CHAPTER 5

SHIFTING NICHES PROMOTE DIVERSIFICATION ALONG A THERMAL GRADIENT

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ABSTRACT

The holy grail of ecology is to explain differences in species richness between clades or regions. The diversification rate of clades is a key parameter for understanding such patterns. Here, we use a time calibrated phylogeny in combination with thermal data for the marine brown algal genus *Dictyota* in order to investigate the evolution of niches through time in relation to diversification rates and species diversity patterns. Our results show that species diversification within this genus is positively associated with the ability of clades to shift their thermal niche. This outcome might have implications for the interpretation of large scale marine diversity patterns, however the generality of our findings should be tested in the future.

INTRODUCTION

Differences in speciation and extinction as well as geographic range changes underlie large-scale biodiversity patterns. Identification of general mechanisms that influence diversification across taxonomic groups and temporal scales, however, has proven a hard nut to crack (e.g. Butlin *et al.*, 2009). Among the many theories to explain the unevenness in biodiversity across large spatial scales, biologists have studied and speculated about a link between species richness and climate for over two centuries (Clarke & Gaston, 2006). This link is most emblematically presented by the latitudinal diversity gradient, a trend of higher biodiversity in the tropics to lower biodiversity towards the poles which has been well characterized for terrestrial (Pianka, 1966; Hillebrand, 2004a; Ricklefs, 2006) as well as marine organisms (Roy *et al.*, 1998; Hillebrand, 2004b). Despite the generality of this trend and a proliferation of different hypotheses, a universally accepted explanation remains elusive (Mittelbach *et al.*, 2007). Differences in diversification rates have featured prominently in several evolutionary explanations. For terrestrial organisms, climate has long been identified as a factor with a pronounced effect on diversification rates. Both rapid shifts (Kozak & Wiens, 2007) as well as conservatism (Kozak & Wiens, 2006) of the climatic niche may interact with rates of diversification. Recently, Kozak & Wiens (2010) demonstrated that rates of ecological niche evolution correlate with diversification rate and these rates are higher in tropical latitudes. The accessibility of global environmental data (Kozak *et al.*, 2008), have created new opportunities for studying species' climatic niches and understanding how past climate changes have shaped extant species diversity. In addition, studies investigating the role of climate on speciation and diversification are receiving renewed attention in the light of anthropogenic climate change (Parmesan & Yohe, 2003; Evans *et al.*, 2009).

Despite covering more than 70% of the earth's surface and hosting a huge diversity of organisms, marine patterns of diversity and the processes underlying these patterns have received considerably less attention compared to terrestrial ecosystems. Moreover some recent studies reveal important contrasts to widely held terrestrial paradigms, which highlight the need to specifically address marine diversification (Tittensor *et al.*, 2010). Accelerated diversification rates for marine organisms have been correlated with large-scale physical restructuring of oceans (Steeman *et al.*, 2009), habitat availability (Williams, 2007; Williams & Duda, 2008) often in combination with increased ecological species interactions (Alfaro *et al.*, 2007; Cowman & Bellwood, 2011) or the acquisition of key innovations(Alfaro *et al.*, 2009; Slater *et al.*, 2010). However, marine studies particularly focusing on the relation between climatic niche evolution and diversification are non-existing.

Temperature has long been regarded a key factor regulating the diversity of organisms and its consistent and dominant role in structuring broad-scale marine diversity patterns was recently endorsed (Tittensor *et al.*, 2010). Seaweeds have featured prominently in studies establishing a crucial role of sea surface temperature in shaping the range and geographical distributions of marine organisms (Pielou, 1977; Van Den Hoek, 1982; Breeman, 1988; Lüning, 1990; Bolton, 1994; Breeman & Pakker, 1994; Santelices & Marquet, 1998; Santelices *et al.*, 2009; Eggert, 2012). Critical temperatures for the completion of the life history were experimentally assessed for many species and correlated well to their respective geographic boundaries (Breeman, 1988). More recently evolutionary studies revealed a strong phylogenetic imprint of temperature and considerable niche conservatism (Breeman *et al.*, 2002; Verbruggen *et al.*, 2009).

Here, we study the evolution of thermal niches through time in relation to diversification rates and species diversity patterns, using the brown macroalga *Dictyota* as model entity.

MATERIALS AND METHODS

STUDY TAXON

We use the brown algal genus *Dictyota* as a model taxon for this study. This widespread genus abounds in tropical to cold-temperate seas and is an important constituent of the marine flora in these regions (De Clerck *et al.*, 2006). It has a rich history of phylogenetic studies (De Clerck *et al.*, 2006; Tronholm *et al.*, 2010) with nearly complete global taxon sampling (80-90%), making it a good candidate for this study. A recent study suggested that species' thermal tolerances have influenced biogeographical patterns in the genus (Tronholm *et al.*, 2012), further promoting its suitability as a model to examine the relationship between climate and diversification.

PHYLOGENY AND DIVERSIFICATION

Testing hypotheses about environmental disparity and diversification requires a time-calibrated phylogeny. We have assembled an 8-locus alignment of 103 *Dictyota* species and 26 outgroup species based on a combination of newly generated and previously published data (De Clerck *et al.*, 2006; Hwang *et al.*, 2009; Tronholm *et al.*, 2010; Tronholm *et al.*, 2012). Phylogenetic trees were inferred using partitioned ML and Bayesian phylogenetic inference, and chronograms were estimated using an auto-correlated clock model with node age constraints derived from a brown algal time-calibrated phylogeny (Silberfeld *et al.*, 2010). We refer to Appendix S1 for details about the construction of the phylogeny and estimation of divergence times. We constructed a consensus tree and selected a random subset of 1,500 chronograms for use in subsequent analyses. Tempo of species diversification was investigated with a three-step procedure (See Appendix S1) taking the consensus tree as the basis for the analyses. The accumulation of lineages over time was first visualized using a lineages-through-time (LTT) plot. We then examined diversity dynamics from the phylogeny using birth–death model of cladogenesis developed by Rabosky (2006) and further elaborated by Morlon *et al.* (2011). The latter are thought to give more realistic estimates of extinction rates while also accommodating for incomplete taxon sampling.

GEOGRAPHIC AND THERMAL DATA

To estimate the thermal affinities of species, we retrieved geographical coordinates from recently collected specimens for which the identification has been confirmed by DNA sequence information. This resulted in 1,144 unique localities for 103 species. Our sampling represented a good balance between tropical (622) and temperate locations (522) (Figure S2.1). We extracted mean sea surface temperature (SST) data for each of these locations from the marine environmental dataset Bio-ORACLE (Tyberghein *et al.*, 2012). The SST data are summarized in Table S2.1.

ANALYSIS OF SPECIATION AND BIOGEOGRAPHY

To quantify the relative importance of different modes of diversification, we evaluated all speciation events that gave rise to at least one individual species (see Malay & Paulay, 2009).

Species occurrence records were mapped in ArcGIS and species ranges were visually analyzed. Species were considered allopatric when they had separate ranges. Species ranges that abut were termed parapatric, whereas species ranges that show a certain degree of overlap were called sympatric. The full list of species' geographic distributions relative to each other can be found in Table S2.2.

THERMAL NICHE EVOLUTION

Patterns of thermal niche evolution were examined with two methods. First, ancestral SST affinities were inferred using a generalized least squares approach implemented in COMPARE (Martins, 2004) and plotted on the chronogram with TreeGradients v1.03 (Verbruggen, 2008). The distribution of thermal affinities was also visualized with a disparity-through-time plot and quantified by calculating a disparity index (MDI = morphological disparity index). Disparity-through-time plots permit a visual exploration of whether for any given time in the phylogeny, environmental differences are more pronounced within subclades or between subclades. The observed disparity for our data was compared with 10,000 simulations under a Brownian motion model of trait evolution (Harmon *et al.*, 2003). The MDI quantifies the overall difference in relative disparity of a clade compared with the expectation under the null model (MDI, Harmon *et al.*, 2003). Analyses were carried out with the 'geiger' package in R (R Development Core Team, 2008; Harmon *et al.*, 2008).

RELATING DIVERSIFICATION TO THERMAL NICHE EVOLUTION

While the methods above can provide insight in the diversification of the genus as well as the evolution of the thermal niche, they do not relate them. To address the principal goal of examining the influence of thermal niche evolution on the rate of species diversification, we set up two analyses.

First, we optimized a model that relates species' traits to diversification rates in a phylogenetic context to establish whether a relationship exists between rates of diversification and SST affinities in *Dictyota*. This method relates net diversification λ to a trait value, in our case SST, as follows:

$$\ln \frac{\lambda}{1-\lambda} = \beta.\mathrm{SST} + \alpha$$

This model, implemented and published by Paradis (Paradis, 2005), is designed to detect monotonic relationships between the trait value (SST) and the rate of diversification (α and β are the model parameters). It was optimized with the yule.cov function in the 'ape' package for R (Paradis *et al.*, 2004). It was compared to the standard Yule model in which the rate of diversification is a constant (and thus unaffected by SST values) with the small sample size-corrected Akaike Information Criterion (AICc). The analysis was performed on the 1,500 posterior trees to take uncertainty in the topology and its time-calibration into account.

Second, we devised a procedure to test the hypothesis that clades with more variable SST affinities show accelerated diversification. This procedure is based on subdividing the tree into major clades and fitting a linear regression model to quantify the association between the rate of thermal evolution and the rate of diversification of the clades. The clades were defined by slicing the phylogeny using a time-specific threshold. The threshold value (55 Ma) was chosen to postdate the radiation of the genus into its major clades. To avoid conditioning our results on a very specific time in the past, we repeated our analyses on a Bayesian posterior sample of trees and sampled threshold values from a normal distribution around that threshold (standard deviation 4 Ma). Clades containing less than four species were discarded from subsequent analyses because parameter values are unlikely to be inferred accurately.

Net diversification rates of clades were estimated from the clade age and the present species diversity of the clade (method-of-moments estimator) (Magallon & Sanderson, 2001). We will indicate the diversification rate of clade i as λ_i. The rate of thermal niche evolution was measured as the rate parameter of a Brownian motion model of evolution optimized on the SST affinities of the species in the clade. This parameter is denoted σ_i^2 for clade i. High σ_i^2 values indicate faster thermal niche evolution.

As an initial test of concept and to visualize the relationship between σ_i^2 and λ_i, we applied this method on the consensus chronogram. Based on the time threshold, the tree was subdivided into independent clades. For each clade, σ_i^2 and λ_i were calculated. The resulting value pairs were plotted, and a linear regression model $\lambda = \beta . \sigma^2 + \alpha$ was fitted to the (σ_i^2, λ_i) data points. This was then repeated with one hundred random threshold values drawn from the normal distribution.

Subsequently, we conducted the same analysis on the posterior sample of 1,500 time-calibrated trees to evaluate the consistency of the obtained pattern against differences in the topology, node ages and threshold values. We inferred the relationship between λ and σ^2 for each tree individually, storing the slope of the relationship for each of the 1,500 replicates. To verify whether the obtained slopes differ from those expected in the absence of a structural relationship between λ and σ^2, we performed the same analysis on datasets generated under the null model in which diversification does not depend on niche evolution. Therefore, we simulated 1,500 trees under a birth-death model (TreeSim: Stadler, 2011) with the parameters obtained from a randomly drawn *Dictyota* tree from the posterior set. Subsequently we simulated credible SST affinities for the species of the simulated trees using fastBM from the phytools package (Revell, 2011) with the rate parameter estimated from a randomly drawn *Dictyota* tree. For each of the 1,500 simulated datasets, we determined the slope of the relationship between λ and σ^2 as described above. The slopes obtained from the real *Dictyota* data were compared to the slopes from the simulated data using a Wilcoxon signed-rank test.

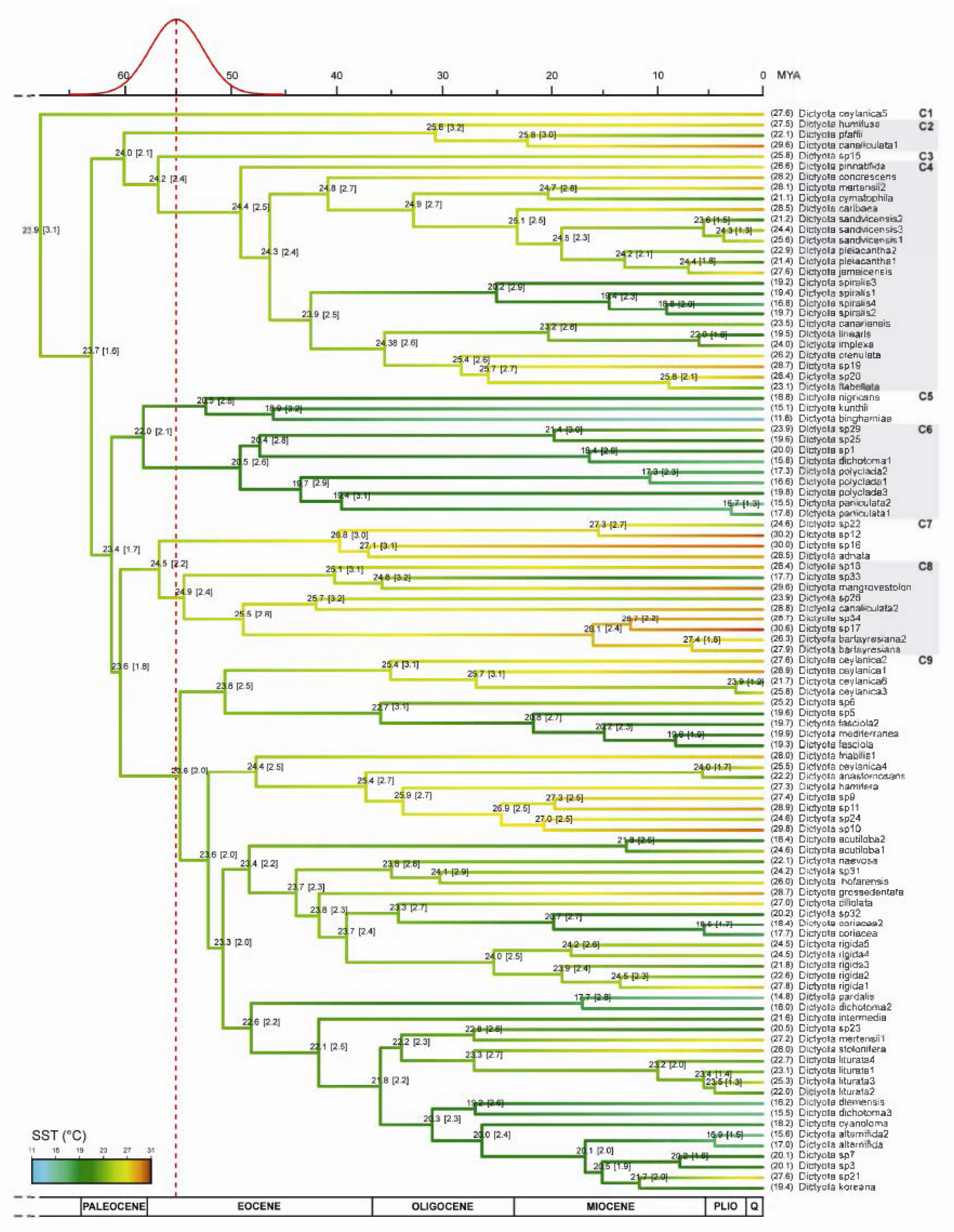


Figure 1: Inferred evolutionary history of the thermal niche in *Dictyota*, showing the scattered distribution of species with warmer and colder sea surface temperature affinities across the tree. The estimated ancestral SST affinities are plotted at nodes and visualized on the phylogeny along a color gradient, with blue indicating cold waters over green and yellow colors indicating temperate waters to tropical waters in red. The dashed red line indicates the temporal threshold used to define clades C1-9. This threshold was varied in the analyses according to the normal distribution shown in red at the top of the figure (see text for details).

RESULTS

Our analyses were aimed at documenting the diversification and thermal evolution of *Dictyota*. Following a brief exploration of some basic results that help introduce the dataset, we will proceed to more detailed analyses that address various details of the relationship between species diversification and thermal niche affinities.

The inferred evolutionary history of sea surface temperature affinities (Figure 1) clearly indicates that evolution along the thermal niche axis has not been homogeneous throughout the genus. While some clades are mainly found in colder water (C5, C6) and others are predominantly tropical (C7, C8), the majority of clades contain a mixture of species from colder and warmer regions. While the ancestral states for the oldest nodes in the tree would suggest that the genus originated in warm-temperate waters, the uncertainty about these estimates is very high (Figure 1). Disparity-through-time plots show that the evolution of SST affinities does not deviate from the expectation under Brownian motion null model (Figure 2; MDI = 0.079, p-value = 0.177).

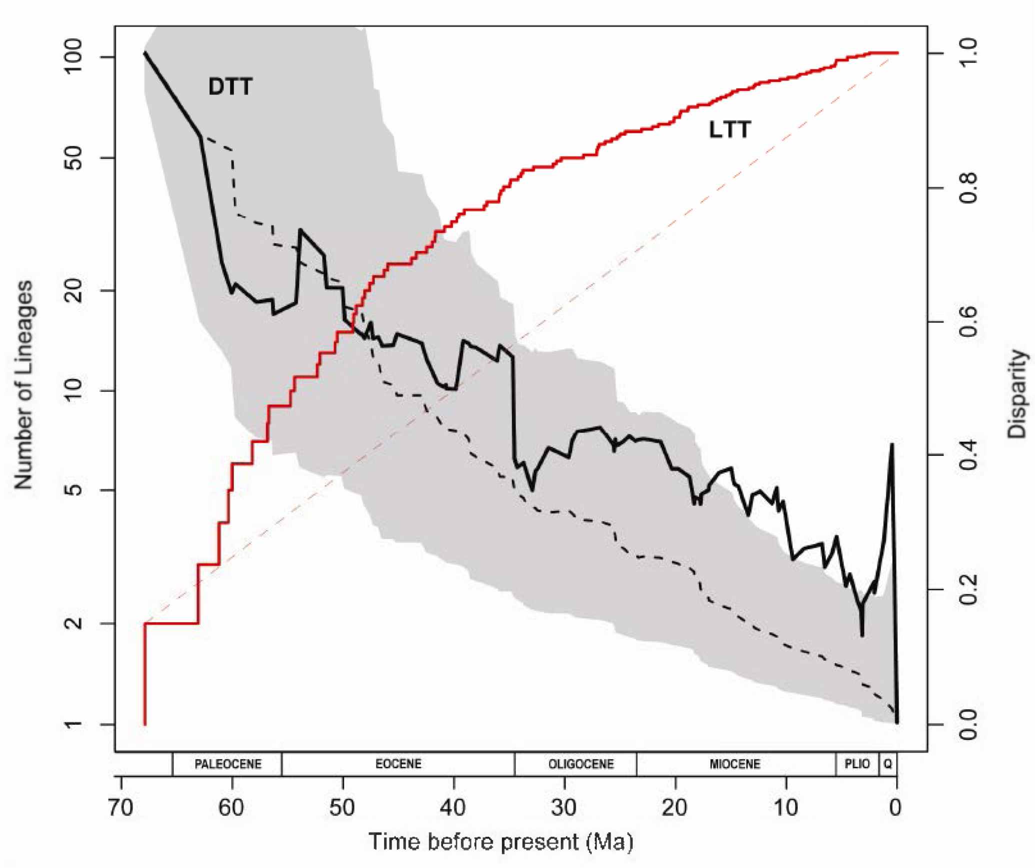


Figure 2: Lineage- and disparity-through-time plots. The lineage-through-time plot (in red) shows that *Dictyota* shows a period of rapid diversification early on and slower diversification later on. This deviates from the pattern expected under homogeneous diversification (pink ribbon). The disparity-through-time plot (black line) largely lies within the expectation under Brownian motion evolution (gray ribbon), indicating that variation in the thermal niche is not found predominantly within or among clades but is more homogeneously spread across the phylogeny. The grey shaded area indicates the 95% DTT range for the simulated data.

The phylogenetic tree and a lineages-through-time plot indicate that the genus experienced an early period of rapid diversification in the Paleocene and early Eocene followed by slower diversification in the remainder of the Cenozoic (Figures 1 &2). This visual assessment is confirmed by the fact that diversification models with decreasing rates of diversification better match the data (Table S1.3). A range of analyses indicates that extinction rates have been very low and that extinction is not likely to have played a major role in the diversification dynamics of the group (Tables S1.3 & S1.4).

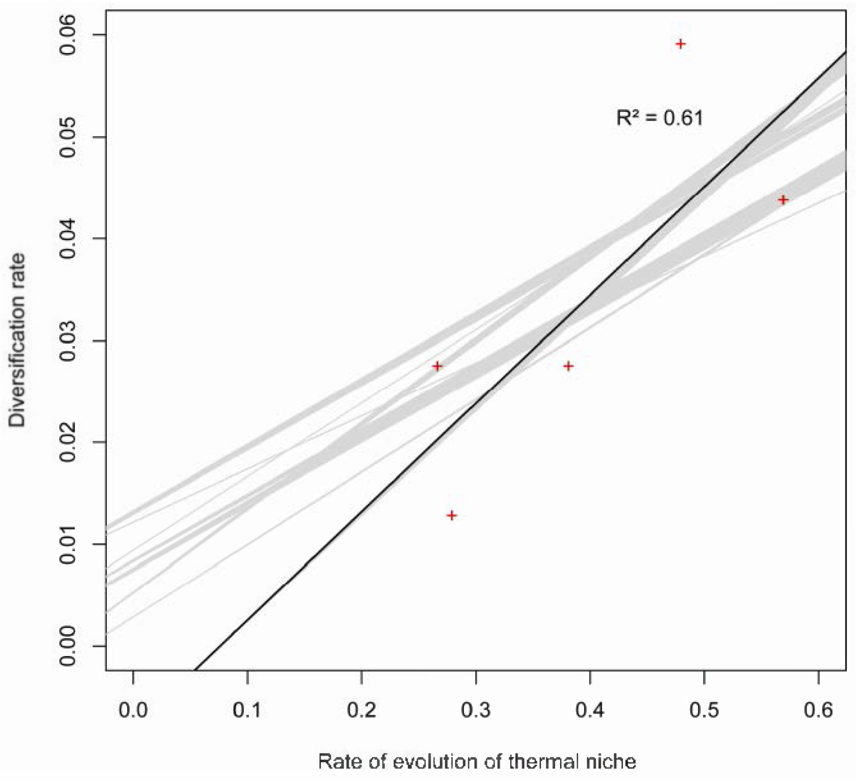


Figure 3: Regression analysis showing the positive relationship between the rate of species diversification and the rate of evolution of the thermal niche among *Dictyota* clades. The black line represents the regression inferred with the temporal threshold set at 55 Ma (red line in Figure 1). Dashed grey lines are regressions based on 100 randomly chosen threshold values from the normal distribution.

A model designed to relate the rate of diversification with species traits shows that the SST affinities of lineages have had very little impact on their diversification rates (β = 0.018 ± 0.021), and that this model is not selected over a simple Yule model of diversification (ΔAICc = –2.05 ± 0.21 in favor of simple Yule model). However, analysis aimed at relating diversification to variability in SST affinities did show that clades with variable thermal niches diversify more rapidly (Figure 3). This result is robust to phylogenetic uncertainty and the exact position of the threshold (slope β = 0.06 ± 0.02 across trees).Furthermore, this result is not a consequence of an autocorrelation that may exist between the number of species in a clade and the thermal niche diversity of that clade, as indicated by the fact that slopes are, on average, an order of magnitude higher in *Dictyota* than in simulations under the null hypothesis assuming is no association between SST affinities and diversification (Figure 4).

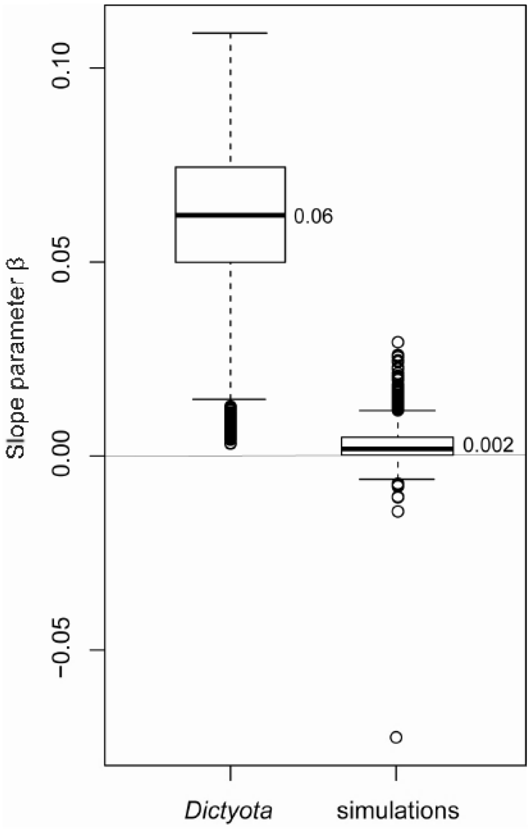
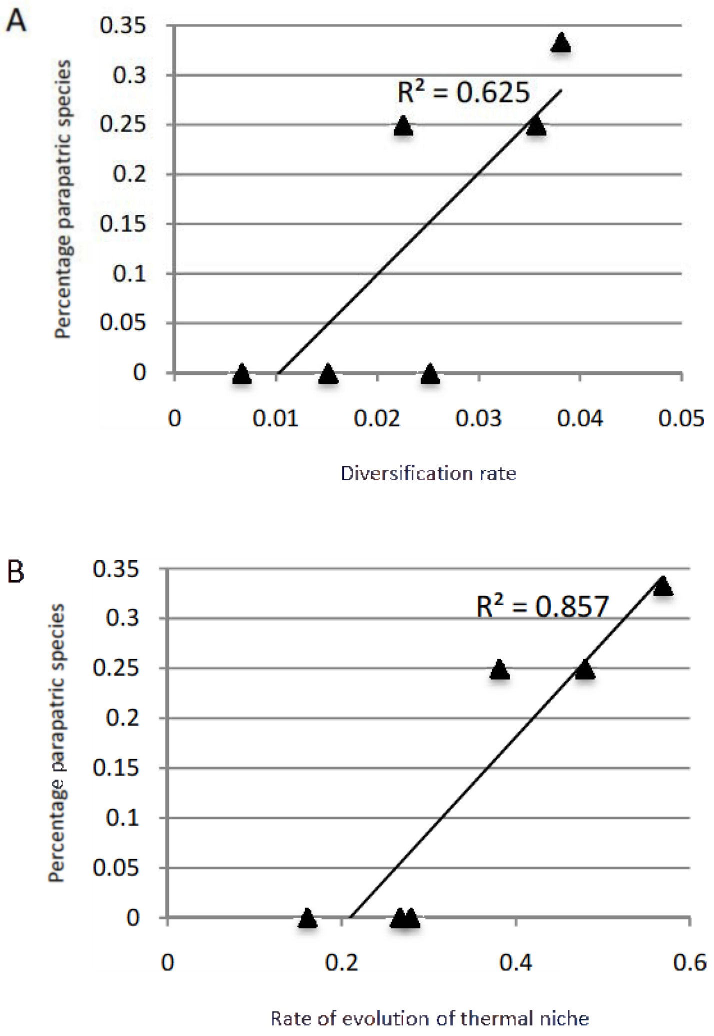


Figure 4: Comparison of inferred slopes of the rate of diversification as a function of the rate of thermal niche evolution (cf. Figure 3) for our dataset (left boxplot) and the null hypothesis that there is no relationship between diversification and thermal niche evolution (right boxplot). The boxplots represent variation in the topology (sampled from the posterior set of *Dictyota* trees) and the threshold values used to define clades. They show median values (thick line), lower and upper quartiles (box), 5% and 95% percentiles (lines) and outliers (circles).

The direction of the great majority of thermal niche shifts is from warmer waters to colder waters (Figure S1.3). Among clades that do not have a conserved thermal niche, those that have shifted from warmer to colder waters have higher rates of diversification than those that have moved from colder water into warmer water (Figure S1.3). Among clades with conserved thermal niches, the rate of diversification does not differ between warm-water clades and colder-water clades (Figure S1.4). Interpreting the observed pattern from a geographical perspective demonstrates that the percentage of sister taxa with contiguous, non-overlapping ranges (parapatric species) is higher in clades with higher diversification rates (R^2= 0.625, Figure 5a). Similarly, the percentage parapatric species correlates with evolutionary rate of the thermal niche, indicating that these speciation events may follow a latitudinal pattern (R^2= 0.857, Figure 5b).



Figuur 5: Regression analysis showing the positive relationship between the percentage of parapatric species and the rate of species diversification (A) and between the percentage of parapatric species and the rate of evolution of the thermal niche among *Dictyota* clades (B).

DISCUSSION

Our results show that species diversification in the marine algal genus *Dictyota* is positively associated with the ability of clades to shift their thermal niche. Despite the seemingly haphazard evolution of the thermal niche and unremarkable diversification dynamics when analyzed separately, the association between both is strong. We demonstrate that this correlation between niche evolution and diversification is robust against topological uncertainty and independent of clade age.

As pointed out by Kozak &Wiens (2010), higher diversification rates are probably caused by higher rates of niche evolution instead of the other way around. A mechanism that can explain increased rates of niche evolution as a consequence of increased diversification is currently unknown. Older, more species rich clades might be expected to spread into more climatic niches by chance alone. However, this possibility is accounted for by evaluating clades comparable of age. In addition to that, the rate of thermal niche evolution within a clade, and not simply the variance in thermal values among species was considered. Indeed, we found no relationship between thermal variance and species richness within a clade.

The evolvability of the niche of a lineage can affect both speciation and extinction rates. In lineages with conserved niches, speciation is more likely to result from vicariance (allopatric) as a result of dispersal limitation than from changes along a niche gradient, which would be a more common speciation mechanism in lineages with higher niche evolvability. This simple model relating the diversification dynamics of a lineage to its niche evolvability is influenced by a number of external elements. An important factor is the steepness and temporal variability of the climatic gradients, in our case the latitudinal gradient in sea surface temperatures. In what follows, we will discuss several aspects of this conceptual model.

The observed diversity pattern in *Dictyota* can be interpreted as an evolutionary response to Cenozoic climatic evolution which established a steep latitudinal temperature gradient. A mechanistic explanation allowing for speciation along such an environmental gradient was offered by Doebeli & Dieckman (2003) who demonstrated that spatial segregation of divergent phenotypes was critically dependent on the steepness of the gradient as well as dispersal capacity (movement). First, compared to the present day, the Early Eocene (55-50 mya) displayed almost no latitudinal SST gradient between subequatorial and subpolar regions (Bijl *et al.*, 2009). Subsequent climatic deterioration established a latitudinal temperature gradient already by the end of the Late Eocene. Secondly, under the model of Doebeli & Dieckman (2003) evolutionary branching and spatial segregation is promoted if movement distances are short. Seaweeds appear to meet this assumption remarkably well, being considered poor dispersers (Kinlan & Gaines, 2003). In other words, local adaptation along a temperature gradient may very well have resulted in higher diversification rates as observed in our data. Clades with higher diversification rates are also characterized by a higher percentage of sister taxa exhibiting contiguous ranges directed along the thermal gradient. The latter forms an indirect source of evidence for a diversification mode which is primarily driven by adaption and subsequent speciation along the thermal gradient. The imprint of extinction toward the diversity pattern is difficult to assess based on phylogenetic evidence only. It has been noted previously that species with more evolvable niches may cope better with changing environmental conditions, decreasing their risk of extinction, while lineages with conserved niches are more likely to suffer extinction (Cooper *et al.*, 2011). By applying analyses which enable to decouple speciation from extinction (e.g. Morlon *et al.*, 2011), extinction rates are consistently estimated very low, regardless of clade (Table S1.4), pointing towards a dominant role for speciation in shaping the observed diversity pattern.

Jablonski et al. (2006) present a model based on genera of fossilized bivalves that is superficially complementary with our findings. The 'out of the tropics model' (OTT model) predicts that taxa preferentially originate in the tropics and expand over time into temperate regions. This is consistent with the directionality of thermal niche evolution of *Dictyota*, whereby the majority of lineages moves from warm to cold waters and not vice versa. However, the OTT model also predicts that diversification should be higher in the tropics, due to higher speciation and lower extinction rates, compared to temperate regions. *Dictyota* lineages constrained to the tropics, however, have consistently lower diversification rates, as do lineages constrained to cold water. Higher diversification rates are observed in those lineages which speciate along a thermal gradient, manifesting itself in high mid-latitudinal diversity.

In addition to the argumentation above linking the ability of lineages to shift niches to their evolutionary success (measured as the rate of diversification), an alternative but not necessarily exclusive scenario is also worth considering. In the marine realm, changes in ocean currents through time are thought to affect connectivity across large geographic scales (Veron, 1995; Paulay & Meyer, 2002; Thiel & Haye, 2006). In periods of low connectivity, population sizes are small and speciation rates increase due to peripatric and allopatric isolation. These isolated populations can evolve more rapidly through genetic drift, creating the potential for rapid thermal niche evolution. Furthermore, if such isolated populations were scattered along various points of the latitudinal thermal gradient, they would be subject to selection for different thermal niche optima, which would also increase their rate of thermal evolution. Similar mechanisms can also affect terrestrial species if climatic cycles lead to speciation by subdividing widespread species into isolated populations. It has to be noted that in both these scenarios, the rate of speciation does not cause increased niche evolution. Instead, an external factor (a selection regime caused by a thermal gradient) impacts simultaneously on rates of speciation and rates of niche evolution, leading to an association between both.

Kozak & Wiens (2010) previously showed a similar association between rates of climatic niche evolution and diversification in plethodontid salamanders. Our study shows that similar mechanisms also affect marine biota. The primary difference between our study and that of Kozak & Wiens (2010) is that the latter analyzed evolution of the multi-dimensional climatic niche whereas we have focused on evolution along the thermal dimension of the niche. Plethodontid salamanders diversify more rapidly in the tropics, where they also have higher rates of niche evolution, for example along the elevational gradient. So, whereas for plethodontids shifts between climatic regimes occur more rapidly in tropical regions where the thermal climate is relatively stable, we find higher diversification in lineages that do vary broadly in their thermal affinities. Differentiation along elevational gradients as found in tropical terrestrial animals is comparable to a latitudinal temperature gradient for algae. A second difference with the study of Kozak & Wiens is that whereas they find rapid niche shifting, our results clearly show that niche evolution is concentrated in a small subset of the branches of the tree, followed by diversification in the newly invaded thermal region. A mere 6% of the branches are responsible for 55% of all thermal niche evolution in the genus. This means that there are a few major niche shifts and other than that thermal evolution is fairly slow and gradual. Almost all of the fast branches move from warmer to colder (one exception) and about half of the fast branches are internal, i.e. they represent an ancestral lineage invading colder water and subsequently diversifying there.

It is intriguing that lineages shown to have a positive association between the rates of niche evolution and diversification also feature a marked decrease in the diversification rate over time. Decreasing diversification has often been interpreted as evidence of diversity-dependent processes (Phillimore & Price, 2008; Rabosky, 2009) acting on speciation-extinction dynamics. Assuming that there are diversity-dependent limits on diversification, the positive association could indicate that niche shifts permits clades to escape from these limits by invading new areas. In the case of

Dictyota, we do not consider this possibility very likely for two reasons. First, the ecological literature suggests that seaweed communities are not saturated and that introduced seaweeds are more likely to establish in naturally more diverse habitats (Mineur *et al.*, 2008). Second, the fact that most niche shifts occur from warmer to colder habitats, coincident with the expansion of temperate habitat on both sides of the narrowing tropical belt during the Cenozoic, suggests that clades that have spawned cold-adapted lineages have been able to invade this new habitat, adding to their diversification potential, while clades with more restricted niches have not benefited from this opportunity.

Our results also have implications for the interpretation of latitudinal diversity patterns. The higher overall diversity in the tropics has been attributed to a number of potential causes. In our dataset, we find no evidence for higher diversification in tropics based on the model relating SST to diversification rates. The same result also falsifies other hypotheses such as a relationship between diversification to energy availability, surface areas (tropical provinces are larger, on average), or the time to diversify (tropics have been around for longer). Interestingly, seaweeds display a bimodal latitudinal diversity pattern, with warm-temperate regions being more species-rich than the tropics (Bolton, 1994; Kerswell, 2006; Santelices *et al.*, 2009). Based on a study of global patterns of generic diversity, Kerswell (2006) concluded that richness patterns of seaweeds are shaped by ocean currents through dispersal. Large ocean gyres, travelling poleward along western ocean boundaries and back towards the tropics along the eastern edges, would result in the greatest algal richness in western ocean regions and depauperate tropical floras in the east. Our results counter that explanation because even though *Dictyota* is present in the tropics as well as the rich temperate regions, it is clearly not a consequence of currents extending it into temperate waters. Our results clearly show that the species occurring at mid-latitudes are temperate-water specialists that are endemic in these regions, and they are not mid-latitude extensions of essentially tropical species. In fact, our results prove that any explanation based only on mechanisms working in an ecological timescale cannot explain the patterns of diversity. It is only using an evolutionary approach that one can discover how temperate water has been colonized from the tropics through niche shifts.

CONCLUSION

The question of what determines rates of diversification is a key problem for both ecologists and evolutionary biologists. We show that for the marine algal genus *Dictyota*, species diversification is positively associated with the ability of clades to shift their thermal niche. This study is the first to present a pattern for marine species in which higher niche evolution leads to higher rates of diversification. Although this is very intriguing, other studies are necessary to investigate the universality of this pattern.

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AUTHOR CONTRIBUTIONS

LT, HV and ODC conceived and designed the study. LT carried out the analyses and wrote the manuscript. HV and ODC assisted LT in writing the final version. CD assembled biological information.

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APPENDIX

S1: PHYLOGENY AND DIVERSIFICATION

Species phylogenies were inferred from a multi-gene alignment (*rbc*L, *psa*A, *psb*A, *nad*1, *cox*1, *cox*3, 18S and 26S) of 129 species, using Bayesian inference (BI) and maximum likelihood (ML). The genera Canistrocarpus, Dilophus, Padina, Rugulopteryx, Scoresbyella and Dictyopteris were used as outgroup.

1. Model Selection

Using the Bayesian information criterion (BIC), a suitable partition strategy and suitable models of sequence evolution were selected. The guide tree used during the entire procedure was obtained by maximum-likelihood (ML) analysis of the unpartitioned concatenated alignment with PhyML, using a JC + Γ8 model (Guindon & Gascuel, 2003). Twelve alternative partitioning strategies were evaluated (table S1.1). All subsequent likelihood optimizations and BIC calculations were carried out with Treefinder (Jobb et al., 2004). The preferential model of sequence evolution and partitioning strategy was a GTR + Γ4 for which all protein coding genes were partitioned in three codon positions and nuclear genes were separated (table S1.2).

Table S1.1: Partitioning strategies

Strategy	Partitions	Details
1	1	All data
2	8	Partitioned by gene
3	3	Mitochondrial genes + Chloroplast genes + Nuclear genes
4	2	Protein coding genes + Nuclear genes
5	**20**	**Protein coding genes (separate codon positions per gene) + Nuclear genes (separated)**
6	19	Protein coding genes (separate codon positions per gene) + Nuclear genes
7	5	Protein coding genes (separate codon positions) + Nuclear genes (separated)
8	4	Protein coding genes (codon positions 1 & 2 + codon position 3) + Nuclear genes (separated)
9	4	Protein coding genes (separate codon positions) + Nuclear genes
10	3	Protein coding genes (codon positions 1 & 2 + codon position 3) + Nuclear genes
11	14	Protein coding genes (codon positions 1 & 2 + codon position 3, per gene) + Nuclear genes (separated)
12	13	Protein coding genes (codon positions 1 & 2 + codon position 3, per gene) + Nuclear genes

Table S1.2: Results top ten

PMTstrategy	substmodel	RAStype	likelihood	parameters	AIC	AICc	BIC
5	**GTR**	**G4**	**-105745.73**	**456**	**212403.5**	**212453.2**	**215635.1**
5	GTR	IG4	-105745.73	476	212443.5	212497.8	215816.8
6	GTR	G4	-105900.63	446	212693.3	212740.8	215854
11	GTR	G4	-106171.06	396	213134.1	213171.4	215940.5
6	GTR	IG4	-105900.63	465	212731.3	212783	216026.6
11	GTR	IG4	-106171.06	410	213162.1	213202.1	216067.7
12	GTR	G4	-106325.95	386	213423.9	213459.3	216159.4
12	GTR	IG4	-106325.95	399	213449.9	213487.7	216277.5
7	GTR	G4	-107217.39	306	215046.8	215068.8	217215.3
7	GTR	IG4	-107217.39	311	215056.8	215079.5	217260.8

2. Phylogenetic analysis

ML analyses were performed using RAxML v. 7.2.8 (Stamatakis, 2006). Statistical support for individual nodes was assessed via bootstrapping with 1,000 replicates. BI was conducted with MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003). Six parallel runs, each consisting of four incrementally heated chains, were run for 30 to 40 million generations, sampling every 2,500 generations. Convergence of log-likelihoods and parameter values were evaluated in Tracer v1.5 (Rambaut & Drummond, 2007). After discarding an appropriate burn-in, we built a consensus tree based on the runs achieving the highest converged likelihoods. The complete BI analysis was then repeated using this consensus tree as a user defined starting tree. The final resulting maximum clade credibility tree is shown in figure S1.2. All analyses were run on the Simon Stevin Computation Cluster at Ghent University, Belgium.

3. Divergence-Time Analysis

Chronograms were estimated using PhyloBayes (Lartillot & Philippe, 2004). We randomly sampled 1,500 trees from the MrBayes posterior set and used a log normal clock model to estimate divergence times. The root of the tree was constrained in geological time based on a brown algal time-calibrated phylogeny (Silberfeld et al., 2010). We applied a gamma root height prior set at 110 Ma (95%: 98 – 134).

Figure S1.1: Maximum likelihood phylogeny based on the combined dataset of eight genes. Numbers at nodes indicate ML bootstrap proportions (as percentages).

Figure S1.2: Bayesian consensus phylogeny based on the combined dataset of eight genes. Numbers at nodes indicate BI posterior probabilities (as percentages).

4. Diversification analyses

Step 1:

A lineage through time plot was developed with the ‘APE’ package in R (Paradis et al., 2004).

Step2:

We used LASER (Rabosky, 2006) to detect temporal variation in diversification rates on the consensus Dictyota phylogeny. We evaluated the fit of the temporal pattern of lineage diversification in Dictyota to a set of rate-constant and rate-variable models:

1. Pure birth model (Yule)
2. Birth-death model
3. Density-dependent model (exponential)
4. Density-dependent model (linear)
5. Yule-2-rate model
6. Yule-3-rate model

The Akaike Information Criterion (AIC) is used for to select among the different models of diversification. The model with the lowest AIC is taken to be the model that best approximates the data. Results are shown in Table S1.3.

Step 3:

In addition to step two, we also made use of a recently published method (Morlon et al., 2011) to estimate diversity dynamics from phylogenies. Morlon presented an approach that provides estimates of present-day diversification rates and how these rates vary across lineages. The Dictyota phylogeny was subdivided in clades similar as in figure 1. All nine models were fit each of these clades. Results are shown in Table S1.4.

Table S1.3: Results of fitting rate-constant and rate-variable birth–death models to the empirical ***Dictyota*** consensus tree (Rabosky, 2006). The best scoring rate-constant model (pink) is a pure birth model. We notice an extinction fraction of 0 (green) when fitting a birth-death model. The best model overall is a yule-3-rate model (blue) with diversification shifts at 33.8 and 3 million years ago. (Legend: np = number of parameters; r1,r2,r3 = net diversification rates; st1,st2 = shift times; a = extinction fraction; x_p = parameter from the ddx model; k = parameter from the DDL model)

model	np	type	lnL	AIC	r_1	r_2	r_3	st_1	st_2	a	x_p	k
pure birth	1	constant	-73.04	148.07	0.033	—	—	—	—	—	—	—
birth-death	2	constant	-73.04	150.07	0.033	—	—	—	—	0.000	—	—
density-dependent (DDX)	2	variable	-56.06	116.11	0.519	—	—	—	—	—	0.702	—
density-dependent (DDL)	2	variable	-56.37	116.74	0.080	—	—	—	—	—	—	116.65
yule2rates	3	variable	-57.27	120.54	0.075	0.023	—	33.79	—	—	—	—
yule3rates	5	variable	-52.90	115.80	0.075	0.026	0.003	33.79	2.96	—	—	—

Table S1.4: A survey of 9 models of diversification (Morlon ***et al.***, 2011) clearly indicates that speciation-only models are the most appropriate for all major clades in Fig 1 (based on the AICc values tabulated here, best-scoring models indicated in blue). When models with variable birth rates were preferred (clades 4,5,8,9), parameter estimates indicated decreasing birth rates through time as also suggested by the results in Table S1.3 above.

model category	model	clade 2	clade 4	clade 5	clade 6	clade 7	clade 8	clade 9
speciation only	B constant	23.28	179.76	24.69	75.37	32.16	76.84	433.37
	B variable E	29.66	177.90	27.15	75.75	35.03	75.50	414.50
	B variable L	28.84	177.69	23.71	76.32	34.44	76.37	416.11
speciation and extinction	BD constant	29.95	181.96	31.36	77.96	36.36	79.43	435.45
	B variable E, D constant	49.66	180.21	44.70	77.32	42.03	77.46	416.49
	B variable L, D constant	48.84	179.64	44.66	77.04	41.42	76.48	414.86
	B constant, D variable E	49.95	184.28	51.36	80.95	43.36	82.42	437.57
	B constant, D variable L	49.92	180.34	44.64	79.90	41.78	81.30	420.03
	B variable E, D variable E		182.65		80.80	56.03	80.90	417.83

Figure S1.3: Diversification as a function of the direction of thermal evolution (TE). The majority of movements are from warmer water into colder water (more points on left side of graph). Rates of diversification are clearly higher in clades shifting their niches from warmer to colder habitats, as indicated by the downward trend in the purple points. This trend is not obvious in clades with more conserved niches (orange points) or clades with intermediate levels of niche evolution (black points). The direction of the thermal niche shift was quantified by subtracting the average SST of contemporary species in the clade from the estimated SST at the ancestral node of the clade in question (dSST). While this metric does not capture the full complexity of niche evolution in the clade, it is a good approximation of the global direction of thermal niche evolution.

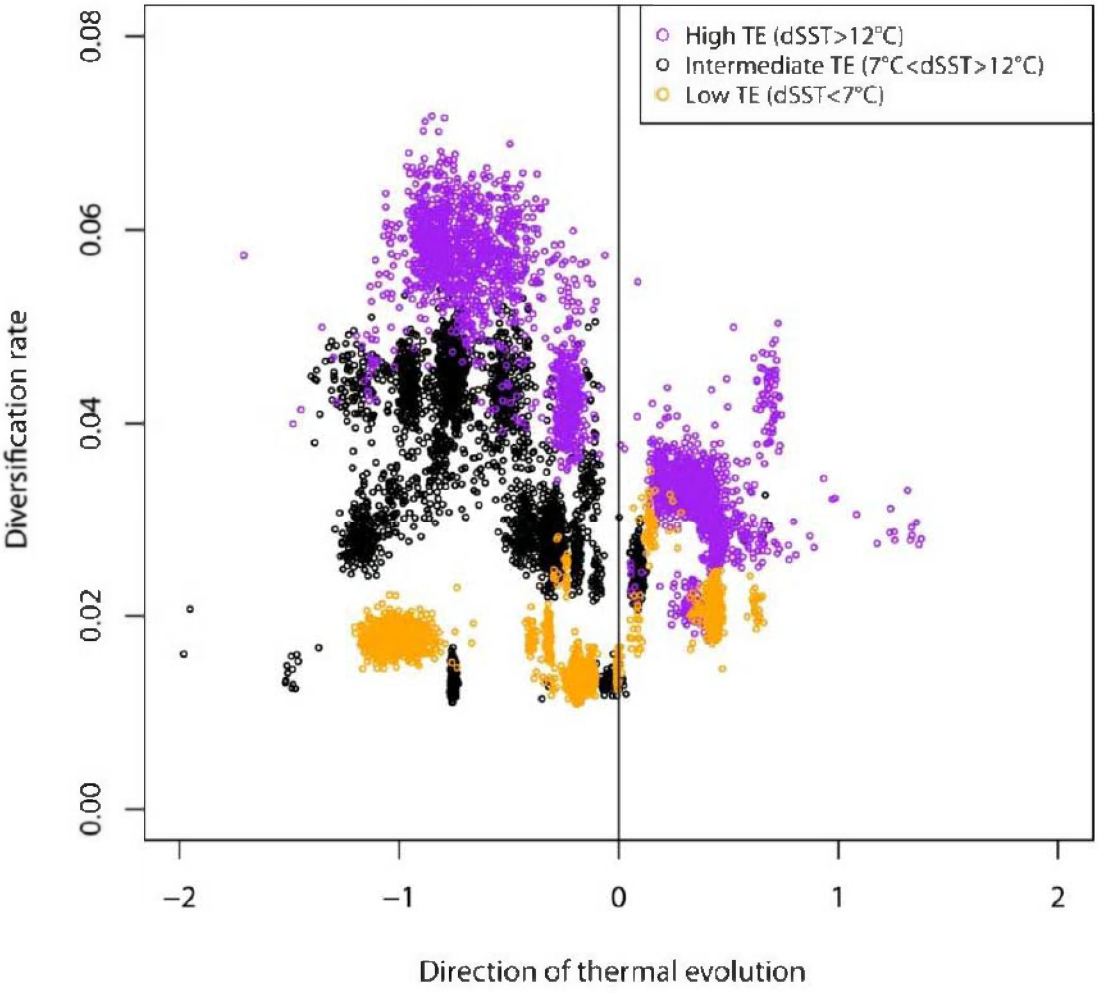

Figure S1.4: There is no clear trend relating the rate of diversification of clades with conservative niches to the thermal niche of those clades. The regression line $y = -2.3\ 10^{-4}\ x + 2.23\ 10^{-2}$ has an adjusted R^2 of 0.057. Conservative clades are defined as above, i.e. its species differ by less than 7°C in average SST.

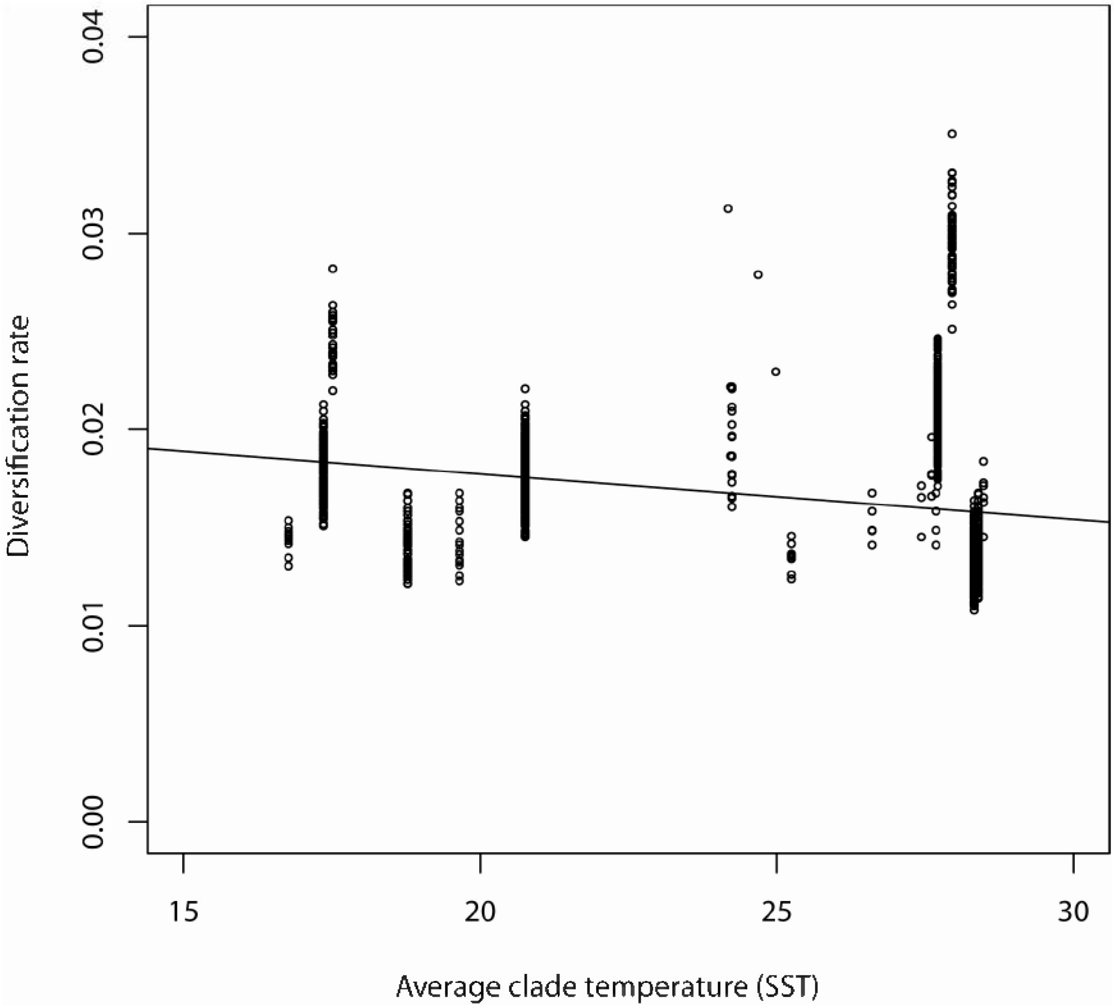

Figure S1.5. Data availability matrix. Graphical representation of the concatenated alignment, showing the availability of sequence data. The color of column and row headers indicate the amount of data available for that column or row. Green indicates high data availability, red indicates low data availability and yellow/orange represents intermediate data availability.

TAXA	18S	26S	cox1	cox3	nad1	psaA	psbA	rbcL
Canistrocarpus cervicornis		GenBank: XX strain: D192 length: 1197 nt	GenBank: XX strain: GWS025739 length: 657 nt		GenBank: GQ425184 strain: D192 length: 729 nt	GenBank: XX strain: HV711 length: 1436 nt	GenBank: XX strain: NR26-20-07 length: 969 nt	GenBank: XX strain: DAP031 length: 1341 nt
Canistrocarpus cervicornis2			GenBank: XX strain: GWS024405 length: 660 nt					
Canistrocarpus crispatus		GenBank: GQ425150 strain: HV721 length: 1182 nt	GenBank: GQ425137 strain: ODC1444 length: 610 nt	GenBank: GQ425146 strain: ODC1444 length: 648 nt	GenBank: GQ425176 strain: ODC1444 length: 734 nt	GenBank: XX strain: HV721 length: 1433 nt	GenBank: XX strain: NR11a-01-12 length: 959 nt	GenBank: GQ425119 strain: HV721 length: 1298 nt
Dictyopteris delicatula						GenBank: EU579898 strain: LBC37 length: 1438 nt	GenBank: XX strain: XX length: 813 nt	GenBank: EU579943 strain: Bit.LBC82 length: 1096 nt
Dictyopteris divaricata	GenBank: AB087112 strain: XX length: 1806 nt					GenBank: AY422600 strain: IK44 length: 1532 nt	GenBank: AY430343 strain: Lee.WJ10 length: 870 nt	GenBank: AY422676 strain: Lee.IK44 length: 1293 nt
Dictyopteris latiuscula						GenBank: AY422601 strain: IK52 length: 1532 nt	GenBank: AY430349 strain: Lee.WJ11 length: 870 nt	GenBank: AY422677 strain: Lee.IK52 length: 1293 nt
Dictyopteris polypodioides	GenBank: AB095293 strain: XX length: 1805 nt	GenBank: DQ472097 strain: ODC1031 length: 1108 nt	GenBank: EU681404 strain: Sil.FRA0513 length: 639 nt	GenBank: EU681445 strain: Sil.FRA0533 length: 654 nt		GenBank: EU579899 strain: LBC38 length: 1488 nt	GenBank: EU681639 strain: Sil.FRA0513 length: 845 nt	GenBank: EU579932 strain: Bit.LBC71 length: 1272 nt
Dictyopteris prolifera	GenBank: AB087114 strain: XX length: 1810 nt					GenBank: AY422602 strain: IK50 length: 1532 nt	GenBank: AY430346 strain: Lee.WJ15 length: 870 nt	GenBank: AY422678 strain: Lee.IK50 length: 1293 nt
Dictyopteris undulata	GenBank: AB087115 strain: XX length: 1806 nt					GenBank: AY528446 strain: IK55 length: 1519 nt	GenBank: AY430353 strain: Lee.WJ14 length: 870 nt	GenBank: AY430333 strain: Lee.WJ12 length: 1293 nt
Dictyota acutiloba1		GenBank: DQ472111 strain: ODC888 length: 1176 nt	GenBank: GU290238 strain: ODC888 length: 605 nt		GenBank: XX strain: JAP047 length: 744 nt	GenBank: XX strain: ODC888 length: 1424 nt	GenBank: XX strain: LT0379 length: 969 nt	GenBank: DQ472056 strain: ODC888 length: 1162 nt

Dictyota acutiloba2		GenBank: XX strain: LT0324 length: 1130 nt			GenBank: XX strain: LT0316 length: 744 nt	GenBank: XX strain: LT0316 length: 1485 nt	GenBank: XX strain: LT0316 length: 969 nt	GenBank: XX strain: LT0316 length: 1060 nt
Dictyota adnata		GenBank: GQ425154 strain: ODC1485 length: 1062 nt	GenBank: XX strain: ODC1485 length: 583 nt	GenBank: XX strain: ODC1485 length: 654 nt	GenBank: GQ425178 strain: ODC1485 length: 714 nt		GenBank: XX strain: SD712204 length: 882 nt	GenBank: GQ425106 strain: SD712204 length: 1234 nt
Dictyota alternifida		GenBank: XX strain: LT0051 length: 580 nt	GenBank: XX strain: LT0051 length: 494 nt	GenBank: XX strain: LT0051 length: 652 nt	GenBank: XX strain: LT0052 length: 738 nt	GenBank: AY422586 strain: NSL1 length: 1532 nt	GenBank: XX strain: LT0052 length: 967 nt	GenBank: AY422662 strain: XX length: 1427 nt
Dictyota alternifida2							GenBank: XX strain: HV2341 length: 967 nt	
Dictyota anastomosans		GenBank: XX strain: HV1949 length: 1103 nt		GenBank: XX strain: HV1949 length: 654 nt	GenBank: XX strain: HV1949 length: 744 nt		GenBank: XX strain: HV1949 length: 969 nt	GenBank: XX strain: HV1949 length: 1229 nt
Dictyota bartayresiana		GenBank: GQ425153 strain: DR7 length: 1106 nt	GenBank: GQ425129 strain: DR7 length: 617 nt	GenBank: XX strain: ODC1513 length: 648 nt	GenBank: GQ425183 strain: ODC1513 length: 738 nt		GenBank: XX strain: D1701 length: 969 nt	GenBank: GQ425107 strain: ODC1588 length: 1280 nt
Dictyota bartayresiana2			GenBank: XX strain: NVT133 length: 608 nt				GenBank: XX strain: JAP028 length: 961 nt	
Dictyota binghamiae		GenBank: XX strain: Lane length: 1183 nt	GenBank: FJ409139 strain: XX length: 657 nt				GenBank: XX strain: HV1542 length: 871 nt	GenBank: XX strain: HV1801 length: 1129 nt
Dictyota canaliculata1		GenBank: GQ425167 strain: SD712709 length: 1105 nt	GenBank: GQ425132 strain: ODC1477 length: 639 nt	GenBank: XX strain: ODC1477 length: 654 nt	GenBank: GQ425177 strain: ODC1477 length: 733 nt		GenBank: GQ425190 strain: ODC1477 length: 824 nt	GenBank: GQ425108 strain: SD712709 length: 1284 nt
Dictyota canaliculata2		GenBank: DQ472117 strain: HV678 length: 1175 nt	GenBank: XX strain: SD712656 length: 617 nt	GenBank: XX strain: SD712656 length: 648 nt	GenBank: XX strain: SD712656 length: 738 nt	GenBank: XX strain: HV678 length: 880 nt	GenBank: XX strain: D1552 length: 969 nt	GenBank: DQ472062 strain: HV678 length: 1300 nt
Dictyota canariensis		GenBank: XX strain: D504 length: 987 nt	GenBank: XX strain: D319 length: 632 nt	GenBank: XX strain: D319 length: 654 nt	GenBank: XX strain: D319 length: 735 nt		GenBank: XX strain: D1559 length: 969 nt	GenBank: XX strain: D504 length: 1276 nt
Dictyota caribaea		GenBank: DQ472116 strain: HV926 length: 1162 nt	GenBank: XX strain: HV926 length: 633 nt	GenBank: XX strain: HV926 length: 653 nt	GenBank: XX strain: HV926 length: 738 nt		GenBank: XX strain: D630 length: 805 nt	GenBank: DQ472061 strain: HV926 length: 1079 nt
Dictyota ceylanica1		GenBank: GQ425152 strain: HV214a length: 1173 nt	GenBank: GQ425122 strain: HV214a length: 621 nt		GenBank: GQ425175 strain: ODC1442 length: 709 nt		GenBank: XX strain: NR15-05-03 length: 969 nt	GenBank: DQ472067 strain: HV214a length: 1328 nt
Dictyota ceylanica2		GenBank: XX	GenBank: XX	GenBank: XX	GenBank: XX		GenBank: XX	GenBank: XX

		strain: D629 length: 1061 nt	strain: RC153 length: 609 nt	strain: D629 length: 538 nt	strain: RC153 length: 733 nt		strain: D629 length: 875 nt	strain: D629 length: 576 nt
Dictyota ceylanica3		GenBank: XX strain: TZ0713 length: 1107 nt	GenBank: XX strain: TZ0713 length: 636 nt	GenBank: XX strain: FG31.5.9.2.13 length: 583 nt	GenBank: XX strain: TZ0713 length: 731 nt		GenBank: XX strain: FG31.5.9.2.13 length: 969 nt	GenBank: XX strain: TZ0713 length: 1280 nt
Dictyota ceylanica4		GenBank: XX strain: SD712460 length: 1031 nt	GenBank: XX strain: MAD0143 length: 608 nt	GenBank: XX strain: ODC1624 length: 654 nt	GenBank: XX strain: ODC1624 length: 734 nt		GenBank: XX strain: HV1891 length: 969 nt	GenBank: XX strain: ODC1624 length: 1281 nt
Dictyota ceylanica5		GenBank: XX strain: HV713 length: 1181 nt	GenBank: XX strain: TZ0173 length: 604 nt	GenBank: XX strain: TZ0173 length: 654 nt	GenBank: XX strain: TZ0173 length: 744 nt	GenBank: XX strain: ODC1662 length: 1470 nt	GenBank: XX strain: CFMX219 length: 964 nt	GenBank: XX strain: ODC1662 length: 1256 nt
Dictyota ceylanica6			GenBank: XX strain: GWS023931 length: 657 nt					
Dictyota ciliolata		GenBank: XX strain: HV723 length: 1183 nt	GenBank: GQ425124 strain: HV632 length: 626 nt		GenBank: GQ425173 strain: D191 length: 744 nt	GenBank: XX strain: TC2 length: 1484 nt	GenBank: XX strain: RD90067 length: 969 nt	GenBank: GQ425109 strain: D191 length: 1317 nt
Dictyota concrescens							GenBank: XX strain: CFMX318 length: 964 nt	
Dictyota coriacea		GenBank: DQ472109 strain: CSUF003 length: 1168 nt	GenBank: GU290234 strain: CSUF003 length: 621 nt		GenBank: GU290251 strain: CSUF003 length: 735 nt		GenBank: XX strain: HV1810 length: 867 nt	GenBank: DQ472054 strain: CSUF003 length: 1223 nt
Dictyota coriacea2			GenBank: HQ990529 strain: GWS018356 length: 654 nt	GenBank: XX strain: HV1940 length: 654 nt		GenBank: AY748318 strain: JALee11 length: 1566 nt	GenBank: XX strain: HV1940 length: 969 nt	GenBank: AY422651 strain: WJ1 length: 1427 nt
Dictyota crenulata		GenBank: GU290231 strain: HV1074 length: 1006 nt	GenBank: XX strain: MX0208 length: 590 nt	GenBank: XX strain: MX0208 length: 643 nt	GenBank: GU290252 strain: HV1074 length: 733 nt	GenBank: XX strain: MX0208 length: 1466 nt	GenBank: XX strain: CFMX393 length: 969 nt	GenBank: GU290253 strain: HV1074 length: 1280 nt
Dictyota cyanoloma		GenBank: XX strain: D502 length: 1020 nt	GenBank: XX strain: GWS016003 length: 660 nt	GenBank: XX strain: D544 length: 654 nt	GenBank: XX strain: D544 length: 734 nt	GenBank: XX strain: D502 length: 1486 nt	GenBank: XX strain: D1567 length: 969 nt	GenBank: XX strain: D544 length: 1284 nt
Dictyota cymatophila		GenBank: GQ425162 strain: D397 length: 1023 nt	GenBank: GQ425128 strain: D406 length: 622 nt	GenBank: XX strain: D306 length: 643 nt	GenBank: GQ425179 strain: D403 length: 738 nt	GenBank: XX strain: D403 length: 1460 nt	GenBank: XX strain: D696 length: 842 nt	GenBank: GQ425111 strain: D397 length: 1136 nt
Dictyota dhofarensis		GenBank: DQ472127 strain: DHO0163 length: 1180 nt	GenBank: XX strain: DHO0163 length: 603 nt		GenBank: XX strain: DHO0163 length: 738 nt		GenBank: XX strain: DHO0163 length: 752 nt	GenBank: XX strain: DHO0163 length: 782 nt
Dictyota dichotoma1		GenBank: GQ425155 strain: D190 length: 1192 nt	GenBank: XX strain: FS244 length: 642 nt	GenBank: AY500368 strain: GenBank length: 654 nt	GenBank: AY500368 strain: Genbank length: 744 nt	GenBank: AY528450 strain: IK81 length: 1519 nt	GenBank: XX strain: RSAD204 length: 969 nt	GenBank: AY527200 strain: IK81 length: 1428 nt

Dictyota dichotoma2	GenBank: AF350227 strain: 1CH length: 1776 nt		GenBank: XX strain: HV1890 length: 600 nt	GenBank: XX strain: HV1890 length: 591 nt	GenBank: XX strain: HV1890 length: 733 nt	GenBank: AY748316 strain: JALee05 length: 1566 nt	GenBank: XX strain: HV1941 length: 969 nt	GenBank: AY422669 strain: IK14 length: 1427 nt
Dictyota dichotoma3		GenBank: XX strain: HV2252 length: 1132 nt	GenBank: XX strain: GWS015099 length: 660 nt	GenBank: XX strain: LT0172 length: 654 nt	GenBank: XX strain: LT0103 length: 733 nt	GenBank: XX strain: LT0103 length: 1062 nt	GenBank: XX strain: LT0172 length: 969 nt	GenBank: XX strain: LT0172 length: 1170 nt
Dictyota diemensis		GenBank: XX strain: LT0108 length: 989 nt	GenBank: HM891273 strain: GWS015568 length: 657 nt	GenBank: XX strain: LT0108 length: 645 nt	GenBank: XX strain: HV2368 length: 733 nt	GenBank: XX strain: HV2368 length: 1476 nt	GenBank: XX strain: HV2350 length: 969 nt	GenBank: XX strain: HV2368 length: 1216 nt
Dictyota fasciola		GenBank: GQ425166 strain: ODC1057 length: 1143 nt	GenBank: GQ425133 strain: ODC1065 length: 639 nt	GenBank: GQ425143 strain: ODC1065 length: 654 nt	GenBank: GQ425172 strain: ODC1065 length: 737 nt	GenBank: XX strain: ODC1065 length: 1486 nt	GenBank: XX strain: D1565 length: 969 nt	GenBank: GQ425110 strain: ODC1065 length: 1291 nt
Dictyota fasciola2							GenBank: XX strain: ODC2027 length: 962 nt	
Dictyota flabellata		GenBank: XX strain: HV1562 length: 1106 nt	GenBank: XX strain: HV1654 length: 604 nt		GenBank: XX strain: HV1564 length: 744 nt	GenBank: XX strain: HV1655 length: 1475 nt	GenBank: XX strain: HV1560 length: 873 nt	GenBank: XX strain: TACO16 length: 1191 nt
Dictyota friabilis1		GenBank: DQ472120 strain: ODC898 length: 1177 nt	GenBank: GU290237 strain: DML67250 length: 533 nt	GenBank: GU290244 strain: ODC898 length: 652 nt	GenBank: GU290249 strain: ODC898 length: 738 nt	GenBank: XX strain: ODC898 length: 1428 nt	GenBank: XX strain: ODC898 length: 866 nt	GenBank: DQ472064 strain: HV153 length: 1328 nt
Dictyota grossedentata		GenBank: XX strain: TZ0490 length: 853 nt	GenBank: XX strain: TZ0490 length: 639 nt	GenBank: XX strain: TZ0490 length: 615 nt	GenBank: XX strain: TZ0490 length: 737 nt		GenBank: XX strain: C29-1-23 length: 969 nt	GenBank: XX strain: TZ0490 length: 1304 nt
Dictyota hamifera		GenBank: DQ472110 strain: HV222 length: 1181 nt	GenBank: GQ425123 strain: HV222 length: 616 nt	GenBank: GQ425141 strain: HV222 length: 654 nt	GenBank: GQ425169 strain: HV222 length: 701 nt		GenBank: XX strain: FS887 length: 958 nt	GenBank: GQ425112 strain: DML67438 length: 1266 nt
Dictyota humifusa		GenBank: XX strain: SD712066 length: 1025 nt	GenBank: XX strain: ODC1659 length: 642 nt	GenBank: XX strain: SD712066 length: 597 nt	GenBank: XX strain: ODC1659 length: 701 nt	GenBank: XX strain: MX0198 length: 1472 nt	GenBank: XX strain: CFCR858 length: 969 nt	GenBank: XX strain: SD712066 length: 1293 nt
Dictyota implexa		GenBank: GQ425163 strain: ODC1238 length: 1179 nt	GenBank: GQ425135 strain: FS271 length: 642 nt	GenBank: GQ425140 strain: LLGO249 length: 654 nt	GenBank: GQ425168 strain: LLGO300 length: 738 nt	GenBank: XX strain: LLGO249 length: 790 nt	GenBank: XX strain: ODC2157 length: 962 nt	GenBank: GQ425116 strain: Kooistra1 length: 1330 nt
Dictyota intermedia			GenBank: XX strain: GWS022767 length: 657 nt	GenBank: XX strain: LT0063 length: 570 nt	GenBank: XX strain: TC1 length: 725 nt	GenBank: XX strain: LT0063 length: 1471 nt	GenBank: XX strain: LT0063 length: 969 nt	GenBank: DQ472086 strain: TC1 length: 1207 nt
Dictyota jamaicensis			GenBank: XX strain: DR27 length: 633 nt		GenBank: XX strain: DR27 length: 738 nt		GenBank: XX strain: FS881 length: 954 nt	
Dictyota koreana	GenBank: AB090387	GenBank: HV1978		GenBank: XX	GenBank: XX	GenBank: AY422591	GenBank: XX	GenBank: AY422665

	strain: SZKIZ067 length: 1812 nt	strain: HV1978 length: 1125 nt		strain: HV1894 length: 654 nt	strain: HV1894 length: 733 nt	strain: IK23 length: 1532 nt	strain: SGAD0909027 length: 969 nt	strain: IK21 length: 1427 nt
Dictyota kunthii		GenBank: GU290231 strain: D104 length: 1172 nt	GenBank: GU290237 strain: D102 length: 598 nt	GenBank: GU290245 strain: D102 length: 620 nt	GenBank: GU290250 strain: D102 length: 738 nt	GenBank: XX strain: D102 length: 1427 nt	GenBank: EU395618 strain: D102 length: 766 nt	GenBank: DQ472057 strain: D102 length: 1253 nt
Dictyota linearis		GenBank: XX strain: ODC1254 length: 1179 nt	GenBank: XX strain: FS335 length: 633 nt	GenBank: XX strain: ODC1254 length: 654 nt	GenBank: XX strain: D391 length: 738 nt	GenBank: XX strain: ODC1254 length: 1460 nt	GenBank: XX strain: ODC2026 length: 962 nt	GenBank: XX strain: ODC1254 length: 1266 nt
Dictyota liturata1		GenBank: XX strain: HEC15721 length: 604 nt	GenBank: XX strain: HEC15816 length: 607 nt		GenBank: GQ425174 strain: HEC15721 length: 736 nt	GenBank: XX strain: HEC15721 length: 1452 nt	GenBank: XX strain: FS892 length: 964 nt	GenBank: XX strain: HEC15721 length: 1212 nt
Dictyota liturata2		GenBank: GQ425159 strain: KZN2282 length: 1185 nt	GenBank: XX strain: MAD0142 length: 605 nt				GenBank: XX strain: FG31.5.9.2.7 length: 969 nt	GenBank: XX strain: KZN2282 length: 1265 nt
Dictyota liturata3			GenBank: XX strain: HV2768 length: 608 nt				GenBank: XX strain: JH88425 length: 955 nt	GenBank: GQ425113 strain: Sole1 length: 1313 nt
Dictyota liturata4			GenBank: XX strain: GWS023781 length: 657 nt					
Dictyota mangrovestolon		GenBank: XX strain: ODC1486 length: 976 nt	GenBank: XX strain: ODC1486 length: 632 nt	GenBank: XX strain: ODC1486 length: 643 nt	GenBank: XX strain: ODC1486 length: 744 nt		GenBank: XX strain: ODC1486 length: 860 nt	GenBank: XX strain: ODC1486 length: 1225 nt
Dictyota mediterranea		GenBank: GU290233 strain: SGAD1116 length: 1178 nt	GenBank: XX strain: LLGO313 length: 612 nt	GenBank: XX strain: LLGO224 length: 646 nt	GenBank: XX strain: LLGO313 length: 744 nt		GenBank: XX strain: ODC2066 length: 962 nt	GenBank: GU290254 strain: D595 length: 1247 nt
Dictyota mertensii1		GenBank: XX strain: HV924 length: 666 nt	GenBank: XX strain: DR30 length: 590 nt		GenBank: XX strain: HV924 length: 719 nt	GenBank: XX strain: D628 length: 1447 nt	GenBank: XX strain: HV924 length: 879 nt	GenBank: DQ472060 strain: HV924 length: 1318 nt
Dictyota mertensii2		GenBank: GQ425158 strain: HV911 length: 1178 nt	GenBank: GQ425130 strain: DR31 length: 607 nt	GenBank: XX strain: HV911 length: 587 nt	GenBank: GQ425180 strain: DR31 length: 724 nt	GenBank: XX strain: HV911 length: 1483 nt	GenBank: GQ425215 strain: DR31 length: 834 nt	GenBank: GQ425114 strain: DR32 length: 1096 nt
Dictyota naevosa		GenBank: DQ472108 strain: KZNb2345 length: 595 nt	GenBank: XX strain: KZNb2345 length: 600 nt	GenBank: XX strain: KZNb2345 length: 560 nt	GenBank: XX strain: KZNb2345 length: 726 nt	GenBank: XX strain: D659 length: 1386 nt	GenBank: XX strain: RSAD482 length: 969 nt	GenBank: DQ472084 strain: KZN2241 length: 1199 nt
Dictyota nigricans		GenBank: XX strain: HV2583 length: 1073 nt	GenBank: XX strain: D92 length: 600 nt		GenBank: XX strain: D92 length: 729 nt		GenBank: XX strain: HV2583 length: 969 nt	GenBank: DQ472077 strain: D92 length: 1328 nt
Dictyota paniculata1		GenBank: XX strain: LT0366	GenBank: XX strain: GWS024729	GenBank: XX strain: D97	GenBank: XX strain: D97		GenBank: XX strain: LT0354	GenBank: DQ472082 strain: D97

		length: 1044 nt	length: 660 nt	length: 654 nt	length: 735 nt		length: 969 nt	length: 752 nt
Dictyota paniculata2			GenBank: XX strain: GWS016687 length: 660 nt				GenBank: XX strain: HV2331 length: 969 nt	
Dictyota pardalis						GenBank: AY422596 strain: IK26N length: 1532 nt	GenBank: AY422633 strain: IK26 length: 765 nt	GenBank: AY422671 strain: IK26 length: 1427 nt
Dictyota pfaffii		GenBank: XX strain: HEC15779 length: 596 nt	GenBank: XX strain: D361 length: 596 nt	GenBank: XX strain: D361 length: 642 nt	GenBank: XX strain: D361 length: 705 nt	GenBank: XX strain: D361 length: 1234 nt	GenBank: XX strain: FS933 length: 937 nt	GenBank: XX strain: D285 length: 1237 nt
Dictyota pinnatifida		GenBank: GQ425157 strain: CLO31302 length: 1171 nt	GenBank: GQ425126 strain: HV902 length: 611 nt	GenBank: GQ425142 strain: HV932 length: 619 nt	GenBank: GQ425171 strain: HV932 length: 744 nt	GenBank: XX strain: HV932 length: 876 nt	GenBank: XX strain: DR4 length: 868 nt	GenBank: GQ425115 strain: Sole3 length: 1317 nt
Dictyota pleiacantha1		GenBank: XX strain: D193 length: 1192 nt	GenBank: XX strain: D404 length: 617 nt		GenBank: XX strain: D404 length: 738 nt	GenBank: XX strain: D310 length: 870 nt	GenBank: XX strain: D1560 length: 969 nt	GenBank: XX strain: D324 length: 1200 nt
Dictyota pleiacantha2							GenBank: XX strain: WNC2009-090 length: 571 nt	
Dictyota polycladal1		GenBank: XX strain: FG79607 length: 1129 nt		GenBank: XX strain: KD88618 length: 643 nt	GenBank: XX strain: FG79607 length: 744 nt	GenBank: XX strain: HV2282 length: 1463 nt	GenBank: XX strain: HV2282 length: 969 nt	GenBank: DQ472050 strain: GWS0139 length: 1202 nt
Dictyota polyclada2		GenBank: XX strain: LT0317 length: 1122 nt		GenBank: XX strain: LT0317 length: 561 nt	GenBank: XX strain: LT0317 length: 731 nt		GenBank: XX strain: LT0317 length: 969 nt	
Dictyota polyclada3		GenBank: XX strain: HV2404 length: 1028 nt	GenBank: XX strain: HV2404 length: 592 nt	GenBank: XX strain: HV2404 length: 583 nt	GenBank: XX strain: HV2404 length: 739 nt		GenBank: XX strain: HV2404 length: 818 nt	GenBank: XX strain: HV2404 length: 1227 nt
Dictyota rigida1		GenBank: XX strain: ODC1623 length: 1112 nt	GenBank: GQ425138 strain: ODC1657 length: 605 nt	GenBank: XX strain: ODC1623 length: 653 nt	GenBank: GQ425181 strain: ODC1657 length: 721 nt		GenBank: XX strain: ODC1623 length: 871 nt	GenBank: GQ425117 strain: ODC1623 length: 1280 nt
Dictyota rigida2				GenBank: XX strain: HV1948 length: 654 nt	GenBank: XX strain: HV1948 length: 721 nt		GenBank: XX strain: HV1948 length: 969 nt	
Dictyota rigida3		GenBank: XX strain: HV2556 length: 554 nt	GenBank: XX strain: HV2572 length: 608 nt	GenBank: XX strain: HV2572 length: 654 nt	GenBank: XX strain: HV2556 length: 701 nt		GenBank: XX strain: HV2556 length: 968 nt	GenBank: XX strain: HV2572 length: 1217 nt
Dictyota rigida4			GenBank: XX strain: MAD2157 length: 598 nt				GenBank: XX strain: RSAD549 length: 969 nt	
Dictyota rigida5		GenBank: GQ425164 strain: TCn6	GenBank: XX strain: TCn6	GenBank: XX strain: TCn6	GenBank: XX strain: TCn6			GenBank: XX strain: TCn6

		length: 1175 nt	length: 479 nt	length: 643 nt	length: 737 nt			length: 1189 nt
Dictyota sandvicensis1		GenBank: DQ472118 strain: ODC896 length: 1058 nt	GenBank: GU290239 strain: ODC889 length: 604 nt		GenBank: GU290248 strain: ODC889 length: 724 nt	GenBank: XX strain: ODC896 length: 1454 nt	GenBank: XX strain: ODC889 length: 867 nt	GenBank: DQ472053 strain: ODC896 length: 1320 nt
Dictyota sandvicensis2		GenBank: XX strain: KD88671 length: 1123 nt	GenBank: XX strain: GWS023922 length: 657 nt		GenBank: XX strain: KD88671 length: 726 nt		GenBank: XX strain: KD88671 length: 969 nt	GenBank: XX strain: KD88671 length: 1217 nt
Dictyota sandvicensis3		GenBank: XX strain: HV1095 length: 1180 nt	GenBank: XX strain: HV1095 length: 440 nt					GenBank: XX strain: HV1095 length: 1094 nt
Dictyota sp1		GenBank: XX strain: D323 length: 568 nt	GenBank: XX strain: D328 length: 614 nt	GenBank: XX strain: D328 length: 647 nt	GenBank: XX strain: D323 length: 744 nt	GenBank: XX strain: D328 length: 1308 nt	GenBank: XX strain: D328 length: 873 nt	GenBank: XX strain: D328 length: 1219 nt
Dictyota sp10			GenBank: XX strain: SD712275 length: 605 nt	GenBank: XX strain: SD712275 length: 644 nt	GenBank: XX strain: SD712275 length: 710 nt		GenBank: XX strain: SD712275 length: 860 nt	GenBank: XX strain: SD712275 length: 1084 nt
Dictyota sp11		GenBank: XX strain: TZ0327 length: 750 nt	GenBank: XX strain: TZ0327 length: 614 nt	GenBank: XX strain: TZ0327 length: 641 nt	GenBank: XX strain: TZ0327 length: 744 nt		GenBank: XX strain: NR02-10-04 length: 969 nt	GenBank: XX strain: TZ0327 length: 1261 nt
Dictyota sp12		GenBank: XX strain: SD712079 length: 988 nt		GenBank: XX strain: SD712079 length: 453 nt	GenBank: XX strain: SD712079 length: 738 nt		GenBank: XX strain: SD712079 length: 826 nt	GenBank: XX strain: SD712079 length: 1136 nt
Dictyota sp15		GenBank: XX strain: CLO12603 length: 556 nt	GenBank: XX strain: CLO12603 length: 608 nt	GenBank: XX strain: SGAD1051 length: 647 nt	GenBank: XX strain: DML68137 length: 741 nt		GenBank: XX strain: DML67430 length: 873 nt	GenBank: XX strain: DML67430 length: 1289 nt
Dictyota sp16		GenBank: XX strain: SD712520 length: 1088 nt	GenBank: XX strain: SD712641 length: 597 nt	GenBank: XX strain: SD712520 length: 595 nt	GenBank: XX strain: SD712641 length: 735 nt		GenBank: XX strain: NR07-25-12 length: 960 nt	GenBank: XX strain: SD712520 length: 1136 nt
Dictyota sp17		GenBank: XX strain: SD712436 length: 988 nt	GenBank: XX strain: SD712436 length: 599 nt		GenBank: XX strain: SD712436 length: 743 nt		GenBank: XX strain: SD712436 length: 847 nt	
Dictyota sp18		GenBank: XX strain: D745 length: 1099 nt	GenBank: XX strain: D745 length: 589 nt	GenBank: XX strain: D745 length: 642 nt	GenBank: XX strain: D745 length: 736 nt		GenBank: XX strain: D745 length: 766 nt	GenBank: XX strain: D745 length: 1179 nt
Dictyota sp19		GenBank: XX strain: MX0335 length: 1076 nt	GenBank: XX strain: MX0335 length: 586 nt	GenBank: XX strain: MX0335 length: 643 nt	GenBank: XX strain: MX0335 length: 737 nt		GenBank: XX strain: CFCR844 length: 969 nt	GenBank: XX strain: MX0335 length: 1227 nt
Dictyota sp20		GenBank: XX strain: HV1590 length: 842 nt	GenBank: XX strain: HV1590 length: 622 nt		GenBank: XX strain: HV1590 length: 738 nt	GenBank: XX strain: MX0334 length: 1439 nt	GenBank: XX strain: CFNI565 length: 969 nt	GenBank: XX strain: HV1590 length: 1216 nt
Dictyota sp21		GenBank: XX strain: MX0360 length: 552 nt	GenBank: XX strain: MX0360 length: 606 nt	GenBank: XX strain: MX0360 length: 654 nt	GenBank: XX strain: MX0360 length: 645 nt		GenBank: XX strain: CFMX389 length: 969 nt	GenBank: XX strain: MX0360 length: 1132 nt
Dictyota sp22		GenBank: XX	GenBank: XX	GenBank: XX	GenBank: XX		GenBank: XX	GenBank: XX

		strain: D1694 length: 1127 nt	strain: D1694 length: 451 nt	strain: D1694 length: 649 nt	strain: D1694 length: 739 nt		strain: HV2568 length: 967 nt	strain: D1694 length: 748 nt
Dictyota sp23		GenBank: XX strain: LT0430 length: 556 nt			GenBank: XX strain: LT0430 length: 709 nt		GenBank: XX strain: LT0430 length: 969 nt	GenBank: XX strain: LT0430 length: 1221 nt
Dictyota sp24		GenBank: XX strain: JH88416 length: 534 nt	GenBank: XX strain: JH88416 length: 591 nt	GenBank: XX strain: JH88416 length: 654 nt	GenBank: XX strain: JH88416 length: 724 nt		GenBank: XX strain: JH88416 length: 671 nt	GenBank: XX strain: JH88416 length: 679 nt
Dictyota sp25		GenBank: XX strain: LT0347 length: 1003 nt		GenBank: XX strain: LT0347 length: 649 nt			GenBank: XX strain: LT0411 length: 969 nt	GenBank: XX strain: LT0347 length: 1222 nt
Dictyota sp26		GenBank: XX strain: KD88202 length: 1093 nt	GenBank: XX strain: KD88202 length: 609 nt	GenBank: XX strain: KD88202 length: 554 nt			GenBank: XX strain: KD88202 length: 937 nt	GenBank: XX strain: KD88202 length: 789 nt
Dictyota sp29							GenBank: XX strain: WNC2009-133 length: 950 nt	
Dictyota sp3		GenBank: XX strain: D321 length: 569 nt	GenBank: XX strain: FS562 length: 608 nt	GenBank: XX strain: HEC15817 length: 654 nt	GenBank: XX strain: HEC15817 length: 733 nt		GenBank: XX strain: D505 length: 873 nt	GenBank: XX strain: HEC15817 length: 1168 nt
Dictyota sp31			GenBank: XX strain: MAD2178 length: 590 nt					
Dictyota sp32			GenBank: XX strain: GWS018563 length: 660 nt					
Dictyota sp33			GenBank: XX strain: GWS016917 length: 660 nt					
Dictyota sp34			GenBank: XX strain: GWS025859 length: 657 nt					
Dictyota sp5		GenBank: XX strain: HEC15763 length: 605 nt		GenBank: XX strain: HEC15763 length: 653 nt	GenBank: XX strain: HEC15763 length: 737 nt		GenBank: XX strain: HEC15763 length: 853 nt	GenBank: XX strain: HEC15763 length: 1227 nt
Dictyota sp6							GenBank: XX strain: FS958 length: 954 nt	
Dictyota sp7		GenBank: DQ472121 strain: KZN2308 length: 1055 nt	GenBank: XX strain: D186 length: 616 nt	GenBank: XX strain: D186 length: 641 nt	GenBank: XX strain: KZN2308 length: 729 nt		GenBank: XX strain: KZN2308 length: 871 nt	GenBank: DQ472066 strain: KZN2308 length: 1338 nt
Dictyota sp9		GenBank: XX strain: ODC1552 length: 565 nt	GenBank: XX strain: ODC1552 length: 537 nt	GenBank: XX strain: ODC1552 length: 654 nt	GenBank: XX strain: ODC1552 length: 715 nt		GenBank: XX strain: ODC1552 length: 873 nt	GenBank: XX strain: ODC1552 length: 1066 nt

Dictyota spiralis1		GenBank: GQ425161 strain: ODC1225 length: 1180 nt	GenBank: XX strain: ODC1029 length: 632 nt	GenBank: XX strain: ODC1225 length: 654 nt	GenBank: XX strain: ODC1225 length: 744 nt		GenBank: XX strain: FS486 length: 857 nt	GenBank: DQ472074 strain: ODC1029 length: 1344 nt
Dictyota spiralis2		GenBank: XX strain: D290 length: 203 nt	GenBank: XX strain: FS302 length: 633 nt				GenBank: XX strain: ODC2116 length: 962 nt	GenBank: XX strain: D290 length: 939 nt
Dictyota spiralis3		GenBank: XX strain: ODC1056 length: 1029 nt	GenBank: XX strain: FS231 length: 633 nt	GenBank: XX strain: HEC15815 length: 643 nt	GenBank: XX strain: HEC15815 length: 694 nt	GenBank: XX strain: HEC15815 length: 657 nt	GenBank: XX strain: ODC2031 length: 962 nt	GenBank: XX strain: HEC15815 length: 1234 nt
Dictyota spiralis4			GenBank: GU290235 strain: ODC1071 length: 633 nt	GenBank: XX strain: ODC1071 length: 637 nt	GenBank: XX strain: ODC1071 length: 733 nt			
Dictyota stolonifera		GenBank: GQ425160 strain: TZ0488 length: 841 nt	GenBank: GQ425139 strain: TZ0488 length: 598 nt	GenBank: XX strain: TZ0488 length: 637 nt	GenBank: GQ425182 strain: TZ0488 length: 740 nt	GenBank: XX strain: TZ0377 length: 887 nt	GenBank: XX strain: RD88740 length: 969 nt	GenBank: GQ425118 strain: D264 length: 1267 nt
Dilophus fastigiatus		GenBank: DQ472123 strain: D96 length: 1171 nt	GenBank: XX strain: KD15-5-09-01-07 length: 590 nt		GenBank: GQ425170 strain: D96 length: 744 nt	GenBank: XX strain: D96 length: 1440 nt	GenBank: XX strain: LT0443 length: 969 nt	GenBank: DQ472068 strain: D96 length: 1196 nt
Dilophus gunnianus		GenBank: XX strain: D1537 length: 1130 nt	GenBank: HM891296 strain: GWS016245 length: 657 nt		GenBank: XX strain: D744 length: 744 nt		GenBank: XX strain: D1537 length: 955 nt	GenBank: XX strain: D744 length: 1231 nt
Dilophus robustus1		GenBank: XX strain: HV2604 length: 681 nt				GenBank: XX strain: HV2497 length: 1371 nt	GenBank: XX strain: HV2604 length: 969 nt	GenBank: XX strain: HV2604 length: 1205 nt
Dilophus robustus2		GenBank: XX strain: D1702 length: 1129 nt	GenBank: XX strain: D1702 length: 448 nt	GenBank: XX strain: D1702 length: 654 nt	GenBank: XX strain: D1702 length: 269 nt		GenBank: XX strain: D1702 length: 969 nt	GenBank: XX strain: D1702 length: 1215 nt
Dilophus robustus3		GenBank: XX strain: ODC1110 length: 1179 nt	GenBank: XX strain: ODC1108 length: 590 nt			GenBank: XX strain: ODC1100 length: 1465 nt	GenBank: XX strain: ODC1119 length: 882 nt	GenBank: XX strain: ODC1120 length: 1153 nt
Dilophus sp1							GenBank: XX strain: LT0215 length: 685 nt	
Padina arborescens	GenBank: AB090392 strain: XX length: 1810 nt	GenBank: EU579996 strain: Bit.LBC135 length: 314 nt		GenBank: AB358939 strain: Win2 length: 654 nt		GenBank: AY430316 strain: IK65 length: 1519 nt	GenBank: AY430357 strain: Lee.IK65 length: 870 nt	GenBank: AB358904 strain: Win2 length: 1238 nt
Padina boergesenii		GenBank: DQ472093 strain: ODC890 length: 978 nt						GenBank: DQ472037 strain: ODC890 length: 1183 nt
Padina crassa	GenBank: AB095297 strain: XX length: 1801 nt			GenBank: AB358943 strain: Win1 length: 654 nt		GenBank: AY430318 strain: IK70 length: 1519 nt	GenBank: AY430361 strain: Lee.WJ21 length: 870 nt	

Padina japonica	GenBank: AB095298 strain: XX length: 1802 nt			GenBank: AB358942 strain: Win4 length: 654 nt		GenBank: AY430319 strain: IK71 length: 1519 nt	GenBank: AY430360 strain: Lee.IK71 length: 870 nt	GenBank: AB358910 strain: Win4 length: 1238 nt
Padina pavonica		GenBank: EU580000 strain: Bit.LBC139 length: 386 nt		GenBank: EU681454 strain: Sil.FRA0509 length: 654 nt	GenBank: EU681498 strain: Sil.FRA0509 length: 713 nt	GenBank: EU579919 strain: LBC58 length: 1463 nt	GenBank: EU681649 strain: Sil.FRA0509 length: 845 nt	GenBank: EU579961 strain: Bit.LBC100 length: 1194 nt
Padina sanctaecrucis		GenBank: DQ472092 strain: CL030305 length: 783 nt		GenBank: AB489969 strain: Win3 length: 654 nt				GenBank: DQ472036 strain: CL030305 length: 885 nt
Rugulopteryx marginatus		GenBank: DQ472098 strain: GWS0111 length: 1176 nt	GenBank: XX strain: GWS023125 length: 657 nt	GenBank: XX strain: LT0291 length: 647 nt	GenBank: XX strain: HV2153 length: 744 nt		GenBank: XX strain: HV2153 length: 969 nt	
Rugulopteryx okamurae	GenBank: AB090388 strain: XX8 length: 1806 nt	GenBank: GQ425149 strain: D194 length: 1124 nt	GenBank: HQ990525 strain: GWS018267 length: 651 nt	GenBank: XX strain: HV1958 length: 654 nt	GenBank: GQ425185 strain: FS280 length: 744 nt	GenBank: AY422598 strain: IK43 length: 1532 nt	GenBank: XX strain: FS328 length: 846 nt	GenBank: AY422675 strain: WJ7 length: 1407 nt
Rugulopteryx radicans		GenBank: DQ472100 strain: D98 length: 599 nt	GenBank: XX strain: D98 length: 419 nt		GenBank: XX strain: D98 length: 728 nt		GenBank: XX strain: HV2449 length: 969 nt	GenBank: DQ472045 strain: D98 length: 1178 nt
Rugulopteryx suhrii		GenBank: DQ472099 strain: KZNb2315 length: 1174 nt	GenBank: XX strain: KZNb2315 length: 617 nt		GenBank: Dic35 strain: KZNb2315 length: 740 nt		GenBank: EU395617 strain: KZNb2346 length: 766 nt	GenBank: DQ472044 strain: KZNb2315 length: 1304 nt
Scoresbyella profunda		GenBank: XX strain: HV2553 length: 1119 nt	GenBank: GQ425121 strain: DIC44 length: 607 nt	GenBank: GQ425148 strain: DIC44 length: 518 nt			GenBank: XX strain: HV2570 length: 969 nt	GenBank: XX strain: HV2553 length: 1230 nt

S2: GEOGRAPHIC AND THERMAL DATA

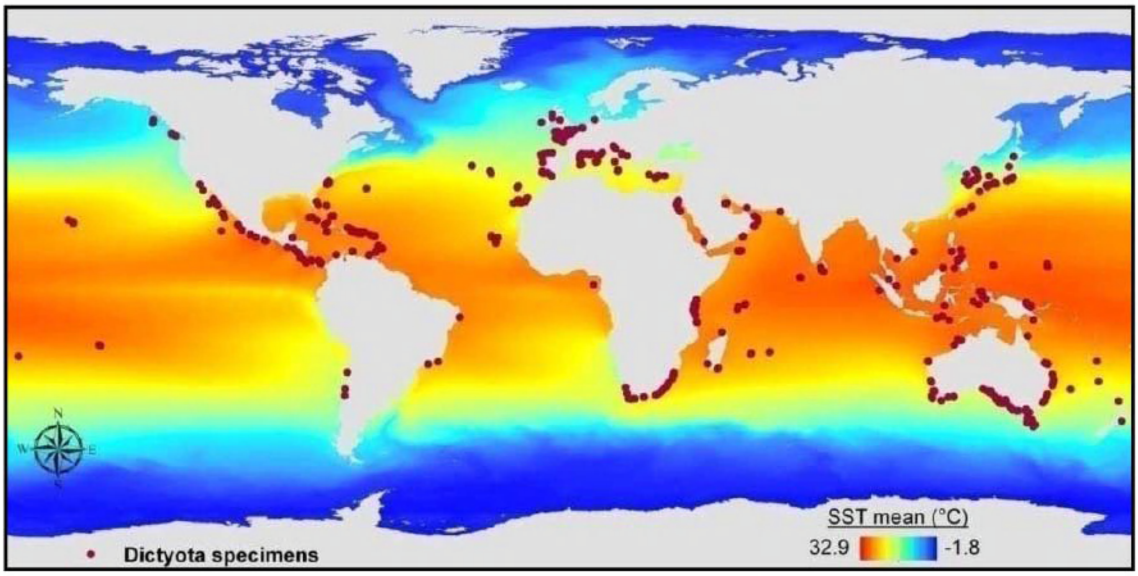

Figure S2.1: Overview *Dictyota* sampling records. The background is represents a mean sea surface temperature layer derived from Bio-ORACLE (Tyberghein *et al.*, 2012).

Table S2.1: Overview *Dictyota* species: amount of samples, amount of unique localities, mean sea surface temperature, standard error of mean sea surface temperature.

Taxa	# samples	# unique localities	mean SST	mean SST Standard Error
Dictyota acutiloba1	35	24	24.55	0.44
Dictyota acutiloba2	6	3	18.37	0.17
Dictyota adnata	24	18	28.48	0.39
Dictyota alternifida	16	13	16.98	0.48
Dictyota alternifida2	2	2	15.62	0.25
Dictyota anastomosans	1	1	22.18	0.00
Dictyota bartayresiana	106	72	27.94	0.13
Dictyota bartayresiana2	12	4	26.31	1.04
Dictyota binghamiae	15	10	11.75	1.00
Dictyota canaliculata1	3	3	29.55	0.42
Dictyota canaliculata2	14	12	28.83	0.37
Dictyota naevosa	17	13	22.06	0.76
Dictyota nigricans	12	12	18.84	0.56
Dictyota paniculata1	9	8	17.77	0.47
Dictyota paniculata2	5	3	15.46	0.21
Dictyota pardalis	2	1	14.80	0.00
Dictyota pfaffii	24	16	22.11	0.40
Dictyota pinnatifida	12	9	26.61	0.71
Dictyota pleiacantha1	13	7	21.42	0.53
Dictyota pleiacantha2	2	2	22.85	0.19
Dictyota polyclada1	11	10	16.55	0.36
Dictyota polyclada2	2	2	17.28	1.26

Dictyota canariensis	25	11	23.47	0.44
Dictyota caribaea	6	6	28.46	0.24
Dictyota ceylanica1	4	3	28.85	0.32
Dictyota ceylanica2	2	1	27.55	0.00
Dictyota ceylanica3	5	3	25.83	0.93
Dictyota ceylanica4	10	8	25.53	1.07
Dictyota ceylanica5	31	24	27.55	0.39
Dictyota ceylanica6	4	3	21.71	0.00
Dictyota ciliolata	147	91	26.97	0.27
Dictyota concrescens	1	1	28.24	0.00
Dictyota coriacea	4	2	17.66	0.10
Dictyota coriacea2	16	13	18.44	0.62
Dictyota crenulata	16	15	26.20	0.95
Dictyota cyanoloma	92	21	18.21	0.48
Dictyota cymatophila	11	7	21.11	0.14
Dictyota dhofarensis	4	4	25.97	0.02
Dictyota dichotoma1	789	107	15.82	0.32
Dictyota dichotoma2	23	15	18.00	0.78
Dictyota dichotoma3	10	5	15.47	0.16
Dictyota diemensis	37	22	16.20	0.26
Dictyota fasciola	38	19	19.30	0.50
Dictyota fasciola2	2	2	19.73	0.68
Dictyota flabellata	21	9	23.12	0.84
Dictyota friabilis1	90	65	27.95	0.21
Dictyota grossedentata	21	15	28.72	0.18
Dictyota hamifera	20	14	27.32	0.54
Dictyota humifusa	69	54	27.49	0.23
Dictyota implexa	75	55	24.03	0.61
Dictyota intermedia	59	31	21.58	0.22
Dictyota jamaicensis	28	25	27.60	0.29
Dictyota koreana	17	14	19.40	0.72
Dictyota kunthii	7	4	15.12	0.56
Dictyota linearis	21	10	19.54	0.58
Dictyota liturata1	16	9	23.11	0.62
Dictyota liturata2	21	14	22.04	0.94
Dictyota liturata3	4	2	25.29	1.61
Dictyota liturata4	3	3	22.70	1.03
Dictyota mangrovestolon	1	1	29.61	0.00
Dictyota mediterranea	27	12	19.94	0.30
Dictyota mertensii1	13	9	27.21	0.54
Dictyota mertensii2	4	3	28.10	0.25
Dictyota polyclada3	5	4	19.75	1.03
Dictyota rigida1	14	9	27.83	0.12
Dictyota rigida2	2	2	22.58	0.41
Dictyota rigida3	4	3	21.78	1.66
Dictyota rigida4	6	6	24.51	0.16
Dictyota rigida5	1	1	24.49	0.00
Dictyota sandvicensis1	4	4	25.62	0.13
Dictyota sandvicensis2	11	6	21.19	0.52
Dictyota sandvicensis3	1	1	24.43	0.00
Dictyota sp1	8	5	19.97	0.45
Dictyota sp10	1	1	29.78	0.00
Dictyota sp11	4	4	28.88	0.39
Dictyota sp12	1	1	30.21	0.00
Dictyota sp15	4	4	25.83	1.00
Dictyota sp16	3	3	30.03	0.42
Dictyota sp17	1	1	30.63	0.00
Dictyota sp18	1	1	28.37	0.00
Dictyota sp19	17	16	28.71	0.19
Dictyota sp20	40	24	28.39	0.31
Dictyota sp21	2	1	27.56	0.00
Dictyota sp22	3	2	24.60	4.09
Dictyota sp23	3	1	20.51	0.00
Dictyota sp24	1	1	24.62	0.00
Dictyota sp25	5	3	19.57	0.60
Dictyota sp26	1	1	23.86	0.00
Dictyota sp29	9	6	23.93	0.25
Dictyota sp3	8	4	20.11	0.97
Dictyota sp31	1	1	24.22	0.00
Dictyota sp32	1	1	20.22	0.00
Dictyota sp33	1	1	17.67	0.00
Dictyota sp34	2	1	28.69	0.00
Dictyota sp5	2	2	19.63	0.70
Dictyota sp6	2	2	25.20	1.16
Dictyota sp7	6	5	20.06	1.11
Dictyota sp9	1	1	27.43	0.00
Dictyota spiralis1	31	21	19.38	0.35
Dictyota spiralis2	8	6	19.74	0.74
Dictyota spiralis3	22	11	19.17	0.81
Dictyota spiralis4	1	1	16.83	0.00
Dictyota stolonifera	37	24	27.95	0.39

Table S2.1: List species' geographic distributions relative to each other.

Clade	X	Y	Speciation
C2	canaliculata1	pfaffii	allopatric
C2	humifusa	canaliculata1, pfaffii	sympatric
C4	flabellata	sp20	parapatric
C4	sp19	sp20, flabellata	sympatric
C4	crenulata	sp19, sp20, flabellata	sympatric
C4	implexa	linearis	sympatric
C4	canariensis	linearis, implexa	sympatric
C4	spiralis2	spiralis4	sympatric
C4	spiralis1	spiralis4, spiralis2	sympatric
C4	spiralis3	spiralis4, spiralis2, spiralis1	sympatric
C4	jamaicensis	pleiacantha1	parapatric
C4	pleiacantha2	pleiacantha1, jamaicensis	parapatric
C4	sandvicensis1	sandvicensis3	allopatric
C4	sandvicensis2	sandvicensis3, sandvicensis1	allopatric
C4	caribaea	pleiacantha1, pleiacantha2, jamaicensis, sandvicensis3, sandvicensis1, sandvicensis2	sympatric
C4	cymatophila	mertensii2	allopatric
C4	concrescens	pleiacantha1, pleiacantha2, jamaicensis, sandvicensis3, sandvicensis1, sandvicensis2, caribaea, cymatophila, mertensii2	allopatric
C4	pinnatifida	rest of clade C4	sympatric
C5	kunthii	binghamiae	allopatric
C5	nigricans	binghamiae, kunthii	allopatric
C6	paniculata1	paniculata2	sympatric
C6	polyclada3	paniculata2, paniculata1	parapatric
C6	polyclada1	polyclada2	sympatric
C6	sp1	dichotoma1	sympatric
C6	sp29	sp25	allopatric
C7	sp22	sp12	allopatric
C7	sp16	adnata	sympatric
C8	bartayresiana	bartayresiana2	parapatric
C8	sp17	sp34	sympatric
C8	canaliculata2	sp26	allopatric
C8	mangrovestolon	sp33	allopatric
C8	sp18	sp33, mangrovestolon	sympatric
C9	koreana	sp21	allopatric
C9	sp3	sp7	parapatric
C9	alternifida	alternifida2	sympatric
C9	cyanoloma	alternifida, alternifida2, sp3, sp7, sp21, koreana	sympatric
C9	diemensis	dichotoma3	sympatric
C9	liturata2	liturata3	allopatric
C9	liturata1	liturata3, liturata2	allopatric
C9	liturata4	liturata1, liturata2, liturata3	allopatric
C9	stolonifera	liturata1, liturata2, liturata3, liturata4	parapatric
C9	sp23	mertensii1	allopatric
C9	intermedia	alternifida, alternifida2, sp3, sp7, sp21, koreana, liturata1, liturata2, liturata3, liturata4, mertensii1, sp23, stolonifera, diemensis, dichotoma3, cyanoloma	parapatric
C9	dichotoma2	pardalis	sympatric
C9	rigida1	rigida2	allopatric
C9	rigida3	rigida1,2	allopatric
C9	rigida4	rigida5	allopatric
C9	coriacea	coriacea2	allopatric
C9	sp32	coriacea, coriacea2	sympatric
C9	ciliolata	sp32, coriacea, coriacea2	sympatric
C9	grossedentata	rigida1, rigida2, rigida3, rigida4, rigida5, ciliolata, sp32, coriacea, coriacea2	sympatric
C9	dhofarensis	sp31	allopatric
C9	naevosa	sp31, dhofarensis	allopatric
C9	acutiloba1	acutiloba2	parapatric

C9	sp10	sp24	parapatric
C9	sp11	sp9	sympatric
C9	hamifera	sp9, sp10, sp11, sp24	sympatric
C9	anastomosans	ceylanica4	parapatric
C9	friabilis1	ceylanica4, hamifera, anastomosans, sp9, sp10, sp11, sp24	sympatric
C9	fasciola	mediterranea	sympatric
C9	fasciola2	mediterranea, fasciola	sympatric
C9	sp5	mediterranea, fasciola, fasciola2	sympatric
C9	sp6	mediterranea, fasciola, fasciola2, sp5	parapatric
C9	ceylanica3	ceylanica6	allopatric
C9	ceylanica1	ceylanica3, ceylanica6	sympatric
C9	ceylanica2	ceylanica1, ceylanica3, ceylanica6	allopatric

APPENDIX REFERENCES

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