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Determinants of tapeworm species richness in elasmobranch fishes: untangling environmental and phylogenetic influences

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Parasite species richness is a fundamental characteristic of host species and varies substantially among host communities. Hypotheses aiming to explain observed patterns of richness are numerous, and none is universal. In this study, we use tapeworm parasites of elasmobranch fishes to examine the phylogenetic and environmental influences on the variation in species richness for this specific system. Tapeworms are the most diverse group of helminths to infect elasmobranchs. Elasmobranchs are cosmopolitan in distribution and their tapeworm parasites are remarkably host specific; therefore, making this an ideal system in which to examine global patterns in species diversity. Here, we 1) quantify the tapeworm richness in elasmobranch fishes, 2) identify the host features correlated with tapeworm richness, and 3) determine whether tapeworm richness follows a latitudinal gradient. The individual and combined effects of host size, factors associated with water temperatures (influenced by latitude and depth), host habitat, and type of elasmobranch (shark or batoid) on measures of species diversity were assessed using general linear models. These analyses included tapeworm host records for 317 different elasmobranch species (124 species were included in our analyses) and were conducted with and without taking into account phylogenetic relationships between host species. Since sharks and batoids differ substantially in body form, analyses were repeated for each host subset. On average, batoids harboured significantly more tapeworm species than shark hosts. Tapeworm richness in sharks was influenced by median depth, whereas no predictor variable included in our models could adequately account for interspecific variation in tapeworm richness in batoid hosts. The taxonomic diversity of tapeworm assemblages of sharks and batoids was influenced by median depth and median latitude, respectively. When the influence of host phylogeny is accounted for, larger hosts harbour a greater tapeworm richness, whereas hosts exploiting wider latitudinal ranges harbour more taxonomically distinct tapeworm assemblages. Species richness and taxonomic diversity of tapeworm assemblages in elasmobranch fishes are influenced by different evolutionary pressures, including host phylogenetic relationships, space constraints and geographical area. Our results suggest that ca 3600 tapeworm species have yet to be described from elasmobranch fishes.

The presence of a greater diversity of species at lower latitudes is the oldest, and possibly the most robust, spatial biodiversity relationship observed for free-living organisms (Pianka 1966, Rohde 1992, Gaston and Blackburn 2000, Willig et al. 2003, Hillebrand 2004a). Despite this fact, there exists a surprising lack of consensus regarding mechanisms to explain the latitudinal gradient in diversity (Rohde 1992, Willig et al. 2003, Hillebrand 2004a, b, Poulin and Morand 2004). Further, this pattern is more consistent in terrestrial than aquatic environments (Clarke 1992, Willig et al. 2003, Hillebrand 2004a). Parasitic organisms show a variety of relationships with latitude (Willig et al. 2003), including a negative (Price et al. 1998, Rohde 2002, Gröbler and Lewis 2008), a positive (Poulin 2001) or no (Fernandes and Price 1988, Hawkins and Compton 1992, Merino et al. 2008) relationship between latitude and species richness This lack of consensus suggests that other variables, or in the case of parasitic organisms, host variables, may influence species richness.

Even though parasites outnumber free-living organisms (May 1992, Windsor 1998), studies investigating patterns of species richness in parasitic organisms are grossly underrepresented. This bias may have important implications in ecology. Over half the species on Earth have adopted a parasitic mode of life. If parasites indeed display latitudinal trends in species richness that are inconsistent with those observed for free-living taxa, then the inverse relationship between species richness and latitude may no longer be considered a ''robust'' pattern. Other host features, such as range size, habitat and diet, may also correlate with parasite species diversity. First, host species with broader geographic distributions (expressed as latitude, longitude, depth, altitude, or area) are likely to encounter more infective stages of different parasite species than hosts with a more restricted distribution (Gregory 1990). Second, species sharing a common evolutionary history are likely to exploit similar habitats (Harper et al. 1961, Davidson 1977) and to encounter the same, or closely related, parasite faunas.

Third, hosts with diverse feeding habits are expected to encounter a greater assortment of infective stages of endoparasites (Chen et al. 2008). Although parasite richness of hosts can be influenced by feeding habits of prey items (Marcogliese 2002), the gaps in our knowledge of lifecycles of certain parasites prevent us form assessing the relative importance of this variable. As one would expect, host range, habitat and diet may act synergistically and be driven by phylogenetic influences. Nevertheless, there is no consensus regarding the relative importance of these variables as determinants of parasite richness (Poulin and Morand 2004). The inconsistencies in published results on parasite richness may be caused by their failure to control for potential confounding effects of sampling effort and phylogenetic influences on host features (Poulin and Morand 2004, Luque and Poulin 2008). Additionally, it has been suggested that taxonomic distinctness (TD) is more sensitive to host ecology than species richness and may be more useful to accurately isolate the host correlates of parasite diversity (Luque et al. 2004, Luque and Poulin 2008).

Tapeworm assemblages of elasmobranch fishes (sharks, skates and rays) are ideal to study host influences on parasite diversity. These parasites exhibit relatively strict host specificity and their hosts have broad geographic distributions. Tapeworms are the most diverse group of parasites exploiting the digestive tract of elasmobranchs (Caira and Healy 2004). Elasmobranch fishes are infected by approximately 1000 described species encompassing six different orders of tapeworms; all generally restricted to these fishes. Furthermore, elasmobranchs are found in all of the world's oceans, spread over 85% of the latitudinal scale, encountered at all depths, and, except for the freshwater stingrays (Myliobatiformes: Potamotrygonidae), cover all marine habitats. Five of the six orders of tapeworms infecting elasmobranchs exhibit relatively strict host specificity, indicating a close association with one or a few closely related host species. Only a small proportion of the life cycles of tapeworms infecting elasmobranchs have been described to date. However, we know that all are acquired by elasmobranchs via ingestion of infected prey (e.g. invertebrates, marine mammals, fish, etc.) serving as intermediate or paratenic hosts (Willams and Jones 1994). The objectives of this study are to: 1) quantify the tapeworm richness in elasmobranch fishes; 2) identify the host features correlated with tapeworm richness; and 3) determine whether tapeworm richness follows a latitudinal gradient. For reasons mentioned above, sampling effort and host phylogenetic history were taken into account. Furthermore, since sharks and batoids differ substantially in body form (Compagno 1999), analyses were repeated at both these taxonomic levels in an effort to control for this difference.

Methods

The data set

The complete tapeworm species diversity dataset was compiled searching through the Zoological Records on ISI Web of Knowledge, which includes records since 1864, using elasmobranch host taxa (Latin name and all known synonyms) in combination with ''Parasit* OR disease OR pathog*'' in September and October 2008. We only included hosts from which at least one tapeworm species has been reported, especially in light of the unavailability of negative data. Additionally, we restricted the dataset to tapeworm taxa. Synonymies and species inquirenda (doubtful species identifications requiring further investigation) were encountered during our search, and whenever possible, we adopted the most recent taxonomic treatment. Despite this, it is likely that not all identifications are accurate. For instance, a recent study revising the tetraphyllidean genus *Uncibilocularis* Southwell, 1925 transferred 5 species to the genus *Acanthobothrium* Van Beneden, 1850 (Jensen and Caira 2008). However, since our analyses focus on species diversity, such taxonomic errors have little bearing on their outcome. Furthermore, the parasite diversity for some hosts is underestimated. For instance, several phyllobothriid tetraphyllidean tapeworms have been recovered during parasite surveys of rajid skates from the North Pacific Ocean in the mid-1990s but have yet to be described (Keeney 1999), whereas trypanorhynch tapeworms recovered during the same surveys from the same hosts have been described (Keeney and Campbell 2001).

In addition to parasite species diversity, we recorded several host features for each elasmobranch species: 1) host length, measured as the maximum length from the tip of the snout to the mid-point of the pelvic fins (Randhawa and Poulin 2009); 2) latitude (range), measured as the number of degrees spanning their geographic distribution; 3) latitude (median), measured as the absolute value of the mid-point of their geographic range; 4) depth (range), measured as the difference between the shallowest and deepest depths at which they occur; 5) depth (median), measured as the mid-point of their depth distribution; 6) type of habitat where they occur (bathydemersal, benthopelagic, demersal, pelagic, and reef-associated); and 7) whether they are sharks or batoids (Compagno 1999) (Table 1). Information for these parameters was obtained from FishBase (Froese and Pauly 2008) or Compagno et al. (2005) and was not available for all species.

Measures of parasite diversity are strongly influenced by sampling/study effort (Walther et al. 1995) and correcting for this confounding variable provides a more accurate measure of diversity (Poulin 2004, Luque and Poulin 2007, 2008). We used five different measures of sampling/study effort (Supplementary material Table S1) to provide an indirect approximation of the number of hosts examined for parasites from the entire host population.

Table 1. List of parameters included in candidate models of tapeworm richness and taxonomic distinctness of tapeworm assemblages in elasmobranchs.

Parameter no.	Definition
1	Log host length
2	Log latitude (range)
3	Log latitude (median)
4	Log depth (range)
5	Log depth (median)
6	Habitat
7	Type of elasmobranch

In addition to tapeworm species richness, we also obtained the taxonomic distinctness (TD) of parasite assemblages for each host species. TD is a measure of diversity that can be more sensitive to host ecology than species richness (Luque et al. 2004, Luque and Poulin 2008). It is based on the average number of steps up the taxonomic hierarchy, based on the Linnean scheme (Phylum, Class, Order, Family, Genus, and Species), to reach a taxon common to 2 species, and computed for all species pairs included in the assemblage analysed (Clarke and Warwick 1998, 1999, Warwick and Clarke 2001, Luque et al. 2004). Since taxa included in this study belong to the same phylum and class, the variance in TD is not expected to provide us with any useful information; therefore, it has not been calculated. We used the most recent taxonomic literature to calculate the TD for each parasite assemblage. Though we based the majority of these on Khalil et al. (1994), Palm (2004), Jensen (2005), and Tyler (2006), the primary literature remained an important source of information. Although a recent proposal to erect a new cestode order has recently been published (Healy et al. 2009) it was not taken into account due to the lack of resolution of intraordinal relationships within this new proposed order. We can provide the complete list of references upon request. We computed the average TD for each host species harbouring at least 4 tapeworm species using the programme Taxobiodiv 1.2 <www.otago.ac.nz/zoology/downloads/poulin/TaxoBiodiv1.2>.

Statistical analyses

All continuous variables were log-transformed (logx + 1 if zeros were present) in order to meet assumptions of normality. We used linear regression analyses to determine the strongest correlate of species diversity (richness and TD) among the 5 measures of sampling/study effort (Supplementary material Table S1). We assessed relationships between tapeworm species richness, or TD, and predictor variables using General Linear Models (GLM). Of the 7 predictor variables included in analyses (Table 1), 5 consisted of continuous (body size, host latitudinal range, host median latitude, host depth range, and host median depth) and 2 of categorical (host habitat and type of elasmobranch) variables. We computed all possible main effects linear regression models. We ranked models according to their corrected Akaike information criterion values (AIC_c). This value was obtained from the Residual Sum of Squares for each model using the method outlined in Anderson (2008). We determined the relative importance and rank of each variable using the AIC_c differences (Δ AIC_c) and model weights (w_i) (Anderson 2008). The latter approach provides insights into the importance of each variable, taking into account the possible multicolinearity between predictor variables and requires running all possible models so that each variable is of equal footing (Anderson 2008). In cases where more than one model was supported, we used the multi-model inference approach (Burnham and Anderson 2002). We obtained model-averaged parameter estimates by weighting parameter estimates according to model probabilities (Anderson 2008). By averaging all models from our a priori set, "bad" models received a weight that tends towards "0", thus keeping model inclusion objective. We calculated the unconditional variances to obtain a 95% confidence interval for each variable. This measure takes into account the sampling variance and the variance component for model selection uncertainty (Burnham and Anderson 2002, Anderson 2008). This approach provides an estimate of the "slope" for each parameter, independent from other variables present in the model (Anderson 2008). We selected a priori sets of potentially biologically significant second-order interactions between predictor variables and compared these to models incorporating main effects included in the interaction. For instance, the relative importance of the interaction between predictor variables A and B was compared to the following models: 1) A; 2) B; 3) A + B; and 4) A + B + (A × B). The evidence ratio between the model including the interaction term and the "best" model from each set (based on AIC_c) was used to determine whether the inclusion of the interaction term improved the model significantly.

Generally, data obtained from organisms sharing a common evolutionary history are not independent from each other (Morand and Poulin 2003, Poulin and Morand 2004). Hence, we repeated analyses taking into account phylogenetic relationships between host species using the phylogenetically independent contrasts method (Felsenstein 1985) to control for confounding effects of host phylogeny on host features and measures of species diversity. We computed these independent contrasts on continuous variables using the PDAP:PDTREE programme (Midford et al. 2005) implemented in Mesquite ver. 2.5 for Mac OSX (Maddison and Maddison 2007). For host habitat, a categorical variable, we derived contrasts by transforming habitat types into dichotomous variables (i.e. pelagic vs other 4, bathydemersal vs other 4, etc.) and computed contrasts using the pairwise comparison algorithm for species pairs contrasting in state for 1 binary character (Maddison 1990, 2000) in Mesquite ver. 2.5 for MacOSX (Maddison and Maddison 2007).

We derived contrasts from a tree based on Shirai (1996), Winchell et al. (2004) and Naylor et al. (2005) [for elasmobranchs], Eitner (1995), De Carvalho (1996), Adnet and Cappetta (2001), Douady et al. (2003), Greig et al. (2005), Iglesias et al. (2005), Shimada (2005), Human et al. (2006), Lopez et al. (2006), and Cavalcanti (2007) [for sharks], and Lovejoy (1996), McEachran et al. (1996), McEachran and Dunn (1998), Rosenberger (2001), Dunn et al. (2003), and McEachran and Aschliman (2004) [for batoids] (tree is available from the authors upon request). Since no information on branch lengths for this host group is available, we estimated branch lengths assuming that characters evolved by Brownian motion (Felsenstein 1985) and verified their statistical adequacy (Garland et al. 1992). Too few resolved phylogenies of elasmobranch genera are available in the literature, thus preventing us from resolving most intrageneric relationships. Consequently, we considered all unresolved nodes (polytomies) as "soft polytomies" (Maddison 1990, Purvis and Garland 1993). Although polytomies were arbitrarily resolved by collapsing all branches within unresolved intrageneric phylogenies (Felsenstein 1985, Purvis and Garland 1993), the number of degrees of freedom was reduced for hypothesis testing

and set to between N − 1 and p − 1 (N, number of independent contrasts; p, number of nodes in the working phylogeny) in order to limit type I error (Purvis and Garland 1993). We computed contrasts following guidelines highlighted in Garland et al. (1992) and corrected for confounding variables when required. Corrections were done using the residuals obtained by regressing a selected variable (e.g. tapeworm richness) against a confounding variable (e.g. sampling/study effort).

All analyses were repeated for 2 subsets: sharks and batoids. These groups differ substantially in body form (Compagno 1999). Both phylogenetically corrected and uncorrected analyses are reported and discussed due to the lack of resolution of the elasmobranch phylogeny.

Results

Complete dataset

The data set included 317 hosts, each harbouring a raw average of 6.0 ± 6.8 (SD) (range = 1 to 47; median = 3.0) tapeworm species (Fig. 1). As Fig. 1 illustrates, 65 elasmobranch species were host to a single tapeworm species. The median study effort (no. of references on ISI Web of Knowledge including the Latin name of hosts and all known synonyms combined with ''Parasit* OR disease OR pathog*'') for these was 1 study (range = 0–13), whereas that for species hosting three or more was of 7 (range = 0–112). Of the 1896 host-tapeworm associations: 1228 involved taxa exhibiting relatively strict host specificity (11 involved the Cathetocephalidea Schmidt and Beveridge, 1990; 83 the Diphyllidea Van Beneden in Carus, 1863; 119 the Lecanicephalidea Wardle and McLeod, 1952; 10 the Litobothriidea Dailey, 1969; and 1005 the Tetraphyllidea Carus, 1863) and 668 the Trypanorhyncha Diesing, 1863. The latter is a group that has been shown to infect multiple genera within a single host family (Palm and Caira 2008).

Current estimates of the global diversity of chondrichthyan fishes are of between 1100 and 1200 species, of which over 95% are elasmobranchs (Whittington and Chisholm 2003, and references therein, Cavanagh and Gibson 2007). Only 317 species of elasmobranchs, or 26% of the upper estimate of the global diversity of these fishes, have been examined for intestinal parasites. Using the average tapeworm species richness (six species) and the average number of host specific taxa (four species) per elasmobranch species, we can thus calculate that there are ca 5400 tapeworm-elasmobranch host records and nearly 3600 undescribed species of tapeworms infecting elasmobranchs yet to be recorded.

Two elasmobranch species seemed to harbour significantly more tapeworm species than others (Fig. 1): the feathertail stingray *Pastinachus sephen* and the giant guitarfish *Rhynchobatus djiddensis*. However no biological rationale could be used to exclude these taxa from our analyses. Although both harboured substantially more tapeworm species (47 each) than others sharing the same familial designation (10.1 ± 10.7, median = 6.0, and 6.5 ± 9.8, median = 3.0, respectively), neither harboured the most taxonomically diverse tapeworm assemblage within their respective families, nor was the largest or inhabited the greatest latitudinal/depth range. Both occupied tropical reef associated habitats, but so do other representatives of their respective families. However, both species are among the best studied and in fact, there are more than ten times the number of publications on *P. sephen* and its parasites, pathogens and diseases than for most other members of the Dasyatidae (55 vs median of 4.5). Hence the importance of correcting species richness for study effort.

All five measures of sampling/study effort (Supplementary material Table S1) were log-transformed to meet assumptions of normality and correlated positively with tapeworm richness (all $p < 0.0001$; n = 306–313), but the number of references obtained from a search on ISI Web of Knowledge including the Latin name of hosts (including all known synonyms) combined with ''Parasit* OR disease OR pathog*'' was the strongest correlate (r = 0.709 vs

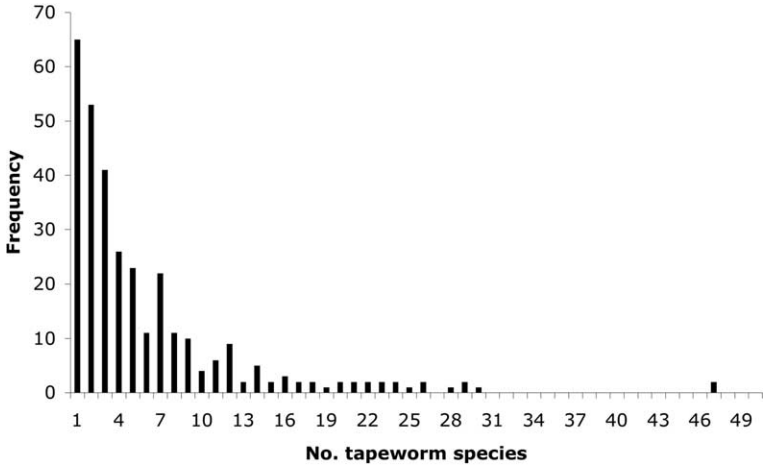

Figure 1. Frequency distribution of the number of tapeworm species per host species (n = 317).

0.273–0.538); therefore, residuals of the linear regression of log tapeworm richness on log measure of study effort (identified above) were computed and used from this point onwards.

The GLM analyses included 124 elasmobranch species for which data were available for all dependent and predictor variables: tapeworm richness and taxonomic distinctness (TD); body size, latitudinal range, median latitude, depth range, median depth, habitat, and type of elasmobranch, respectively. The "best" model ($AIC_c = -344.59$) explaining interspecific variation in tapeworm species richness included median depth + type of elasmobranch (Table 2). The 10 "best" models included a combination of median depth (n = 8), type of elasmobranch (n = 7), depth range (n = 3), latitudinal range (n = 3), median latitude (n = 1), and body size (n = 1) (Table 2). None of these included habitat as an important predictor variable. Parameter estimates obtained using a model-averaging approach, indicate that the relative importance of each variable mirrors that of the frequency inclusion (descending order) in the 10 "best" models, except that "type of elasmobranch" is more important than median depth (Table 3). However, none of the model-averaged parameters had confidence intervals bounded away from "0" (Table 3) indicating that none of the included predictor variables in our model explain the observed variation in tapeworm richness on their own. Additionally, main effects models were not improved significantly by the inclusion of their respective interaction terms.

The "best" model ($AIC_c = -648.04$) explaining interspecific variations in TD of tapeworm assemblages included latitudinal range (Table 2). The 10 "best" models included a combination of latitudinal range (n = 9), depth range (n = 4), median depth (n = 2), body size (n = 2), median latitude (n = 2), and type of elasmobranch (n = 1) (Table 2). None of these included habitat as an important predictor variable. Latitudinal range was the most important predictor variable (Table 3). None of the model-averaged parameter estimates have confidence intervals bounded away from "0" (Table 3) indicating that none of the included predictor variables in our model explain the observed variation in tapeworm richness on their own. Additionally, main effects models were not improved significantly by the inclusion of their respective interaction terms.

Prior to using the phylogenetically independent contrasts method, the adequacy of our branch lengths was verified (Garland et al. 1992) and an exponential transformation of branch lengths was deemed necessary. Correcting for host phylogeny, larger hosts harboured a greater tapeworm richness ($r = 0.226$; $p < 0.0001$; $n = 305$; $DF = 132$) (Fig. 2a). Hosts with a wider latitudinal range harboured more taxonomically diverse tapeworm assemblages ($r = 0.215$; $p = 0.0088$; $n = 153$; $DF = 60$) (Fig. 3a). When host phylogeny was considered, tapeworm richness was not influenced significantly by habitat. On the other hand, hosts exploiting bathydemersal habitats and [bathydemersal + benthopelagic] habitats harboured tapeworm assemblages of lower taxonomic diversity than those inhabiting [benthopelagic + pelagic + demersal + reef] (Pairwise comparisons; 16 pairs; $p = 0.0107$ to 0.0327) and [demersal + pelagic + reef] (22 pairs; $p = 0.0037$ to 0.0112) habitats, respectively.

Sharks vs batoids

The data set included 128 shark and 189 batoid species, each harbouring an average of 5.7 ± 5.7 (range = 1 to 26; median = 3.0) and 6.2 ± 7.4 (range = 1 to 47; median = 4.0) tapeworm species, respectively. Although this difference was not statistically different, when we corrected for sampling effort those values included in our analyses, batoids had a greater richness than sharks ($p = 0.0056$). However, GLM analyses of the complete dataset revealed that type of elasmobranch was a pretending variable, thus this difference is not explained by this particular predictor. Of the 726 shark-tapeworm associations: 11 involved the Cathetocephalidea; 15 the Diphyllidea; 12 the Lecanicephalidea; 10 the Litobothriidea; 325 the Tetraphyllidea; and 353 the Trypanorhyncha. Of the 1170 batoid-tapeworm associations: 68 involved the Diphyllidea; 107 the Lecanicephalidea; 680 the Tetraphyllidea; and 315 the Trypanorhyncha. Representatives of neither the Cathetocephalidea nor the Litobothriidea have been reported from batoids.

The GLM analyses included 56 shark and 68 batoid species for which data were available for all dependent and predictor variables (see above). For sharks, the "best" model ($AIC_c = -152.80$) explaining interspecific variations in tapeworm richness included median depth (Table 2). The frequency of inclusion of the various predictor variables of the 10 "best" models, and the relative importance of each, are similar to those observed for the complete dataset (Table 2 and 3). Furthermore, consistent with analyses of the complete dataset, none of the model averaged parameters for the sharks subset had confidence intervals bounded away from "0" (Table 3). On the other hand, the "best" model ($AIC_c = -194.26$) explaining interspecific variations in tapeworm richness of batoids was the "null" model (Table 2). Consequently, none of the predictor variables included in our models could adequately explain the variation in tapeworm richness observed in batoid hosts (Table 2 and 3). Additionally, main effects models for neither shark nor batoid subsets were improved significantly by the inclusion of their respective interaction terms.

The "best" model ($AIC_c = -315.21$) explaining interspecific variations in TD of tapeworm assemblages in sharks included depth range (Table 2). The 10 "best" models included a combination of depth range (n = 3), habitat (n = 2), body size (n = 2), latitudinal range (n = 2), median latitude (n = 2), and median depth (n = 1) (Table 2). Depth range was the most important predictor variable. However, the range of relative importance was narrow (0.7028–1.0000) (Table 3). Only the model-averaged parameter of the demersal component of habitat had a confidence interval bounded away from "0" (Table 2) indicating that other variables included in other plausible models are pretending variables. The "best" model ($AIC_c = -337.64$) explaining interspecific variations in TD of

Table 2. Summary of the top 10 models for tapeworm richness and taxonomic distinctness of tapeworm assemblages based on AIC_c. Models are shown including the number of parameters (K), Log Likelihood (Log (L)), $\Delta -$ AIC_c, and Akaike weights (w_i) of each model given the data. Model parameters shown in brackets are listed in Table 1.

Comprehensive dataset											
Tapweworm species richness						Taxonomic distinctness					
Model	K	Log (L)	AIC_c	Δ AIC_c	w_i	Model	K	Log (L)	AIC_c	Δ AIC_c	w_i
{57}	4	176.4636	−344.5910	0.0000	0.0811	{2}	3	327.1210	−648.0421	0.0000	0.0877
{457}	5	177.0336	−343.5588	1.0322	0.0484	{24}	4	327.9481	−647.5601	0.4820	0.0689
{47}	4	175.8015	−343.2668	1.3242	0.0418	{25}	4	327.8021	−646.8682	1.1739	0.0488
{257}	5	176.7268	−342.9451	1.6460	0.0356	{245}	5	328.4757	−646.4429	1.5992	0.0394
{5}	3	174.5507	−342.9015	1.6895	0.0348	{–}	2	325.1761	−646.2531	1.7889	0.0359
{357}	5	176.7026	−342.8966	1.6944	0.0347	{27}	4	327.1406	−645.9451	2.0970	0.0307
{25}	4	175.5684	−342.8009	1.7902	0.0331	{23}	4	327.1210	−645.9059	2.1361	0.0301
{157}	5	176.6248	−342.7411	1.8499	0.0321	{12}	4	327.1210	−645.9059	2.1361	0.0301
{245}	5	176.5351	−342.5617	2.0293	0.0294	{234}	5	328.0274	−645.5464	2.4956	0.0252
{7}	3	174.3615	−342.5230	2.0680	0.0288	{124}	5	327.9878	−645.4671	2.5750	0.0242
Sharks											
{5}	3	79.6309	−152.8003	0.0000	0.1258	{4}	3	160.8333	−315.2051	0.0000	0.0761
{235}	5	81.7673	−152.3346	0.4657	0.0997	{–}	2	159.6260	−315.0256	0.1794	0.0696
{234}	5	81.4107	−151.6214	1.1789	0.0698	{6}	5	164.2153	−314.7163	0.4888	0.0596
{4}	3	78.9125	−151.3635	1.4369	0.0613	{5}	3	160.5845	−314.7076	0.4975	0.0594
{23}	4	80.0386	−151.2929	1.5075	0.0592	{1}	3	160.3841	−314.3066	0.8985	0.0486
{25}	4	80.0220	−151.2598	1.5406	0.0582	{26}	4	164.9653	−313.5973	1.6077	0.0341
{35}	4	79.9680	−151.1518	1.6485	0.0552	{2}	3	160.0176	−313.5737	1.6313	0.0337
{45}	4	79.9480	−151.1118	1.6885	0.0541	{34}	4	161.0843	−313.3843	1.8207	0.0306
{15}	4	79.6396	−150.4948	2.3055	0.0397	{14}	4	161.0528	−313.3213	1.8837	0.0297
{2345}	6	81.9431	−150.1719	2.6284	0.0338	{3}	3	159.8815	−313.3014	1.9037	0.0294
Batoids											
{–}	2	99.2216	−194.2585	0.0000	0.1419	{2}	3	172.0083	−337.6417	0.0000	0.1400
{1}	3	100.2294	−194.0838	0.1747	0.1300	{12}	4	172.7807	−336.9264	0.7153	0.0979
{3}	3	99.5592	−192.7434	1.5152	0.0665	{1}	3	171.4617	−336.5484	1.0933	0.0810
{5}	3	99.2586	−192.1422	2.1163	0.0493	{23}	4	172.1503	−335.6658	1.9759	0.0521
{2}	3	99.2280	−192.0811	2.1774	0.0478	{24}	4	172.0398	−335.4448	2.1969	0.0467
{4}	3	99.2271	−192.0792	2.1793	0.0477	{25}	4	172.0083	−335.3818	2.2599	0.0452
{12}	4	100.3411	−192.0473	2.2112	0.0470	{3}	3	170.7260	−335.0771	2.5646	0.0388
{15}	4	100.2570	−191.8792	2.3793	0.0432	{13}	4	171.7574	−334.8798	2.7619	0.0352
{13}	4	100.2513	−191.8677	2.3908	0.0429	{–}	2	169.5123	−334.8400	2.8017	0.0345
{14}	4	100.2341	−191.8334	2.4251	0.0422	{124}	5	172.8209	−334.6741	2.9675	0.0317

tapeworm assemblages in batoids included latitudinal range (Table 2). The 10 "best" models included a combination of latitudinal range (n = 6), body size (n = 4), median latitude (n = 3), depth range (n = 2), and median depth (n = 1) (Table 2). None of these included habitat as an important predictor variable. The relative importance of each variable mirrored that of the frequency of inclusion (descending order) in the 10 "best" models (Table 3). However, none of the model-averaged parameters had confidence intervals bounded away from "0" (Table 3). Main effects models for neither shark and batoid subsets were improved significantly by the inclusion of their respective interaction terms.

When correcting for host phylogeny, larger sharks and batoids harboured more tapeworm species ($r = 0.233$; $p = 0.0092$; $n = 126$; $DF = 73$ and $r = 0.223$; $p = 0.0035$; $n = 178$; $DF = 57$, respectively) (Fig. 2b and c, respectively). Additionally, shark TD was not correlated with any of the model parameters included in our analyses, whereas batoid TD was positively correlated with latitudinal range ($r = 0.247$; $p = 0.0243$; $n = 90$; $DF = 24$) (Fig. 3b and c, respectively).

When host phylogeny was considered, shark tapeworm richness was not influenced significantly by habitat. Shark hosts exploiting pelagic habitats harboured tapeworm assemblages with significantly lower TD than those inhabiting [bathydemersal + benthopelagic + demersal + reef] habitats (pairwise comparisons; 6 pairs; $p = 0.03125$). When host phylogeny was considered, batoid tapeworm richness of hosts associated with reef habitats was greater than that of those associated with [bathydemersal + benthopelagic + pelagic + demersal] habitats (pairwise comparisons; 10 pairs; $p = 0.0107$), but TD of batoid tapeworm assemblages was not influenced significantly by habitat.

Discussion

Our dataset is the most comprehensive compilation of tapeworms infecting elasmobranchs to date and provides a thorough assessment of tapeworm community diversity for these hosts over the entire range of their sampled distributions. It is clear from our results that tapeworm species richness and diversity in elasmobranchs are two measures which complement each other and are under different selective pressures. First, we found no significant differences in raw tapeworm richness between shark and batoid hosts, although a significant difference was observed in richness

Table 3. Relative importance of predictor variables for tapeworm species richness and taxonomic distinctness of tapeworm assemblages, including weights [$w_+(i)$], ranks (R), weighted model average parameter estimates (PE), and 95% confidence interval (CI). Parameter estimates in bold indicate those bounded away from "0".

Comprehensive dataset									
Tapeworm richness					Taxonomic distinctness				
Variable	$w_+(i)$	R	PE	CI	Variable	$w_+(i)$	R	PE	CI
Host length	0.4119	6	0.0106	−0.0385 to 0.0597	Host length	0.4519	4	0.0051	−0.0104 to 0.0208
Latitude (range)	0.6516	4	−0.0418	−0.1050 to 0.0213	Latitude (range)	1.0000	1	0.0257	−0.0002 to 0.0516
Latitude (median)	0.5155	5	−0.0187	−0.0583 to 0.0208	Latitude (median)	0.4345	5	−0.0010	−0.0106 to 0.0085
Depth (range)	0.6701	3	0.0332	−0.0777 to 0.1441	Depth (range)	0.6349	2	−0.0128	−0.0337 to 0.0081
Depth (median)	0.9718	2	−0.1072	−0.2443 to 0.0298	Depth (median)	0.5248	3	0.0047	−0.0161 to 0.0255
Habitat (BD)	0.0525	7	0.0030	−0.0039 to 0.0099	Habitat (BD)	0.0166	7	0.0041	−0.0020 to 0.0102
Habitat (BP)	0.0525	7	−0.0009	−0.0059 to 0.0040	Habitat (BP)	0.0166	7	0.0003	−0.0042 to 0.0048
Habitat (D)	0.0525	7	0.0008	−0.0024 to 0.0039	Habitat (D)	0.0166	7	0.0008	−0.0021 to 0.0037
Habitat (P)	0.0525	7	−0.0033	−0.0088 to 0.0021	Habitat (P)	0.0166	7	−0.0044	−0.0092 to 0.0003
Type of elasmobranch	1.0000	1	0.0327	−0.0076 to 0.0731	Type of elasmobranch	0.3902	6	−0.0004	−0.0041 to 0.0033
Sharks									
Host length	0.3867	5	0.0057	−0.0619 to 0.0734	Host length	0.8102	4	−0.0013	−0.0202 to 0.0177
Latitude (range)	0.8252	2	−0.1618	−0.3713 to 0.0477	Latitude (range)	0.7987	5	0.0045	−0.0177 to 0.0267
Latitude (median)	0.8165	3	−0.0744	−0.1674 to 0.0187	Latitude (median)	0.7028	6	−0.0008	−0.0090 to 0.0106
Depth (range)	0.7366	4	−0.0015	−0.1541 to 0.1512	Depth (range)	1.0000	1	−0.0098	−0.0294 to 0.0098
Depth (median)	1.0000	1	−0.1587	−0.3580 to 0.0406	Depth (median)	0.8890	3	−0.0023	−0.0235 to 0.0189
Habitat (BD)	0.0426	6	0.0023	−0.0031 to 0.0077	Habitat (BD)	0.9716	2	0.0064	−0.0152 to 0.0279
Habitat (BP)	0.0426	6	−0.0010	−0.0045 to 0.0025	Habitat (BP)	0.9716	2	−0.0084	−0.0234 to 0.0066
Habitat (D)	0.0426	6	−0.0011	−0.0038 to 0.0016	Habitat (D)	0.9716	2	0.0142	**0.0026 to 0.0258**
Habitat (P)	0.0426	6	−0.0006	−0.0034 to 0.0021	Habitat (P)	0.9716	2	−0.0006	−0.0034 to 0.0021
Batoids									
Host length	1.0000	1	0.0692	−0.0364 to 0.1749	Host length	0.7737	2	0.0283	−0.0096 to 0.0661
Latitude (range)	0.5650	5	−0.0059	−0.0436 to 0.0318	Latitude (range)	1.0000	1	0.0293	−0.0017 to 0.0603
Latitude (median)	0.6439	4	−0.0121	−0.0528 to 0.0286	Latitude (median)	0.5028	3	−0.0061	−0.0216 to 0.0094
Depth (range)	0.6678	3	0.0315	−0.0429 to 0.1059	Depth (range)	0.4218	4	−0.0046	−0.0211 to 0.0119
Depth (median)	0.6681	2	−0.0333	−0.1125 to 0.0460	Depth (median)	0.4163	5	0.0041	−0.0132 to 0.0214
Habitat (BD)	0.0379	6	0.0007	−0.0035 to 0.0049	Habitat (BD)	0.1407	6	0.0044	−0.0030 to 0.0118
Habitat (BP)	0.0379	6	0.0018	−0.0021 to 0.0057	Habitat (BP)	0.1407	6	0.0042	−0.0023 to 0.0107
Habitat (D)	0.0379	6	0.0008	−0.0015 to 0.0031	Habitat (D)	0.1407	6	−0.0005	−0.0043 to 0.0034
Habitat (P)	0.0379	6	−0.0034	−0.0110 to 0.0042	Habitat (P)	0.1407	6	−0.0092	−0.0216 to 0.0033

once we corrected for sampling effort. Second, the most important predictor variable for tapeworm richness was host type (shark or batoid), whereas that for taxonomic distinctness (TD) of tapeworm assemblages was host latitudinal range (the former, a proxy for host phylogenetic influences, the latter, a proxy for geographical area). Third, when considering host phylogenetic relationships, a different pattern emerged; host size was positively correlated with tapeworm species richness, whereas latitudinal range remained the most important predictor for TD of tapeworm assemblages in elasmobranchs. These differences highlight the necessity of accounting for both host and parasite evolutionary relationships in assessing parasite richness.

The inverse relationship between species richness and latitude is a well-established pattern in free-living organisms, although it is less consistent in aquatic systems (Clarke 1992, Willig et al. 2003, Hillebrand 2004a). Our results

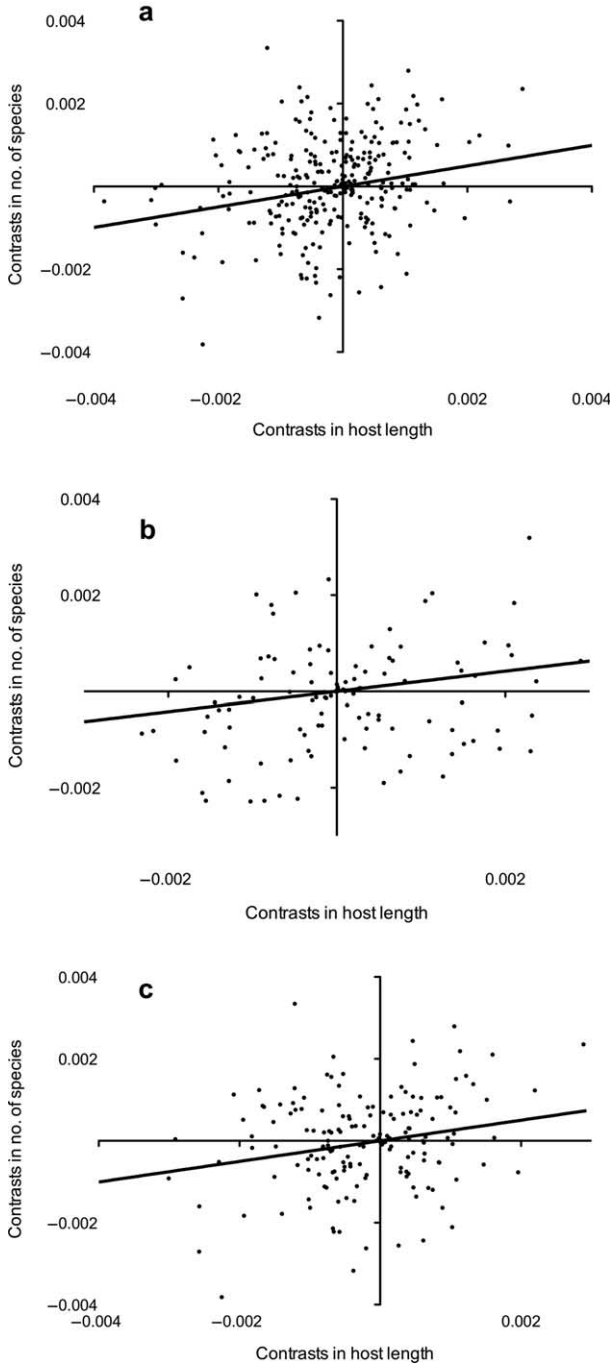

Figure 2. Relationship between the corrected number of tapeworm species and length of their (a) elasmobranch, (b) shark, and (c) batoid hosts, based on 305, 126, and 178 phylogenetically independent contrasts, respectively. The lines represent the best fit line for a simple linear regression.

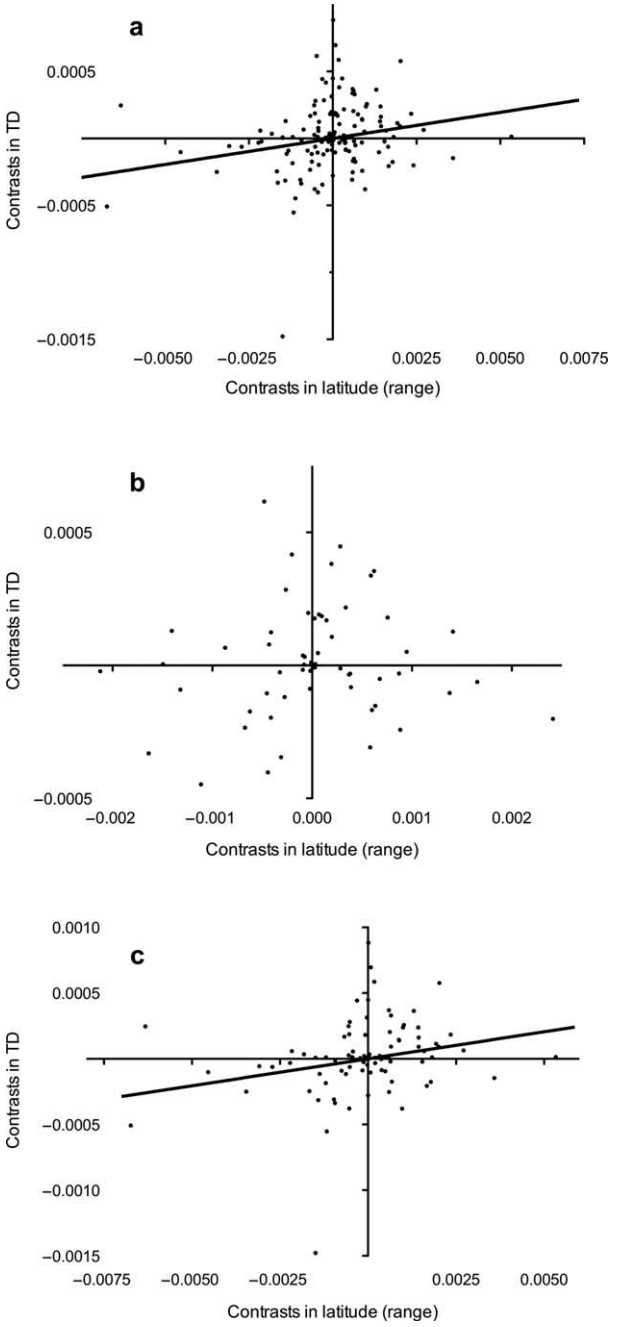

Figure 3. Relationship between the average TD and latitude (range) of their (a) elasmobranch, (b) shark, and (c) batoid hosts, based on 153, 62, and 90 phylogenetically independent contrasts, respectively. The lines represent the best fit line for a simple linear regression.

show that latitude is not a suitable predictor of tapeworm species richness and suggest that temperature may not correlate with latitude in marine systems. However, depth, another proxy for environmental temperature, is a good predictor of species richness. In oceans, temperature within the surface layer (top 100–200 m) and the deep layer (below 1500 m) do not vary with depth. The two layers differ in that the surface layer is influenced by seasonality and latitudinal gradients in climate, while the deep layer is uniformly cold (3–4°C) across time and space (Castro and Huber 2003). Conversely, the intermediate layer of the ocean, the main thermocline, shows sudden changes in temperature associated with depth (Castro and Huber 2003). Therefore, elasmobranchs inhabiting coastal waters (i.e. along the continental shelf to depths of ca 200 m), are probably exposed to temperature gradients driven by latitude. In contrast, those inhabiting bathydemersal (the sea floor at depths >200 m) and pelagic habitats may be exposed to temperature gradients driven by depth. Most host species included in this study are not associated with coastal waters, which may explain influence of depth on tapeworm species richness across latitudes.

When considering the shared evolutionary histories of hosts included in these analyses, we identified host body size as the only predictor variable to influence tapeworm species richness for all datasets analysed. Generally, tapeworms infecting elasmobranchs are restricted to the spiral intestine. Although no data are available on the relationship between elasmobranch length or weight and size of the spiral intestine, some evidence suggests it is very likely to be strongly positive (Randhawa unpubl.). We reiterate that host body size, as obtained herein (Randhawa and Poulin 2009), is a better proxy for size of the spiral intestine than host length. Larger habitats, spiral intestines in this particular case, should provide more space, nutrients and niches for different tapeworms species to exploit. However, there is a general lack of consensus as to whether host body size and endoparasite species richness are correlated (Table 4.1 in Poulin and Morand 2004). The inconsistency among published results may in part be due to the fact that some studies have corrected their analysis for host phylogeny, whereas other have not. Among studies correcting for host phylogeny, the nature of the relationship between host size and endoparasite species richness in fish is not consistent (Sasal et al. 1997, Morand et al. 2000, Takemoto et al. 2005, Munoz et al. 2006, Luque and Poulin 2008). We are aware of only a single study that has investigated the endoparasite richness in elasmobranchs while considering the common evolutionary histories of elasmobranch hosts (Luque and Poulin 2008). Whereas our study found a positive significant relationship between host size and tapeworm richness in all datasets, Luque and Poulin's (2008) results showed no significant correlation between endoparasite richness and host size. This discrepancy may reflect the breadth of endoparasitic taxa included in both studies (tapeworms only, present study vs all endoparasites, Luque and Poulin [2008]) or their geographical scale (global, present study vs Neotropical, Luque and Poulin [2008]).

Only recently have scientists identified taxonomic distinctness as a key indicator of biodiversity in aquatic conservation research (Ellingsen et al. 2005, Bhat and Magurran 2006, Leonard et al. 2006). Consistent with Luque et al. (2004) and Luque and Poulin (2008), our findings demonstrate that parasite richness and average taxonomic distinctness of parasite assemblages are sensitive to different host properties (median depth and latitudinal range, respectively, herein). We show that elasmobranch hosts occurring over a greater latitudinal range harbour more taxonomically distinct tapeworm assemblages than those with restricted ranges, regardless of whether hosts share an evolutionary history. Hosts found over a greater range are likely exposed to a greater diversity of prey items. For instance, the diet of elasmobranch species may differ substantially in different areas of their geographical range, thus increasing the potential of being exposed to, and acquiring, a greater diversity of tapeworms. Our findings, in conjunction with those of Luque et al. (2004), illustrate that species richness and taxonomic diversity are two measures that complement each other, even though they provide different explanations of the selective forces affecting parasite biodiversity.

Our analyses did not identify host habitat as a predictor of tapeworm richness. However, when taking into account the common evolutionary history of hosts using the phylogenetic independent contrast method, pairwise comparisons revealed that habitat did influence the TD of tapeworm parasite assemblages in elasmobranchs. All 37 bathydemersal and 55.6% (10 of 18) of benthopelagic elasmobranchs included in this study are found at depths beyond the continental shelf. They harbour tapeworm assemblages with lower TD than those exploiting other types of habitats. Furthermore, these species are exposed to the oceanic thermocline. The lack of information regarding host diet and lifecycles of tapeworms infecting elasmobranchs prevents us from making inferences about the influence of the prey biota associated with these habitats on the diversity of tapeworm assemblages in these hosts. However, since host diet is an expected predictor of parasite diversity in vertebrates (Poulin and Morand 2004) and since tapeworms are generally acquired via ingestion of an infected prey item, one would assume that elasmobranch tapeworm diversity is influenced by host diet. Furthermore, parasite diversity is not randomly distributed (Poulin 1995, Chen et al. 2008) and is in part affected by host diet (Poulin and Morand 2004). Hosts with broader diets generally harbour a greater parasite diversity (Chen et al. 2008). The latter can also be affected by the diet and feeding habits of prey items (Marcogliese 2002). In light of this, it is possible that our general linear model analyses of tapeworm richness did not recover a single best model due to the absence of an important predictor variable such as host diet. Repeating these analyses to include breadth of the host diet, if and when this information becomes available, as a predictor variable may reveal that diet has influenced tapeworm richness in elasmobranchs.

Different factors influence the richness of the respective tapeworm faunas of sharks and batoids. The absence of a clear predictor variable influencing the tapeworm richness of batoids indicates that our selection of variables did not include the most influential one. Similarly, although we identified median depth as the most important predictor

variable included in our models, it did not drive the evolution of tapeworm richness in sharks. For reasons identified above, repeating our analyses to include breadth of host diet may reveal it to be an important predictor variable. Additionally, the demersal (i.e. just above the benthic zone) component of shark habitat is the only predictor variable included in our models to influence tapeworm richness. Parasite faunas of pelagic fishes are depauperate compared to those demersal ones (Manter 1934, Collard 1970, Noble 1973, Campbell et al. 1980). Helminth transmission in demersal habitats occurs in a two-dimensional plane, whereas that in pelagic habitats occurs in a three-dimensional volume (Collard 1970, Campbell et al. 1980). The dilution of helminth infective stages through the water column may contribute to a decrease in diversity in fish exploiting pelagic habitats. Furthermore, prey biota associated with demersal habitats are denser and more diverse than in pelagic habitats (Campbell et al. 1980), two factors likely to facilitate transmission of helminth parasites.

Our study included 317 elasmobranch species, or 26% of the global diversity of elasmobranchs, from which at least one species of tapeworm has been reported. Nearly 900 species were not included, some of which may have been examined for intestinal parasites, but their negative records were never reported. Nevertheless, our findings are significant from a biodiversity perspective and suggest that elasmobranchs contribute but a fraction of the global biodiversity in marine ecosystems compared to that of their tapeworm parasites. Even though the exact mechanisms that have contributed to the diversity of tapeworm assemblages in elasmobranchs have not been clearly untangled, it is evident that host size, factors associated with environmental temperature (such as latitude and depth) and host phylogeny have influenced current patterns of richness and taxonomic diversity.

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