating it.  
 21 Importantly, it is possible to estimate the number of individuals lost to intraguild predation using  
 22 observed abundance information (Lafferty et al. 1994). Because the dominance hierarchy is  
 23 known for these species, and is based on gross morphological characters (e.g., body size) that are

1 stable throughout our study area (personal observations), it is also possible to quantify the  
 2 intensity of intraguild predation across latitudes.

3 Here, we examine trematode species richness and interaction intensity in populations of  
 4 two horn snail species from temperate North America to tropical southern Central America in  
 5 both the Atlantic and Pacific Oceans. We hypothesized that if broad-scale factors or habitat/niche  
 6 variability were the primary drivers of the LDG, we would not see a typical decrease in diversity  
 7 with latitude. However, if local ecological factors are important in driving diversity gradients we  
 8 would see an LDG. Consistent with this, we also hypothesized that the intensity of interspecific  
 9 interactions would track species diversity gradients. We found that, in contrast to general  
 10 patterns, trematode species richness in both snail species was positively correlated with latitude,  
 11 exhibiting a “reversed” LDG, where the tropics are relatively low in trematode species richness  
 12 compared to temperate regions. Further, consistent with this reversed latitudinal pattern, we  
 13 found that the strength of interspecific interactions, measured as the intensity of intraguild  
 14 predation, also increased from low to high latitudes.

## 15 MATERIALS AND METHODS

### 16 Data collection

17 We sampled snails across 27 degrees of latitude along both coasts of North and Central  
 18 America, covering most of the geographic distribution of both Pacific and Atlantic horn snails,  
 19 *Cerithideopsis californica* and *C. pliculosa*, respectively (we note that, given the molecular  
 20 genetic evidence in Miura *et al.* (2010), we consider *C. californica* to include the nominal  
 21 species: *C. californica* (Haldeman), *C. mazatlanica* (Carpenter) and *C. valida* (Adams)). In the  
 22 eastern Pacific, our southernmost sampling locations correspond to the peak of nearshore  
 23 molluscan diversity and sea surface temperature (Roy *et al.* 1998, Valdovinos *et al.* 2003) which

1 is shifted slightly to the north of the equator. We collected snails from 43 locations within five  
 2 countries in North and Central America, however, to standardize sampling effort, prevalence  
 3 analyses included only sites for which we were able to dissect at least 100 snails and parasite  
 4 species richness analyses included those sites where we encountered at least 100 trematode  
 5 infections (see below). Sampling locations were selected using Google Earth and previous  
 6 experience to identify suitable estuarine habitats for snails. From January 2007 through March  
 7 2010, at each location we used a standard searching procedure for horn snail populations at  
 8 several sites (each  $< 200 \text{ m}^2$ ) by first identifying suitable habitat and then searching for snails  
 9 (generally within mangrove roots or near salt-marsh vegetation). Most sites were located in  
 10 different estuaries, but in a few cases sites in the same large system were separated by a few  
 11 kilometers (Fig. 2, Appendix A). We treated sites as independent samples for our analyses,  
 12 because these snails have very low mobility and trematode diversity varies over small spatial  
 13 scales (Hechinger and Lafferty 2005, Torchin et al. 2005, Hechinger et al. 2007). We targeted the  
 14 largest snails from each site for dissections as these are generally older and have a higher  
 15 probability of being infected with parasites (e.g., Sousa 1993, Kuris 1990, Torchin et al. 2005).

16 Snails were measured from the apex of the spire to the apertural base with Vernier  
 17 calipers and processed for parasites following Torchin et al. (2005). Trematode species were  
 18 identified following Martin (1972) and Hechinger and Huspeni (unpublished). While we use the  
 19 same morphospecies codes for both Pacific and Atlantic horn snail trematodes (Fig. 1, Appendix  
 20 B), we recognize that the Atlantic species may actually be very similar cryptic species.

### 21 **Species richness and prevalence**

22 We used rarefied species richness estimates to control for sampling effort (Sanders 1968,  
 23 Gotelli and Colwell 2001, Colwell et al 2012) of trematodes by rarifying parasite species

1 richness to a sample size of 100 trematode infections from each site using Estimates 9.10  
 2 (Colwell and Elsensohn 2014). We used a general linear model (GLM) to analyze the effect of  
 3 latitude, ocean (Atlantic, Pacific) and their interaction on species richness. We used the same  
 4 approach to evaluate the association of prevalence (proportion of snails infected per site) with  
 5 snail size and latitude from sites where we collected dissected more than 100 snails (either  
 6 infected or uninfected). GLMs were made using JMP version 10 (SAS Institute).

7 **Intensity of interspecific interactions**

8         To measure the intensity of intraguild predation among trematode species, we estimated  
 9 the total proportion of trematode infections killed by other species at each site using the formulas  
 10 in Lafferty et al. (1994). These formulas require information on the trematode species dominance  
 11 hierarchy, which was first constructed by Kuris (1990). We used the most recent version of this  
 12 hierarchy, as presented in Hechinger (2010). The formulas estimate the number of recruited  
 13 parasites killed by other trematodes by applying the observed prevalence of each species in  
 14 “dominant-free” snails to the portion of the snail population infected by dominant trematodes.  
 15 This prevalence, minus observed co-infections with dominants, represents the amount of  
 16 trematode infections killed via intraguild predation. We summed the killed and observed  
 17 infections across all species to obtain the total amount of recruits for a study site and calculated  
 18 intensity of intraguild predation as the proportion of total recruits lost to intraguild predation. We  
 19 then used a GLM to examine the strength of intraguild predation versus latitude, ocean and their  
 20 interaction.

21 **RESULTS**

22 **Species richness and prevalence**

1 We quantified parasitism in over 27,000 snails from 43 locations within five countries in  
 2 North and Central America across 27 degrees latitude in both the Pacific and Atlantic Oceans.  
 3 Parasite species richness was greater in the temperate zone, increasing with latitude from about 7  
 4 to 30-35 degrees in both the Pacific and Atlantic Oceans ( $F_{1,19}=14.7$ ,  $R^2 = 0.48$ ,  $P = 0.0011$ , Fig.  
 5 3). There was a marginally significant effect of ocean ( $F_{1,19}=3.7$ ,  $P = 0.069$ ) but no significant  
 6 interaction between ocean and latitude ( $F_{1,19}=2.1$ ,  $P = 0.16$ ) indicating that a single slope could  
 7 explain the diversity-latitude relationship in both oceans (Fig. 3).

8 Prevalence, or the proportion of infected snails, also increased with latitude in both  
 9 oceans ( $F_{1,32}=23.7$ ,  $R^2 = 0.52$ ,  $P < 0.0001$ , Fig. 4). There was no significant ocean effect ( $F_{1,32}=$   
 10  $2.3$ ,  $P = 0.14$ ) nor interaction between ocean and latitude ( $F_{1,32}=0.22$ ,  $P = 0.64$ ). Although  
 11 prevalence increased with latitude, a GLM incorporating prevalence as a predictor indicated that  
 12 it did not influence the effect of latitude on species richness in either ocean ( $F_{1,18} = 0.68$ ,  $P =$   
 13  $0.42$ ,  $F_{1,18} = 0.10$ ,  $P = 0.75$  interaction). That is, species richness increased with latitude,  
 14 regardless of the increase in prevalence.

15 Mean shell size was greater in the Pacific compared to Atlantic ( $F_{1,31} = 44.6$ ,  $P < 0.0001$ )  
 16 but did not consistently vary with latitude in either ocean ( $F_{1,31} = 1.4$ ,  $P = 0.23$ , interaction  $P =$   
 17  $0.30$ ), nor did mean size influence species richness in either ocean (main effect  $F_{1,17} = 0.38$ ,  $P =$   
 18  $0.54$ , interaction  $F_{1,17} = 2.1$ ,  $P = 0.16$ ).

### 19 **Intensity of interspecific interactions**

20 The intensity of interspecific interactions, measured as intraguild predation also increased  
 21 with latitude ( $F_{1,19}= 24.7$ ,  $R^2 = 0.62$ ,  $P < 0.0001$ , Fig. 5). Here, all effects were significant  
 22 (ocean,  $F_{1,19}= 6.4$ ,  $P = 0.02$ , interaction,  $F_{1,19}= 5.1$ ,  $P = 0.037$ ), reflecting that interaction  
 23 intensity increased more strongly in the Atlantic than in the Pacific. In both oceans, at low

1 tropical latitudes, less than 5% of trematode recruits were estimated to be lost to intraguild  
 2 predation, while this percentage increased to approximately 15% in the Pacific and  
 3 approximately 30% in the Atlantic in the temperate zone. As expected, prevalence and species  
 4 richness combined explained a substantial amount of the variation in intraguild predation ( $R^2 =$   
 5  $0.94$ ,  $P < 0.0001$ ,  $n = 23$ ), and both maintained independent effects in the model (prevalence:  
 6  $F_{1,20} = 218.5$ ,  $P < 0.0001$ , richness:  $F_{1,20} = 8.1$ ,  $P = 0.0098$ ), with no interaction between the two  
 7 ( $F_{1,19} = 0.43$ ,  $P = 0.52$ ).

## 8 **DISCUSSION**

9 Counter to typical species diversity patterns, trematode species richness in two  
 10 congeneric marine snails increased from the tropics to the temperate zone across  $27^\circ$  latitude in  
 11 both the Pacific and Atlantic oceans. Trematode prevalence (proportion of snails infected) was  
 12 also greater at higher latitudes. Consistent with these reversed latitudinal patterns, we found that  
 13 the strength of interspecific interactions, measured as the intensity of intraguild predation, also  
 14 increased from low to high latitudes. Below, we (1) provide possible explanations for the  
 15 observed reversed gradients of parasite species richness and intensity of interspecific  
 16 interactions, (2) highlight how parasites can serve as useful tools for examining general  
 17 mechanisms underlying LDGs, and (3) discuss implications of our results for understanding  
 18 global patterns of parasite diversity.

### 19 **Possible explanations for the reversed LDGs**

#### 20 *Parasite species richness*

21 In our study, the rapid and widespread dispersal of trematodes by birds (e.g., Miura et al. 2006)  
 22 precludes broad-scale factors from driving the reversed LDGs. Hence, we postulate that the  
 23 reversed LDGs for these trematodes are driven by local ecological factors such as demographic

1 attributes of the host snail populations (the primary resource and habitat for these trematodes).  
 2 Our preliminary observations suggest that, at lower latitudes, the horn snail populations are  
 3 characterized by greater spatial patchiness, greater mortality rates, greater temporal instability  
 4 (stochastic population persistence), and potentially smaller populations. For instance, we  
 5 compiled independent qualitative observations from two of us (MET and OM) concerning the  
 6 density and patchiness characterizing the horn snail populations at each of the study sites. GLM  
 7 analyses of these data suggest that, indeed, densities increased and patchiness decreased by about  
 8 an order of magnitude at our highest latitude study sites compared to those in the lowest latitudes  
 9 (Appendix C).

10         These demographic attributes of their host snails would drive lower trematode  
 11 recruitment rates, higher mortality rates, and higher rates of local extinction. Any of these factors  
 12 would result in local diversity of trematodes being lower in the tropics compared to the  
 13 temperate zone, supporting the idea that snail demographic changes may explain the reversed  
 14 LDG, Aguirre-Macedo et al. (2011) document how trematode parasite diversity dropped and  
 15 then slowly recovered over a few years following a major disturbance (a hurricane wiped out a  
 16 local population of *C. pliculosa* in the Yucatan Peninsula, Mexico). Such greater environmental  
 17 instability and habitat turnover (snail mortality) in the tropics could prevent parasite diversity  
 18 from reaching the high levels characterizing temperate zone communities. Future research  
 19 carefully examining infection rates (recruitment), host density (resource abundance), and host  
 20 mortality (turnover) would provide strong tests of mechanisms driving the observed reversed  
 21 LDGs.

22         Another potential explanation, which we discount, is that variation in trematode diversity  
 23 could be fueled by other hosts in the trematodes' complex life cycles (usually two additional

1 hosts: birds as final hosts, and benthic invertebrates or fishes as second intermediate hosts).  
 2 Because the diversity and abundance of these additional hosts correlates with species richness  
 3 and prevalence of trematodes infecting horn snails at small spatial scales (Smith 2001, Hechinger  
 4 and Lafferty 2005, Hechinger et al. 2007), these final and second intermediate hosts might drive  
 5 some of the observed diversity patterns. However, both bird and second intermediate host  
 6 richness are likely greater in the tropics considering general diversity patterns in the ocean  
 7 (Hillebrand 2004, Roy and Whitman 2009). Hence, if trematode latitudinal diversity tracked the  
 8 diversity of potential second intermediate and final hosts, it would likely lead to patterns  
 9 opposite to the observed reversed latitudinal diversity gradients.

10

11 *Intensity of interspecific interactions*

12 Consistent with the typical pattern of high diversity at low latitudes, available studies  
 13 suggest that interspecific interactions are also stronger in the tropics (Schemske et al. 2009,  
 14 Freestone and Osman 2011, Freestone et al. 2011). In fact, in their review, Schemske et al.  
 15 (2009) could not find a single study indicating stronger interactions in the temperate zone  
 16 compared to the tropics. In contrast to this general trend, our data for trematodes infecting horn  
 17 snails indicated that interspecific interactions increase with latitude in both oceans, and that they  
 18 do so in two different ways.

19 First, the proportion of horn snail hosts infected (and castrated) by trematodes was higher  
 20 in the temperate zones of both oceans. This is counter to the general trend where levels of  
 21 interactions, including levels of parasitism, tend to be higher in the tropics (Schemske et al.  
 22 2009). For instance, Salkeld et al. (2008) show that blood parasite loads (but not prevalence) in  
 23 lizards are higher in the tropics. Similarly, Robar et al. (2010) indicate that there is a general

1 trend for parasite-induced mortality to be greater at lower latitudes. Although trematode  
 2 parasitism does not result in death of infected horn snails, infected individuals are castrated and  
 3 reproductively dead, and this happens more frequently at higher latitudes.

4         Second, our results also indicate that the intensity of intraguild predation among  
 5 trematodes increases 3 to 6-fold at higher latitudes. This was expected considering the reversed  
 6 latitudinal gradient observed for trematode species richness and prevalence, key determinants for  
 7 intraguild predation in this system; the different species cannot kill one another if they do not co-  
 8 occur in the same individual snail. The probability of such interspecific encounter increases with  
 9 species richness and as the proportion of habitat occupied (prevalence) increases. Although  
 10 readily explainable, this result is noteworthy as it is contrary to general trends, consistent with  
 11 the reversed LDGs. Interestingly, unlike the biotic interactions hypothesis, which proposes that  
 12 strong species interactions cause diversification (Dobzhansky 1950, Mittelbach et al. 2007,  
 13 Schemske et al. 2009), the observed increase of intraguild predation is most likely a consequence  
 14 of greater species richness and prevalence. However, while intraguild predation does not drive  
 15 the reversed LDGs, it could have influenced the shape of the reversed gradient. Specifically,  
 16 intraguild predation could decrease rarer species below detection limits disproportionately in the  
 17 temperate zone. In other words, the reversed LDG is potentially stronger than it appears.

18 **Using parasite LDGs to inform general principles**

19         We propose that additional examination of parasitism across latitudes can help reveal  
 20 mechanisms driving the general LDG. For example, both mortality of individual host snails and  
 21 extinction of host snail populations can be considered to represent habitat disturbance or turn  
 22 over, and disturbance is one of the oldest proposed general mechanisms for the LDG, with lower  
 23 disturbance fostering greater diversity (Dobzhansky 1950). Further, because snail populations are

1 the sole resource for these trematode communities, the standing stock biomass or productivity of  
 2 the snail populations—not ecosystem primary productivity—represents the energy relevant to the  
 3 popular species-energy hypothesis (see Brown 1981, who noted the importance of focusing on  
 4 the appropriate pool of energy when testing the species-energy hypothesis). Because attributes of  
 5 the snail populations are both readily quantifiable and readily expressed in general terms, this  
 6 system is particularly amenable to further experimental testing of hypotheses concerning the role  
 7 of local factors in driving the general LDG.

8         There are two previously reported reversed LDGs that are relevant here. Both  
 9 ichneumonid wasps (which are parasitoids of insects) (Owen and Owen 1974) and aphids (which  
 10 are pathogens on plants) (Dixon et al. 1987), also appear to be less diverse in the tropics (but see  
 11 Quickie (2012) who questions this pattern for ichneumonids). The “resource fragmentation  
 12 hypothesis” has been proposed to explain these “reversed” patterns (Kindlmann et al. 2007). The  
 13 idea is that increased host diversity in the tropics results in smaller or more fragmented host  
 14 population sizes, which in turn support fewer numbers and species of specialist consumers in the  
 15 tropics. The underlying mechanism behind the resource fragmentation hypothesis appears to be  
 16 similar to one of the explanations we posited above: host populations represent the relevant  
 17 energy pool (resource base) for the specialist species under consideration, and those pools may  
 18 be smaller or more patchy in the tropics, driving lower recruitment rates or smaller population  
 19 sizes, thereby supporting lower diversity. However, the above studies examine the LDG at the  
 20 aggregate taxon-level over all possible host species, versus a single host species (as with the  
 21 trematodes studied here). Further, the scale of recruitment by broadly dispersing trematodes in  
 22 our study contrasts with the small spatial scale over which both ichneumonids and aphids  
 23 disperse. Hence, while there may be common mechanisms underlying parasite LDGs, these sorts

1 of differences may provide for insightful examination of the general factors influencing broad-  
 2 scale diversity gradients.

3 **Parasite latitudinal gradients in general**

4 A large proportion of species on Earth are parasitic (de Meeus and Renaud 2002, Dobson  
 5 et. al, 2008, Poulin 2014) but we know relatively little about their geographical distributions  
 6 (Poulin 2014). Most previous studies that have examined parasite distributions across latitudes  
 7 have used data assembled from the limited literature on parasites and hosts belonging to different  
 8 species among latitudes (e.g., Poulin 1995, Rohde and Heap 1998, Gregory et al. 1991, Nunn et  
 9 al. 2005, Krasnov et al. 2004, Lindenfors et al. 2007). The outcomes of these studies have been  
 10 mixed, and this has been reflected in two reviews: Schemske et al. (2009) suggested a general  
 11 trend of higher parasite richness and prevalence at low latitudes, while a meta-analysis by  
 12 Kamiya et al. (2014) detected no overall effect of latitude on parasite species richness. These  
 13 mixed results are likely at least partly a reflection of true differences between particular host-  
 14 parasite groups. However, the lack of clear results is also likely due to variation in analytical  
 15 methods and problems with underlying data, which are assembled from a limited literature. For  
 16 instance, the tropics are often poorly represented, or not represented at all, which can preclude  
 17 detection of LDGs (Willig et al. 2003). To cite two relevant examples, Poulin and Mouritsen  
 18 (2003) detected that trematode richness appeared to increase with latitude across snail host  
 19 species and that the relationship disappeared after accounting for host phylogeny. Additionally,  
 20 further, within-species analyses for the few snail species with sufficient compiled data found no  
 21 LDG (Thieltges et al. 2009). However, as noted in both studies, the lack of tropical data makes it  
 22 difficult to seriously evaluate latitudinal diversity gradients for parasites. However, even two  
 23 comparative studies that did include some tropical data (Rohde and Heap 1998; Nunn et al.

1 2005) report mixed results. Hence, on the whole, we agree with Schemske et al. (2009) that  
 2 available data are too limited to adequately understand how the LDG pertains to parasites, and  
 3 note, along with Poulin (2014), that we may most effectively improve our understanding of  
 4 parasite LDGs by undertaking studies of parasite diversity in widespread host species, as done  
 5 here.

6 To our knowledge, there has only been one previous study that examined the LDG for  
 7 parasites of a single host species that naturally spans temperate to tropical latitudes. In their  
 8 examination of human parasites, Guernier et al. (2004) reported greater parasite richness in the  
 9 tropics. In addition, humans appear to experience higher levels of infection by parasites in the  
 10 tropics (Low 1990, Cashdan 2001). Although these results may be confounded by differences in  
 11 wealth, the extent of public health programs across these regions, and geographic origins of  
 12 human diseases, both patterns for humans are consistent with general latitudinal diversity and  
 13 species interaction gradients. Our results run counter to what has been documented for humans,  
 14 with parasite diversity being lower and interactions being weaker in the tropics. The differences  
 15 in these two systems underscore that we can clearly benefit from additional studies of parasite  
 16 diversity on widely distributed host species to better develop empirical generalizations and test  
 17 mechanistic hypotheses concerning parasite LDGs.

18 Our study has focused on parasite communities infecting two widespread host species,  
 19 and therefore cannot directly resolve the question of how overall parasite species diversity will  
 20 vary with latitude. It has been reasonably postulated (e.g., Rohde 1992, Poulin 2014) that overall  
 21 parasite diversity (total parasite species in all hosts per unit area) will increase in the tropics as a  
 22 consequence of parasite diversity tracking host diversity (i.e., more host species = more parasite  
 23 species). Our documentation of reversed LDGs suggests that the situation will be more complex

1 and may not follow a simple linear relationship. Specifically, although increasing host richness  
 2 should tend to drive increased parasite diversity, this will be countered to the extent that parasite  
 3 diversity is lower per host species. Hence, a thorough understanding of the relationship of overall  
 4 parasite richness with latitude must account for the interplay of these two potentially antagonistic  
 5 trends.

6 **CONCLUSION**

7 The two host-trematode systems that we examined exhibit latitudinal gradients in species  
 8 diversity and interaction strength that are opposite to typical patterns. These reversed gradients  
 9 are broadly interesting because the nature of the study system rules out explanations based on  
 10 large-scale mechanisms, permitting a focus on more local, ecological mechanisms. These  
 11 trematode communities are amenable to further experimental studies testing general hypotheses  
 12 concerning how local factors influence LDGs. Hence, the reversed LDGs documented here may  
 13 be exceptions that help prove a general rule for the role that local factors have in driving LDGs.  
 14 In general, parasite communities in widespread host species— perhaps even more widespread  
 15 than the hosts studied here—could provide useful tools to understand the LDG and aid in  
 16 deciphering the mechanisms that shape patterns of biological diversity.

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12 **SUPPLEMENTAL MATERIAL (ECOLOGICAL ARCHIVES) Appendices A-C.**

13 **Appendix A (Table A1).** Collection localities, site IDs (corresponding to Fig. 2), number of  
 14 snails dissected, parasite prevalence, and total parasite species encountered for the Pacific  
 15 *Cerithideopsis californica* and the Atlantic *C. pliculosa*.

16 **Appendix B (Table B1).** Trematode species and four letter codes (Fig. 1).

17 **Appendix C (Figure C1).** Crude estimates of (a) density ( $F_{1,34} = 11.6$ ,  $P = 0.0017$ ) and (b)  
 18 occurrence (inverse of patchiness) ( $F_{1,34} = 15.6$ ,  $P = 0.0004$ ) characterizing the horn snail  
 19 populations across latitudes.

20

21 **FIGURE LEDGENDS**

22 **Figure 1.** Latitudinal ranges for the trematode species comprising the guild of parasitic castrators  
 23 that infect the (a) Pacific (*Cerithideopsis californica*) and (b) Atlantic (*C. pliculosa*) horn snails.

1 X axis labels are trematode species codes (see Appendix B for species names). The black  
 2 shading indicates species ranges recovered in the current study's sampling, while the grey  
 3 shading provides the broader ranges known by using information from additional sampling by  
 4 the authors, J. C. Buck (pers. comm., Atlantic SMCY), and Wardle (1974, Atlantic ACAN). The  
 5 data indicate that most or all species are found throughout the entire range of their habitat (host  
 6 snails), as expected given the wide dispersal provided by migratory birds. Local richness is likely  
 7 a result of ecological factors influencing species' abundances.

8  
 9 **Figure 2.** Location of sampling sites throughout North and Central America (a) entire region; (b)  
 10 Santa Barbara, California; (c) Nayarit, Mexico; (d) Oaxaca, Mexico; (e) Nicaragua (f) Panama  
 11 (g) Galveston, Texas; (h) Veracruz, Mexico; (i) Belize (j) Nicaragua

12  
 13 **Figure 3.** Species richness (mean  $\pm$  SD) of trematode parasites versus latitude in the Pacific horn  
 14 snail, *Cerithideopsis californica* (dashed line and **O** symbols) and the Atlantic horn snail,  
 15 *Cerithideopsis pliculosa* (solid line and **▲** symbols). Regression lines are fit separately for each  
 16 ocean.

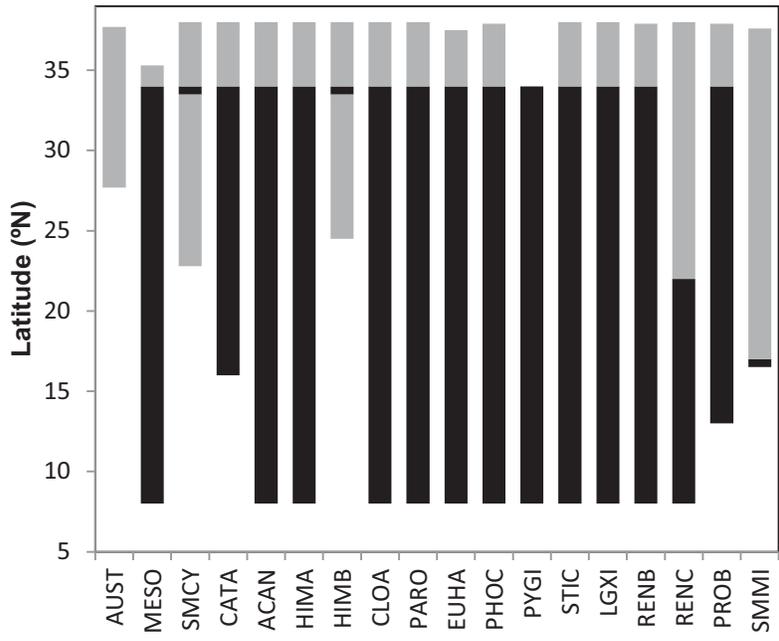
17  
 18 **Figure 4.** Trematode prevalence (proportion of snails infected) versus latitude in the Pacific horn  
 19 snail, *Cerithideopsis californica* (dashed line and **O** symbols) and the Atlantic horn snail,  
 20 *Cerithideopsis pliculosa* (solid line and **▲** symbols). Regression lines are fit separately for each  
 21 ocean. Data include only sites where  $N \geq 100$  snails dissected.

22

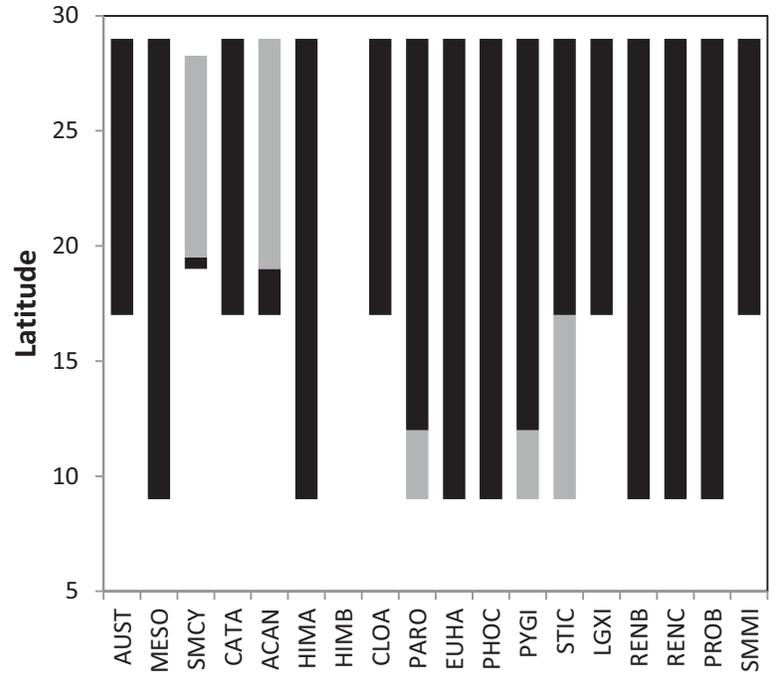
- 1 **Figure 5.** Intensity of interspecific interactions (intraguild predation) versus latitude in the
- 2 Pacific horn snail, *Cerithideopsis californica* (dashed line and **O** symbols) and the Atlantic horn
- 3 snail, *Cerithideopsis pliculosa* (solid line and **▲** symbols). Regression lines are fit separately for
- 4 each ocean. Only includes sites where  $N \geq 100$  infected snails.

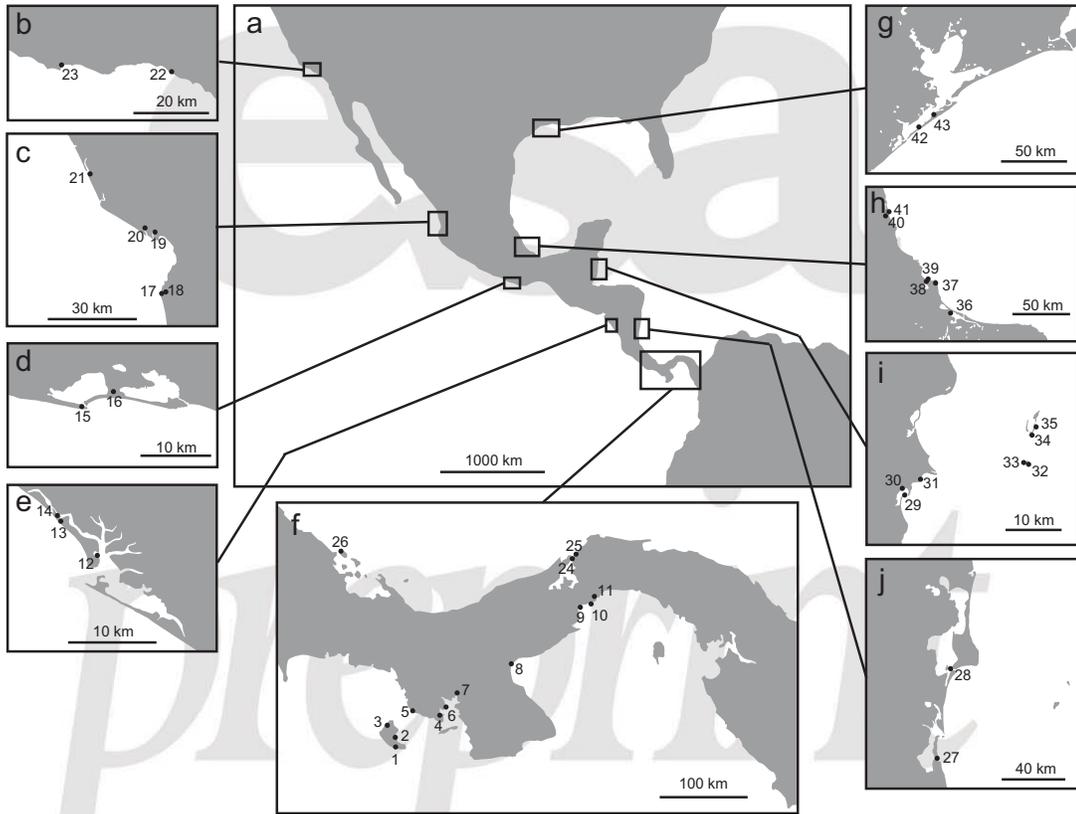
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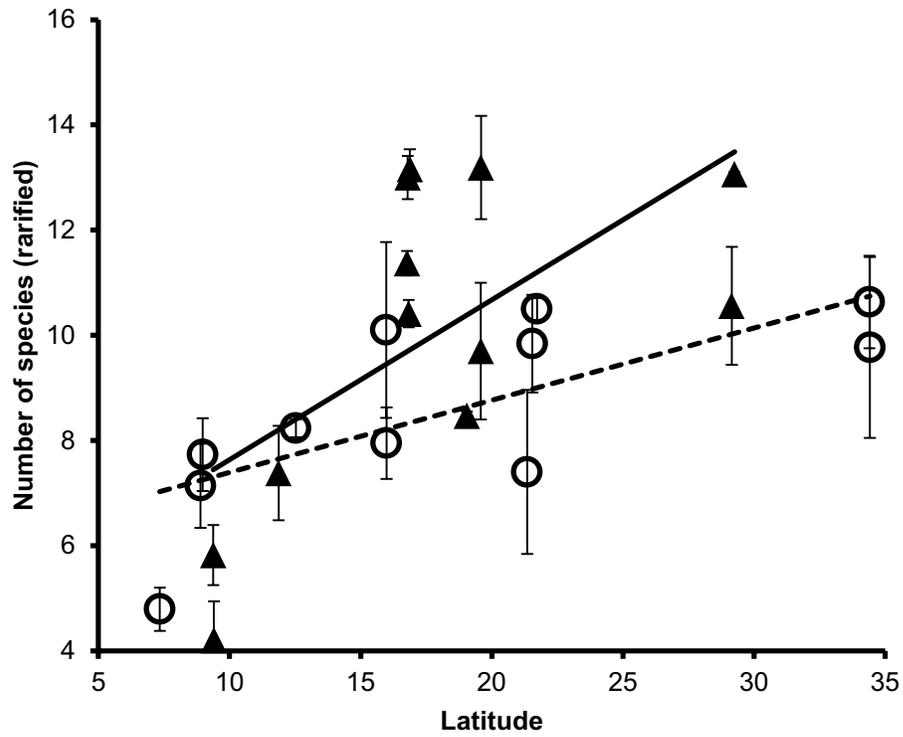
(a) Pacific



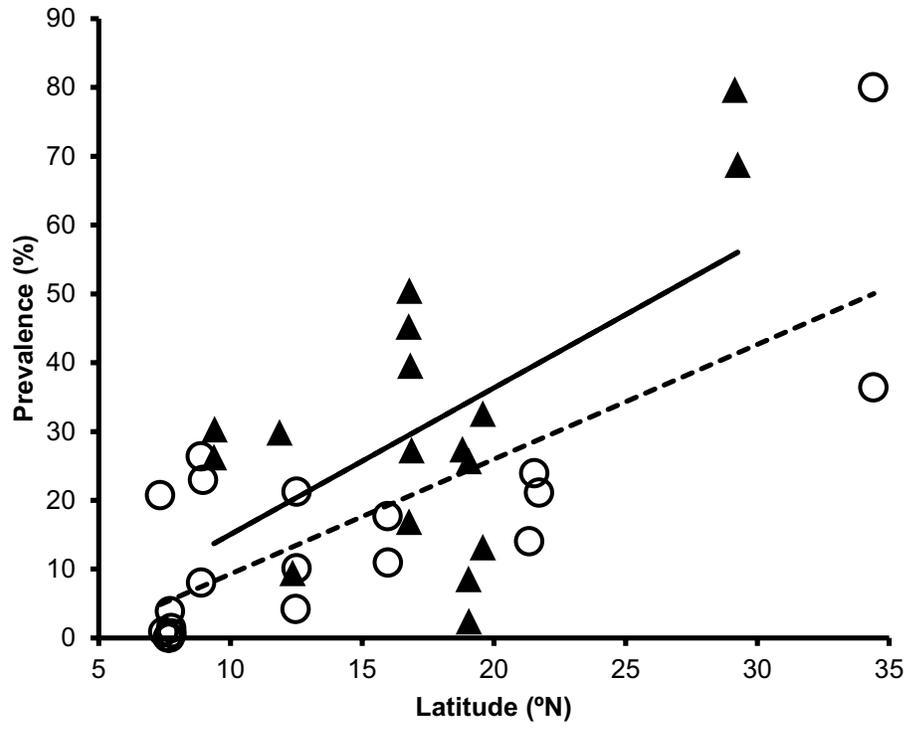
(b) Atlantic



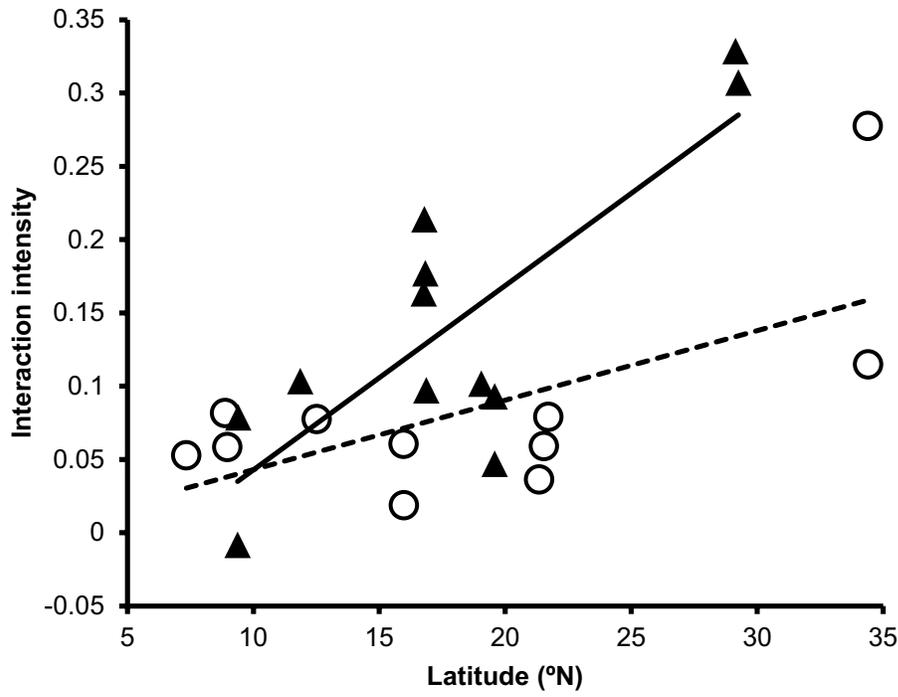




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