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“Fatores Determinantes da Posição Trófica em Consumidores Aquáticos, Fatores
Macroecológicos e Evolutivos”

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General abstract:

The maintenance of a positive energetic budget is critical for a consumer's survival and reproductive success, strategies that maximize the energy acquirement and minimize expenditure fundamentally shape biological interactions, organisms that present the most efficient strategies for the assimilation of nutrients and energy can allocate more resources on reproduction and can propagate their characteristics. Species may develop different adaptations in order to maximize the relationship between energy assimilation/expenditure depending on morphological, physiological or environmental constraints. On this thesis I focus on the body size – trophic position relationship in marine consumers given that the relationship between these two traits can be very important on species energy budget influencing their means to acquire resources and on their metabolic rates and is also influenced by climatic and environmental conditions. On the first chapter I used a dataset published by Jennings & Cogan (2015) to investigate the body size – trophic position relationship in fish and squid species exploring intra and interspecific variations in order to understand the mechanisms that lead to the pattern of a positive relationship between trophic position amplitude and body size in ectothermic aquatic consumers, I found out an overall positive relationship between body size and trophic position and specific responses on the relationships between body size and trophic position amplitude within species. On the remainder of the thesis I focus on the effect of climatic and environmental variables on the body size trophic position, comparing temperate, tropical, marine and freshwater bony fish species, ectothermic species have their metabolic rates regulated by the environmental temperature, meaning that ectothermic species inhabiting warm regions have different, usually higher metabolic rates than species inhabiting colder regions, also environment type may influence on the availability of resource, for example freshwater environments are usually smaller and very influenced by allochthonous input of organic matter, leading to differences on the

characteristics related to feeding strategies and energetic expenditure, for example trophic position and body size, as well as on the relationship between these characteristics. The last two chapters focus on the effects of climate and environment on the evolutionary relationships between body size and trophic position in bony fish. In the second chapter I investigated the evolutionary rates and rates of correlated evolution of body size and trophic position using a global dataset fitted to the latest published evolutionary tree on bony fish to date, I found out that the body size – trophic position relationship is more evident on the tropical climate and that this pattern is likely caused by different evolutionary correlation between body size and trophic position on different climates. In the last chapter I am worked with species diversification models taking into account climatic region as well as species trophic guilds to identify which factors lead to more rapid or slow species diversification, finding out that the prevalence of herbivory in the tropics may be due to higher diversification of low trophic position guilds in these regions.

Resumo geral:

A manutenção de um saldo energético positivo é crítica para a sobrevivência e sucesso reprodutivo de um consumidor, estratégias que maximizem a aquisição de energia e minimizem seu gasto modelam fundamentalmente as interações biológicas, organismos que apresentam as estratégias mais eficientes para a assimilação de nutrientes e energia podem alocar mais recursos na reprodução e podem propagar suas características. Espécies podem desenvolver diferentes adaptações para maximizar a razão entre energia assimilada e gasta dependendo de restrições morfológicas, fisiológicas ou ambientais. O foco desta tese é a relação entre o tamanho corporal e a posição trófica em consumidores marinhos partido do pressuposto de que a relação entre tais características pode ser muito importante para o saldo energético das espécies influenciando em seus meios de aquisição de recursos e em suas taxas metabólicas, sendo também influenciado por condições climáticas e ambientais. No primeiro capítulo foi utilizado um banco de dados publicado por Jennings & Cogan (2015) investigando a relação entre o tamanho corporal e a posição trófica em espécies de peixes e lulas explorando variações intra e interespecíficas com vistas a entender os mecanismos que levam a uma relação positiva entre o tamanho corporal e uma maior amplitude de posições tróficas ocupadas por consumidores ectotérmicos aquáticos. Foi encontrada uma relação geral positiva entre tamanho corporal e posição trófica e respostas específicas para a relação entre tamanho corporal e amplitude de posições tróficas dentro das espécies. No restante da tese foco no efeito de variáveis climáticas e ambientais sobre o tamanho corporal e a posição trófica de espécies de peixes ósseos, comparando espécies de climas temperados e tropicais assim como ambientes marinhos e de água doce, espécies ectotérmicas tem suas taxas metabólicas reguladas pela temperatura ambiente, sendo que espécies ectotérmicas habitando regiões quentes tem taxas metabólicas diferentes, geralmente mais altas, do que espécies habitando regiões mais frias, além disso o tipo de ambiente pode influenciar na

disponibilidade de recursos, por exemplo, ambientes de água doce são geralmente menores e altamente influenciados pela entrada alóctone de matéria orgânica, levando a diferenças nas características relacionadas a estratégias alimentares e no gasto energético, por exemplo na posição trófica e no tamanho corporal, assim como na relação entre estas características. No segundo capítulo investiguei as taxas evolutivas e taxas de evolução correlacionada entre tamanho corporal e posição trófica utilizando um banco de dados global relacionado à árvore filogenética para peixes ósseos mais recente até a data, encontrei que a relação positiva entre tamanho corporal e posição trófica é mais evidente no clima tropical e que este padrão é possivelmente causado por diferenças na correlação evolutiva entre tamanho corporal e posição trófica entre diferentes climas. No último capítulo trabalhei com modelos de diversificação de espécies levando em conta a região climática de ocorrência das espécies e a guilda trófica à qual as espécies pertencem para identificar quais fatores levam à mais rápida ou lenta diversificação de espécies, encontrando que a prevalência da herbivoria nos trópicos pode ser devida à mais alta diversificação de guildas que apresentam posições tróficas baixas nestas regiões.

General Introduction:

Body size and trophic position are among the most important features of consumers and have been acknowledged to influence all levels of ecological organization, from individual ecology and behavior, aspects of species life histories, species interactions to ecosystem function (Layman et al. 2005, Arim et al. 2007, Romanuk et al. 2011). In aquatic food webs the relationship between body size and trophic position is usually positive (Cohen et al. 1993, France et al. 1998, Jennings et al. 2001, Woodward and Hildrew 2002, Jennings and Mackinson 2003), both within and among species (Dalponti et al. 2018) where older bigger individuals within a species occupying higher trophic positions than young smaller ones and with larger species usually representing predators and small species representing herbivores and omnivores. The mechanisms leading to the positive body size – trophic position relationship is likely to be related to morphological constraints on small individuals that can't handle big prey and are, therefore, limited to prey on smaller consumers, filter feed on phyto or zooplankton, resort to detritivory or to feed directly on producers such as algae and aquatic plants, on the other hand, energetic optimization might drive big consumers to prey on the biggest prey available in order to maximize energy acquirement per predation event (Cohen et al. 1993, Arim et al. 2007, Costa 2009, Romanuk et al. 2011).

Within species, for example, ontogenetic niche shifts are responsible for changes in individual's diets and habitat use influencing species interactions (Mittelbach 1981, Werner and Gilliam 1984) and can be caused by morphophysiological changes as well as cognitive enhancement through learning, older individuals, therefore, have new opportunities and a different foraging optimum as they are more capable of chasing and handling bigger prey and

they also have more knowledge of their environment and their prey's behavior which allows them to make strategies to optimize foraging events (Charnov 1976, Mittelbach et al. 1981, Werner and Gilliam 1984, Hughes et al. 1992). Besides the opportunities raised by a larger body, energy requirements also change as aquatic consumers grow larger because metabolic rate scales positively with body size (Bennett 1987, Clarke and Johnston 2002, Killen et al. 2010) this leads to the need for bigger consumers to maximize their energy intake, therefore it is expected that bigger fish adopt foraging strategies that involve capturing the largest prey possible in a single strike, avoiding the necessity of several energy-costly predation events, the continuity of this pattern leads to size-structured food chains where predators prey on the immediate smaller and may fall prey to the immediate bigger consumers present on their environment.

Environmental and climatic conditions may also influence the optimal foraging strategies and body size – trophic position relationships of aquatic ectotherms (Díaz et al 2013, Stuart-Smith et al 2013, Bakker et al. 2016, Dantas et al. 2019), different environments can offer variable food resources that can pose opportunities for foraging or restrict the options species have in a determined region (Tanentzap et al. 2014), for example: shallow lakes and other inland freshwater environments receive a great proportion of organic matter from runoff (Jepsen and Winemiller 2002, Ou et al. 2017) that can serve as food resource for herbivorous and detritivorous species, therefore we may expect that these species represent a larger proportion of the fauna than in other environments (Lowe and MacConnell 1987, Jepsen and Winemiller 2002,). Climate for instance, has effects on metabolic rates (Gillooly et al. 2001) and also on the digestibility of plants and algae, that are usually more edible on warm regions (Cronin et al 1997, Violle et al. 2007, Bakker et al. 2016).

Variation in biodiversity, including species distributions and the distribution of traits throughout the tree of life is ultimately driven by the result of the balance between speciation and extinction during evolutionary time, which are, for instance, generated by differences in species fitness in their environment (Darwin 1869, Rosenzweig 1995, Coyne and Orr 2006, Rangel et al 2018). In this case-study body size and trophic position can be viewed as traits which optimal values are subjected to a variety of factors, for example ontogeny, environmental availability of resources, climate and even may have an influence of one trait on the other, as, for example, body size having an effect on the optimal value of trophic position. Therefore, elucidating the drivers of diversification and extinction of body size and trophic position is of pivotal importance to better understand evolutionary dynamics drawing the patterns I observe (Benton 2009, Barnosky et al 2011, Condamine et al 2013, Burin et al 2015). Much of the theory regarding evolutionary dynamics focuses on abiotic factors as a cause of disruption on the balance of biological communities (Condamine et al 2013) while some focus on the role of biotic interactions and species traits, e.g. trait-dependent diversification models (Burin et al 2015). Promoting the interaction between both kind of approaches is still an open question.

The objective of this thesis is to investigate the trophic ecology of fishes focusing on the effects of body size, climate and environment on the trophic position of fishes, to address this issue I investigated the trophic and evolutionary dynamics in three chapters guided by three main questions that are looked upon as following:

Chapter one:

Does a positive body size – trophic position holds both within and among species?

In this chapter I focus on the body size – trophic position among and within species in a temperate region using a dataset with individual-recorded trophic positions for fish species (and some squids to add some extra layer of variety) and standard phylogenetic-corrected statistics.

Chapter two:

Is the positive body size – trophic position relationship related to an evolutionary trend and is it influenced by climate and environment?

This time with a global dataset comprising species body size, trophic position, climate occurrence and environment usage I used a Bayesian Markov Chain Monte Carlo approach to investigate the evolutionary relationship between body size and trophic position under varying climatic and environmental conditions.

Chapter Three:

How are diversification dynamics of trophic guilds on temperate and tropical regions?

I investigated the evolutionary dynamics of speciation, extinction and diversification that drive the differences in the proportions of trophic guilds between the tropical and temperate climate through State-Dependent Speciation and Extinction models.

Chapter 1

Hunting high or low: body size drives trophic position among and within marine predators

Abstract:

The positive relationship between trophic position and body size is a remarkable ecological pattern. Based on mobility and gape size, a positive relationship between body size and trophic position amplitude is expected. Using a dataset of the diet of marine consumers, I elucidated mechanisms driving the relationship between consumers body mass (a proxy for body size) and trophic position parameters within and among populations. I found that across a body size gradient, maximum trophic position increased, while minimum trophic position remained invariant, with a positive relationship between species body size and trophic position amplitude. However, using single individuals as data points I found a positive correlation between trophic position and body mass, and such correlation becomes stronger for larger species, indicating that as mean species body size increased, smaller individuals tended to forage on lower levels while larger individuals mainly foraged on higher levels. Therefore, the wider variation in trophic positions I observed for larger species is possibly related to an ontogenetic diet shift in size-structured populations. These results corroborate with the general idea that larger consumers do not show a positive relationship between body size and diet niche breadth, and supports the notion that ontogenetic niche differences can act as a driver of trophic position amplitude among marine predators.

Keywords: trophic chain, ontogenetic diet shifts, niche breadth, consumer-resource interactions, food web topology

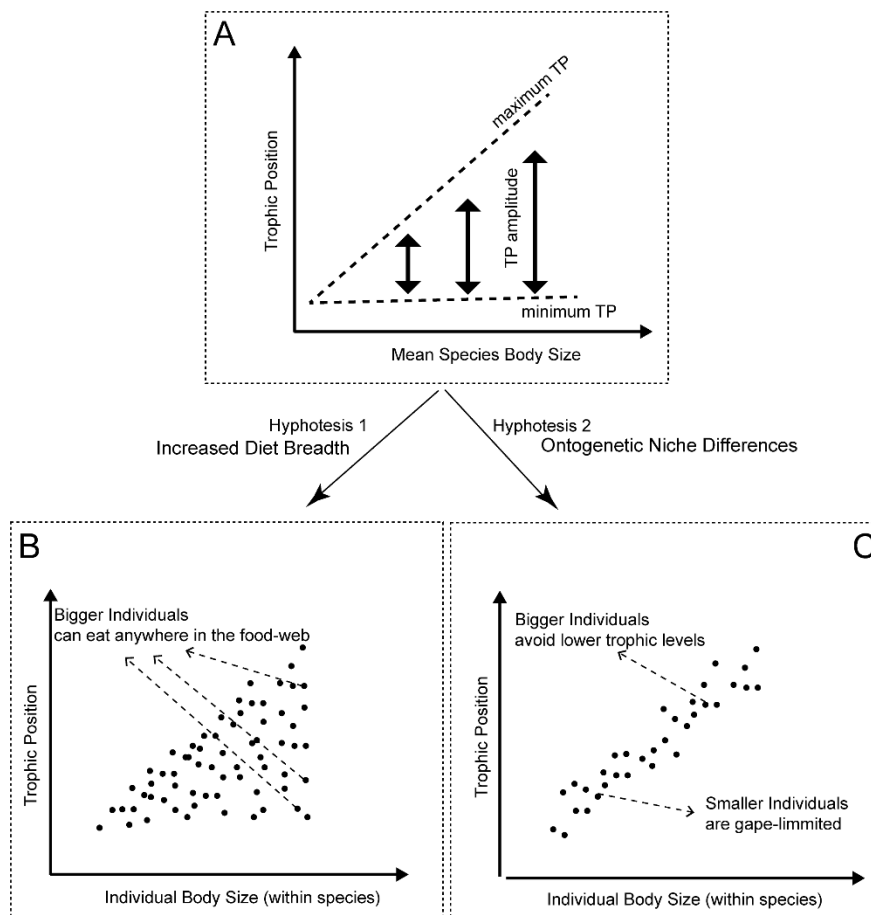
Introduction:

Body size is a fundamental trait that affects ecological dynamics from individuals to ecosystems (Cohen et al. 1993, Arim et al. 2007, Jennings & Cogan 2015). This trait also shapes energetic demands (Elliott & Hurley 2000, West & Brown 2005) and plays an important role in structuring ecological interactions within and among species (Peters & Wassenberg 1983), which influences food web dynamics and ecosystem functioning (Emmerson & Raffaelli 2004, Basset & Angelis 2007, Séguin et al. 2014). In general, body size constrains the size of prey that predators can consume (Cohen et al. 1993, Woodward et al. 2005, Arim et al. 2007), as well as the cognitive ability an organism has to forage throughout various food webs (Edmunds et al. 2016). The constraint of gape limitation and the opportunities of enhanced foraging capabilities due to body size cause a body size hierarchy in many aquatic food webs (Williams & Martinez 2000, Petchey et al. 2008), characterized by a positive relationship between a predator's trophic position (hereafter TP) and body size in aquatic food webs (Hairston & Hairston 1993, Jennings et al. 2001, Layman et al. 2005, Arim et al. 2007, Romanuk et al. 2011). Therefore, I predicted that a positive relationship between predator body size and maximum TP exists at the species level, whereas this relationship with minimum TP should remain constant or increase slightly, with a TP amplitude that is positively correlated to species' body mass (Fig. 1A).

Although most studies use mean body size as a predictor for species TP (Schoener 1971, Williams & Martinez 2000, Ou et al. 2017), ecologists have only recently considered the implications that interactions among species with size-distributed populations have on TP patterns (Ramos-Jiliberto et al. 2011, Rudolf & Lafferty 2011). Previous studies have shown that individuals from the same species have different prey preferences (e.g., ontogenetic diet shifts), with minimum and maximum prey size increasing according to predator size (Thompson 1975, Cohen et al. 1993, Scharf et al. 2000, Costa 2009). These studies highlighted that large predators

might avoid smaller prey because the energetic costs may exceed energetic gain, constraining the shape of the relationship between body size and diet niche breadth (Costa 2009). Therefore, two distinct mechanisms may lead to the same proposed pattern of TP-body size relationship (Fig. 1A): 1) The lack of gape size limitation for large predators, allowing them to feed anywhere in the food web (Fig. 1B) or 2) ontogenetic diet shifts, leading to increased dietary niche breadth, but only at the population level (Fig. 1C). In this study, I explored the relationships between consumer body size and minimum, mean, maximum, and standard deviation of TP across and within species of marine fishes and squids. I tested the hypothesis that maximum TP increases, while minimum TP remains constant along a gradient of mean species body size, which leads to an increase in trophic position amplitude within each population. I also investigated if such relationship emerges because larger individuals forage throughout the whole food web (i.e., large dietary niche breadth) or if it is due to restrictions related to individual size distribution within populations (i.e., ontogenetic niche specialization).

Figure 1: Hypotheses that larger consumer species present wider trophic niche breadth (A). Possible mechanisms by which trophic niche breadth is positively correlated with mean species size: gape size limits small individuals to forage only on lower trophic levels, while large individuals forage on both higher and lower trophic levels (B), both minimum and maximum TP increase with similar slopes, and greater diet niche breadth is only observed at the population level (C).



Methods:

Sampling: The original dataset contains TP measurements and body sizes for 5535 individuals of 62 fish and squid species (Jennings & Cogan 2015). Trophic positions of individual organisms were estimated using the variation in stable nitrogen isotopes ($\delta N 15$) concentrations from consumers' tissues related to increased trophic positions and environmental variables. For marine environments, which vary in depth, temperature, salinity, and the main source of nitrogen in the food web (e.g pelagic vs benthic environments) consumer TP calculated by $\delta N 15$ must be evaluated in relation to a baseline $\delta N 15$, since such variables affect $\delta N 15$ at the base of the food web and how it transfers through food chains (Layman et al. 2012). Trophic fractionation, or the increase in $\delta N 15$ between consumer and resource ($\Delta 15N$), has been described by two models: one model that considers a fixed increase of 3.4‰ per TP and a scaling model that accounts for the decrease of $\Delta 15N$ for higher TP (Hussey et al. 2014). For this dataset the relationship between $\delta N 15$ and TP is based in the diet of a basal consumer - the suspension-feeding queen scallop (*Aequipecten opercularis*), accounting for $\delta N 15$ variation and uncertainty related to environmental variables. A three-stage TP calculation was used: First, a statistical relationship between the $\delta N 15$ of queen scallops, temperature, and salinity was established. The highest predictive power was achieved with models considering annual mean bottom temperature, annual mean bottom salinity, and minimum salinity with an interaction between bottom temperature and salinity. Second, the statistical relationship between the $\delta N 15$ of queen scallops, temperature, and salinity was established was used, in conjunction with modeled temperature and modeled salinity data and TP estimates for queen scallops. Trophic position for queen scallops were calculated from the main source of nitrogen in the water column where the scallops were

collected to predict baseline δN_{15} (δN_{15} baseline) and create a model of mean TP fluctuation in response to environmental variables. Therefore TP_{baseline}'s were set as 2.4 in depths < 40m (where phytoplankton is the main source of food), 3 in depths > 100m, where phytoplankton is absent and was considered to increase linearly with depth between 40 and 100-m depth. Third, δN_{15} measurements of sampled fish and squids were used to predict individual TP using the queen scallop model as a basis for the relationship between the increase in δN_{15} and TP. The increments in δN_{15} were used to build a fixed and a scaled trophic fractionation models. Information about confidence intervals of 5, 25, 50, 75 and 95% for estimated TP for all individuals are available in Jennings & van der Molen (2015). I used the median value to estimate TP of every individual. Trophic position estimations from isotopic $\delta^{15}N$ are integrative measurements of an organisms' diet from the short to mid-term before sampling (Post 2002). Values of $\delta^{15}N$ in organisms' body may vary from months to years, depending on the speed of growth and body size of the organism (Peters 1983, Hesslein et al. 1993, Post 2002). In general, small short-living organisms present faster turnover rates than large long-living organisms. Therefore, $\delta^{15}N$ can be considered a good proxy of proportional importance of food items consumed by an organism along its lifespan (Post 2002, Perkins et al. 2014). Body mass was used as a measurement of body size. To guarantee a good representation of size distributions and TP variation within species, especially in the analysis using individuals as data points, I only used species with more than 20 individuals in my analyses. This procedure reduced the final data set to 5378 individuals belonging to 48 species, representing a reduction of 20% of the species pool, of particularly under sampled species.

Statistical analyses: To account for species relatedness on TP, I used standardized phylogenetic independent contrasts (PIC) on consumer body size and minimum, mean,

maximum, and standard deviations of TP (as a proxy for trophic niche amplitude). Here, I used population standard deviation of TP as a proxy for trophic niche amplitude, instead of differences between maximum-minimum TP in order to avoid giving too much weight on outliers. Phylogenetic hypotheses address the influence that species relatedness has on their responses to the variables, reducing biases caused by species relatedness and improving statistical power in trait analysis, (Felsenstein 1985, Garland et al. 1992). PIC was calculated using the PIC function in the R package ape (Paradis et al. 2004) for independent phylogenetic contrasts. I built a composite phylogenetic hypothesis for the 48 species used in the analyses (Appendix A) based on different phylogenies and the tree of life project (available at <http://tolweb.org/tree/>). Because branch length was not available, all branches were set to a value of one, a method that reduces Type I error rates (Purvis et al. 1994). This proxy method provides a simple but reasonable estimate of evolutionary relationships among species of diverse assemblages and is widely used in trophic chain studies (Costa 2009, Ou et al. 2017). I present results of slopes and r^2 of both non-phylogenetic and phylogenetic analysis. Some authors suggest this approach (Price 1997, Blackburn and Gaston 1998) because, despite the apparent strengths of the arguments for an explicit consideration of phylogeny in comparative analyses, their use has been the subject of considerable debate in the ecological literature on both conceptual and practical grounds (Ricklefs and Starck 1996), especially because controlling for phylogenetic relatedness can affect the sign of predictor estimates (Elgar and Harvey 1987; Blackburn 1991; Harvey et al. 1991; Nee et al. 1991; Kelly and Purvis 1993; Kelly and Beerling 1995). Significance levels for non-phylogenetic analysis are omitted because they are biased (Costa 2009).

Previous to analysis I log₁₀-transformed all variables to meet linearity assumptions. To assess the overall trend between body mass and TP at the individual level I performed a linear

regression using each individual's TP as the dependent variable and body mass as the predictor variable. To investigate the relationships between body size and TP parameters at the species level I regressed mean, minimum, maximum, and amplitude of species TP against mean species body mass.

To uncover the relationship between body size and TP for different sized individuals within the same species I carried out a Pearson correlation analysis between individual body mass and TP for each species (Appendix B). To evaluate the consistency of the body size (TP relationship across species with different sizes), I regressed the Pearson correlation coefficients against species mean body mass. All analyses were performed in the R software version 3.2.1 (R development core team 2016).

Results:

I observed a positive relationship between body size and TP using individuals as data points regardless of species (Fig. 2A; adjusted $R^2 = 0.14$; slope = 0.028; $P < 0.005$). Within species, I observed a positive relationship between individual body mass and trophic position (Appendix B). The PIC values of Pearson correlations between TP and body mass increased significantly as mean species body mass increased (Fig 2B) (adjusted $R^2 = 0.19$; slope = 0.107; $P = 0.001$). Across species, I observed significant positive relationships for mean, maximum, and amplitude of TP with species' mean body mass (Fig. 3 A, C and D). However, I did not observe a significant relationship between species' minimum TP and body mass (Fig. 3B). I observed that, when controlling for the phylogeny, the signs of slopes are preserved despite differences in their magnitudes. Highlighting that controlling for phylogeny does not affect the overall trend. The slopes and r^2 of linear models using both the raw data and PIC values and P values of linear models using PIC values are presented in Table 1.

Figure 2 Individual-level and species-level analyses: linear regression between log-transformed body mass and log-transformed trophic position (TP), for all individuals in the data set (A) and linear regressions between Phylogenetic Independent Contrasts (PIC) of Pearson correlations between trophic position/body mass and species mean body mass (B).

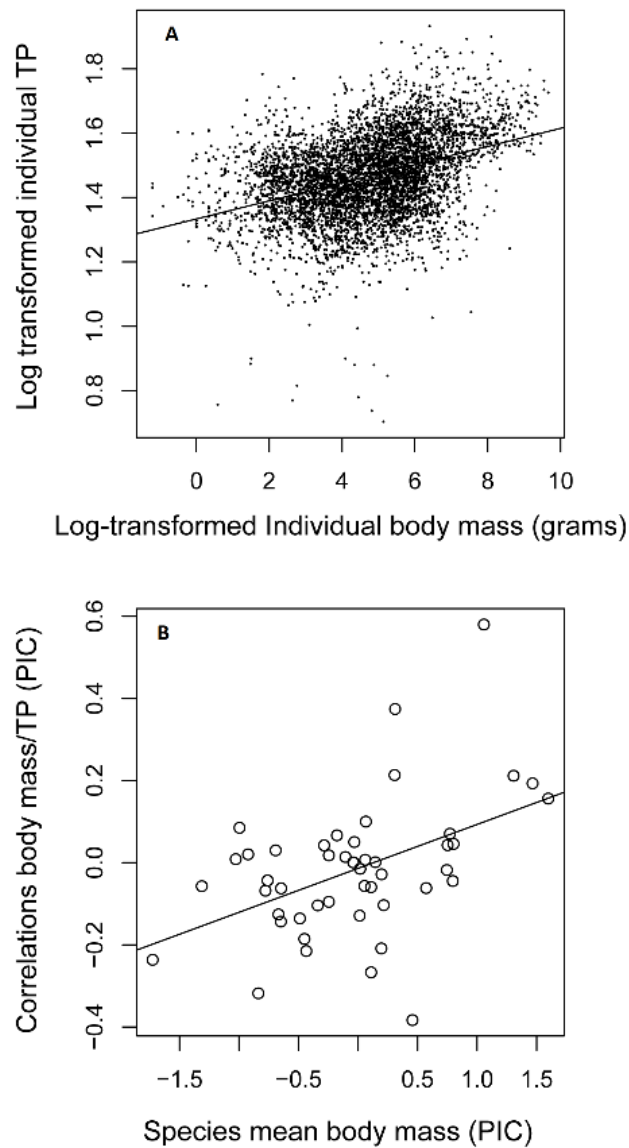


Figure 3 Species-level analyses: linear regressions between Phylogenetic Independent Contrasts (PIC) of species' mean body mass and Phylogenetic Independent Contrasts of TP parameters: species' maximum TP (A), species' minimum TP (B), species' mean TP (C) and amplitude of TP (measured by species' TP one standard deviation).

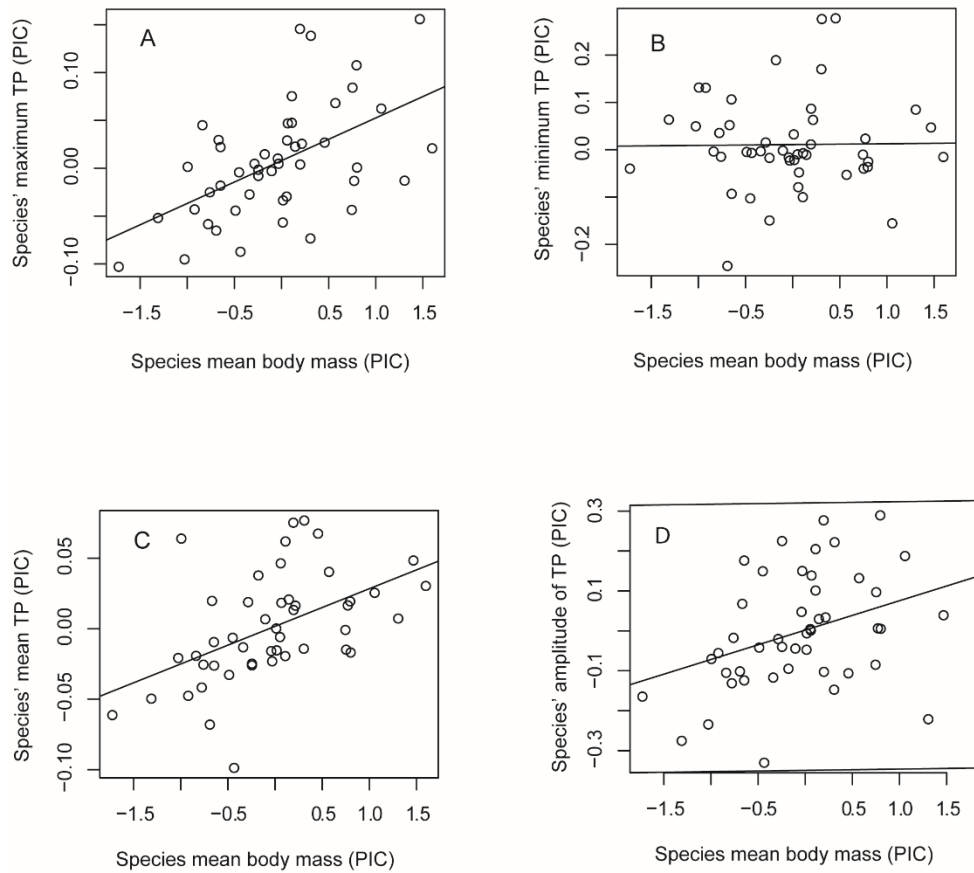


TABLE 1: Results of linear models of species-level analysis: I analyzed the influence of species mean body mass on TP amplitude (one standard deviation), mean, maximum, minimum and of correlation among TP and body mass using both the raw table of data and Phylogenetic Independent Contrasts (PIC).

Species-level analysis					
	Raw Data		PIC		
	Slope	r ²	Slope	r ²	P
Amplitude of TP	3.4x10 ⁻²	0.15	0.073	0.11	0.01
Mean TP	2.1x10 ⁻²	0.15	0.026	0.23	0.0003
Maximum TP	0.037	0.25	0.044	0.27	<0.001
Minimum TP	-1.0x10 ⁻²	0.0057	0.001	0.02	0.932
Correlation mass/TP	9.0x10 ⁻²	0.23	0.107	0.19	0.001

Discussion:

The results showed that smaller individuals of both small and large species presented low TP, therefore, they primarily forage lower in the food web, highlighting that gape limitation may play a strong role on maximum TP. However, large individuals occupied higher TP, suggesting that they primarily forage on high TP organisms. Additionally, body size was positively correlated with mean and variance of TP at the species level and had no relation with minimum species TP, leading to an increased amplitude of TP within species as mean species body size increased. Overall, larger individuals rarely occupied low TP and such pattern becomes more evident in species that attain bigger maximum body size, as the correlation between individual's TP and body size increase with the increase in mean species body mass. Thus, increased amplitude of TP was found to be related to species body size but not to individual body size. Therefore, the amplitude of TP within species was consistent with ontogenetic niche shifts in size-structured populations. Species known to have piscivorous habits as adults showed the most pronounced correlations between body size and TP, regardless of preferred habitat and hunting behaviour, with bottom-dwelling (*Amblyraja radiata*) as well as pelagic species e.g Cod (*Gadus morhua*). Species that showed weak negative correlations between body size and TP were small bodied (min = 22g, max = 90g, mean = 48g, sd = 34g), most often zooplanktivorous or invertebrate-feeding species. For this species, gape limitation may not play a role, as organisms forage throughout their lives on small preys that can be swallowed by adults as well as by younglings.

Also, flatfishes (Pleuronectiformes) and the lesser weever (*Echiichthys vipera*), were found to have weak positive correlations between body size and TP, a pattern generated due to large individuals presenting either low or high TP. This result may be related with the life history of these fish, which although may forage on large prey when adults, therefore being able to reach high TP, have benthic behaviours, defending foraging grounds where they usually forage on the most abundant food resources in their life areas, which consists in a strategy that maximizes food intake regardless of the quality of the resource by diminishing the effect of competition on the abundance of food resources as well as optimizes foraging time by limiting the search area to a resource-rich plot (Pucket and Dill 1985, Canterle et al. 2020). Studies on these species feeding ecology show that adults have piscivorous habits but also include in their diets throughout their lifespan a great proportion of macrobenthic invertebrate prey, mainly Polychaeta and thin-shelled Mollusca, if they are fairly available in their environment, therefore lowering the TP for some adult individuals (Amara et al. 2001, Andersen et al. 2005, Guedes & Araujo 2007).

Overall, the positive relationship between body size and TP is a general pattern observed in several food webs across different systems (Elton 1927, Scharf et al. 2000, Romanuk et al. 2011), although energetic and maneuverability constraints may cause a hump-shaped pattern where trophic positions increase with size until a threshold when very large animals (e.g., baleen whales) start to feed on lower trophic levels (Webb et al. 1996, Arim et al. 2007). However, if the organisms comprising the TP-size relationship are mostly omnivorous and carnivores an increasing linear relationship is expected (Arim et al. 2007, Romanuk et al. 2011). Body masses of individuals used in this study ranged from 2 to 15750 grams, and all samples belong to marine environments. Therefore, these observations may only concern the ascending part of the body size-TP relationship of marine food webs (Romanuk et al. 2011). In addition, ecosystem size of

marine environments may play an important role in structuring longer food webs where larger individuals may find enough resources to meet their energetic demands also in upper trophic levels, for species in this environment have access to larger foraging areas where they can move with ease to less explored areas once food resource levels start to decrease locally (Post et al. 2000).

In size-structured populations, as most fish assemblages in temperate regions, the compartmentalization of individuals in ontogenetic niches is a well-documented pattern (Werner & Gilliam 1984). My results indirectly corroborate the notion that a positive relationship between consumer body size and diet niche breadth does not exist at the individual level and the broader dietary niche breadth observed for larger species results from ontogenetic niche shifts (Olson 1996, Costa 2009), a well-documented pattern size-structured populations, as most fish assemblages in temperate regions are, where the compartmentalization of individuals within a species in ontogenetic niches is common (Werner & Gilliam 1984). Overall, the absence of low $\delta^{15}\text{N}$ signature as body size increased suggests that marine consumers may avoid preying upon small organisms, and highlights the generality of this macroecological pattern for both marine and terrestrial ecosystems (Costa 2009). The consistent positive relationship between body mass and TP across species and among all individuals reinforces a constraint on foraging throughout the food web for animals comprised of the size range and clades studied. It is important to notice however that among vertebrates, when other niche axes are examined, such as microhabitat and home range, a positive relationship between body size and niche breadth can be observed (Pyron 1999).

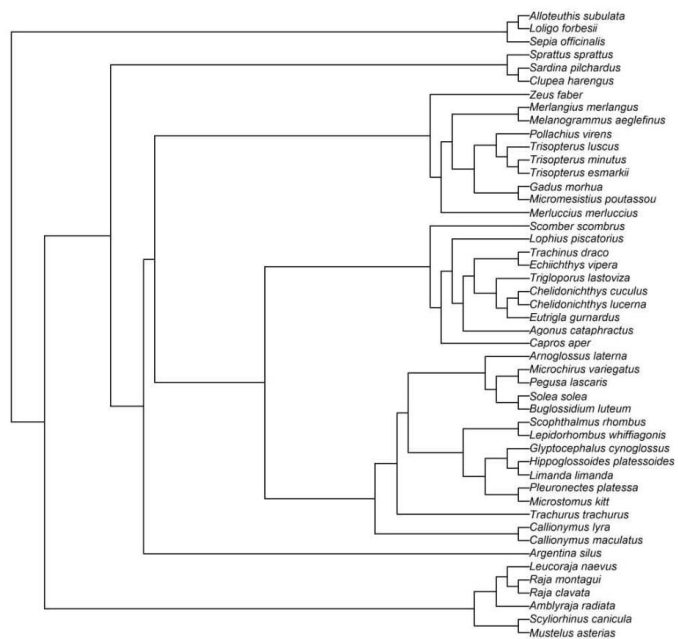
The restrictions for individuals in a certain size class to explore different trophic levels may arise from constraints that hinder smaller individuals from feeding higher in the food web,

like gape limitation, a bottleneck for small individuals to select food resources, as most consumers are limited by what they can swallow, except for a few specialized taxa that take chunks of large prey (e.g., Serrasalmiinae family in freshwater environments and Squatiniformes in saltwater environments) (Werner & Gilliam 1984, Romanuk et al. 2011). For large individuals the constraints that limit feeding throughout the food web could be related to optimal foraging behaviour, considering the time spent in searching and handling prey, with the net calories gained in single feeding events of larger prey much greater than compared to capturing several smaller preys (Harper & Blake 1988, Akin & Winemiller 2008, Costa 2009). Among the many factors that inhibit large predators to feed on small prey, reduction in maneuverability in large bodied animals and difficult recognition of very small prey may be an important aspect, making it hard for large aquatic consumers to find and pursuit small prey, deeming handling time of too long and single predation events of these prey not profitable, very specialized species can overcome this issue by feeding on large clusters of prey indistinctively as if they were a single large individual, as baleen whales and whale sharks that swallow schools of krill or fish in only a few strikes and not in single predation events (Breck and Gitter 1983, Persson 1987, Heglund & Taylor 1988, Webb et al. 1996, Dudley 2002). In addition, the patchy distribution of large prey (Kerr 1974) may be perceived differently by predators that diverge in size as larger individuals are less affected by water viscosity, are able to accomplish for faster and more sustained movements in the water, have enhanced visual acuity and have more body reserves that provide endurance to starvation (Webb 1978, Ware 1978, Mittelbach 1981, Hubbs and Blaxter 1986, Müller et al 2000, Cohen & Jonsson 2003). For larger individuals, therefore, scattered rates of encounter with large prey are compensated by their different perception of the habitat and use of wider areas (Mittelbach 1981, Scharf et al. 2000, Truemp & Lauer 2005). At last, as the basal

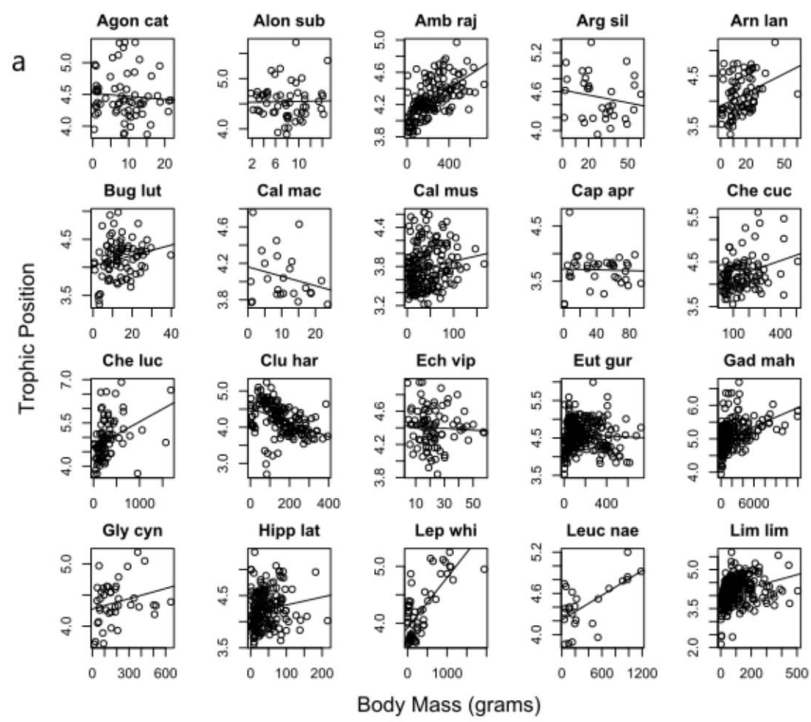
metabolic rate of animals scales with body mass, bigger animals have higher requirements for food resources, hence must select resources which satisfy the minimum energy requirements for sustaining their activities (Schoener 1971, Crowder & Cooper 1982, Robinson & Peters 1983, Clarke & Johnston 1999, Gillooly et al 2001, De Roos et al 2003, Krebs & Davies 2009).

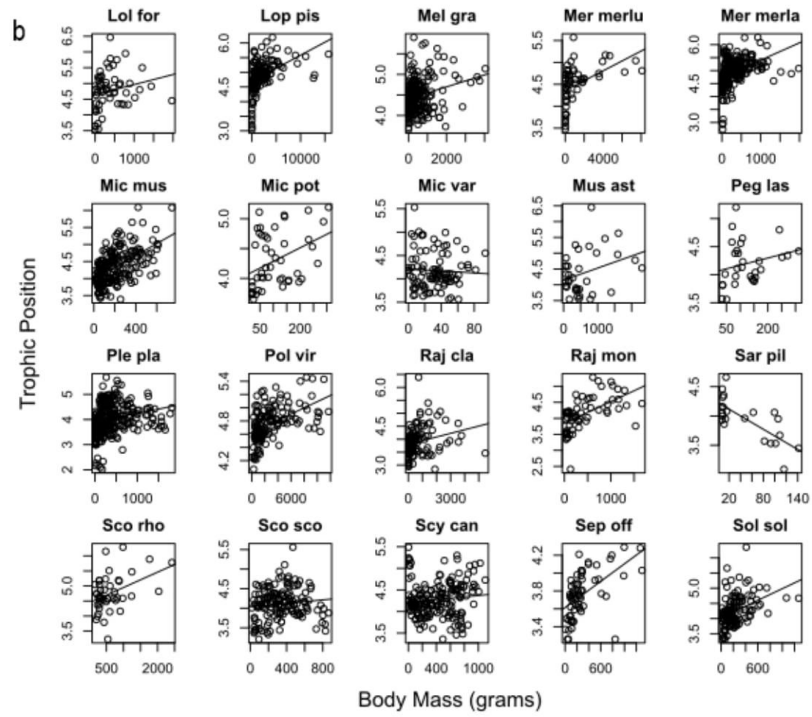
This work prompts to the fact that to disentangle the structure of aquatic food webs, a framework considering different life stages is needed to recognize the role that a single individual may play during its lifespan. As larger species need food resources obtained from specific trophic levels at specific stages of their life histories (Sharf et al. 2000, Costa 2009), environmental changes can affect their populations via impacts at the lowest to the highest trophic levels in the food web (Persson 1985, Persson 1987, Petchey et al. 1999). Furthermore, these results support recent models which suggest that TP and body size are positively correlated (Cohen et al. 1993, Jennings et al. 2001, Costa 2009), and that this relationship is not contingent on evolutionary history, therefore having evolved in different marine consumer lineages. I also suggest that morphological constraints associated with gape limitation may determine a species maximum TP, but ontogenetic diet niche shifts, regarding population size structure, with larger species presenting a wide array of body sizes, may represent the major ecological drivers in determining fish TP amplitude for marine consumer species, since individual body size did not affect TP amplitude and larger individuals rarely occupied lower trophic positions

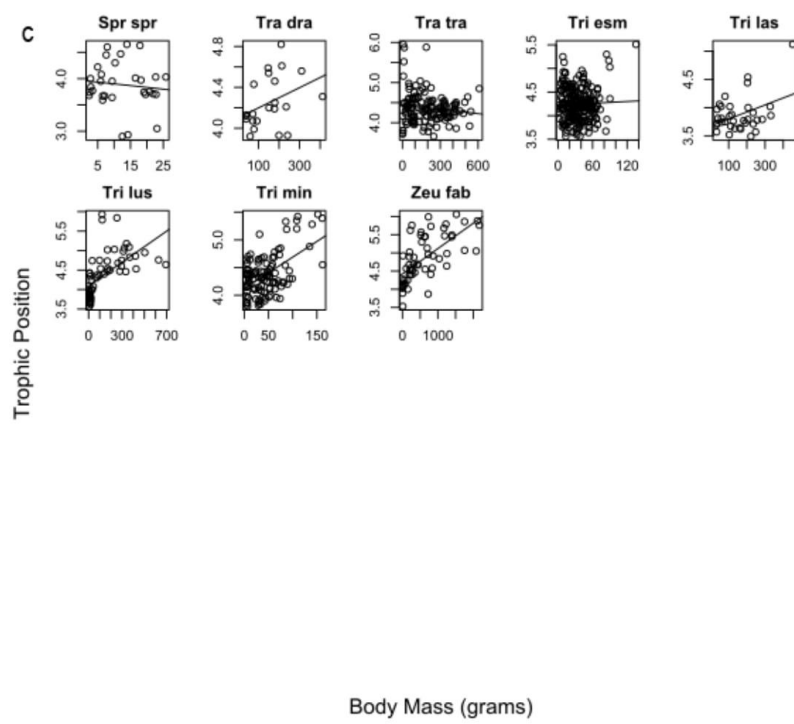
Appendix A: Phylogenetic tree constructed for the 48 species on the data set.



Appendix B: Individual-level analysis Pearson correlations between TP and body mass for individual consumers in all species analyzed. List of abbreviations: Ago cat (*Agonus cataphractus*), Alo sub (*Alloteuthis subulata*), Amb rad (*Amblyraja radiata*), Arg sil (*Argentina silus*), Arn lat (*Argoglossus laterna*), Bug lut (*Buglossidium luteum*), Cal lyr (*Callionymus lyra*), Cal mac (*Callionymus maculatus*), Cap ape (*Capros aper*), Che cuc (*Chelidonichthys cuculus*), Che luc (*Chelidonichthys lucerna*), Clu har (*Clupea harengus*), Ech vip (*Echiichthys vipera*), Eut gum (*Eutrigma gumardus*), Gad mor (*Gadus morhua*), Gly cyn (*Glyptocephalus cynoglossus*), Hip pla (*Hippoglossoides platessoides*), Lep whi (*Lepidorhombus whiffiagonis*), Leuc nae (*Leucoraja naevus*), Lim lim (*Limanda limanda*), Lol forb (*Loligo forbesi*), Lop pis (*Lophius piscatorius*), Mel aeg (*Melanogrammus aeglefinus*), Mer merla (*Merlangius merlangius*), Mer merlu (*Merluccius merluccius*), Mic kitt (*Microstomus kitt*), Mic pou (*Micromesistius poutassou*), Mic var (*Microchirus variegatus*), Mus ast (*Mustelus asterias*), Peg las (*Pegusa lascaris*), Ple pla (*Pleuronectes platessa*), Pol vir (*Pollachius virens*), Raj cla (*Raja clavata*), Raj mon (*Raja montagui*), Sar pic (*Sardina pilchardius*), Sep off (*Sepia officinalis*), Sco sco (*Scomber scombrus*), Scy can (*Scylirhinus canicula*), Sco rhom (*Scophthalmus rhombus*), Spr spr (*Sprattus sprattus*), Sol sol (*Solea solea*), Tra dra (*Trachinus draco*), Tri esm (*Trisopterus esmarkii*), Tri las (*Trigloporus lastoviza*), Tri min (*Trisopterus minutus*), Tri lus (*Trisopterus luscus*), Zeu fab (*Zeus faber*),







Chapter 2

Macroevolutionary dynamics of the body size - trophic position relationship in ray-finned fishes

Abstract:

Trophic position and body size are usually positively correlated across aquatic consumers, but such a relationship is expected to be less pronounced for tropical than temperate species. Using phylogenetic comparative methods, I investigated the influence of the climate (tropical vs temperate) and environment (freshwater vs marine) on the relationship between body size and trophic position in ray-finned fishes and estimated the evolutionary rates and rates of correlated evolution of these characteristics. I found that the slope of the body size – trophic position relationship is lower for organisms in the tropics and not significantly different from zero for freshwater tropical organisms and when I exclude herbivores from the analysis all combinations of climate and environment even out. Through evolutionary time, I found evidence of higher evolutionary integration between body-size and trophic position in temperate climates for both marine and freshwater environments and even when accounting for the influence of herbivory in this pattern evolutionary integration is higher for the temperate species in relation to tropical marine species. This work's results indicate that the observed difference in the body size-trophic position relationship between tropical and temperate climates is driven by the prevalence of herbivory in the tropics and can be explained by evolutionary dynamics inherent to climate.

Keywords: Actinopterygii, FishBase, Food-web, Global warming, Bayesian.

Introduction:

Body size and trophic position are usually positively correlated among consumer species in aquatic food webs (Cohen et al. 1993, Jennings et al. 2001, Woodward et al. 2005, Arim et al. 2010, Jennings & Cogan 2015). One of the main drivers of the body size-trophic position relationship is gape limitation (Arim et al. 2010, Dalponti et al. 2018), where gape size imposes a mechanical limit to the trophic position of consumers, preventing small individuals from consuming large prey, resulting in a positive correlation between trophic position and consumer size. However, as consumer size increases, it also increases absolute energy expenditure (Schmidt-Nielsen & Knut 1984, Blaxter 1989). Optimal foraging drives large aquatic predators to forage on the largest prey available, minimizing foraging costs (Scharf et al. 2000, Williams & Martinez 2000, Petchey et al. 2008). Alternatively, the increase in energy demand with body size and the reduced availability of energy at high trophic positions may impose an energetic constraint to food chain length and promote a negative correlation between trophic position and body size (Burness et al. 2001, Arim et al. 2007, Arim et al. 2016). When combined across a large range in body size variation, these opposing trends can generate a humped relationship between trophic position and body size (Arim et al. 2007, Segura et al. 2015, Arim et al. 2016). Therefore, the size-structured nature of aquatic food webs, and the organism trophic position, can be related to both morphological constraints and metabolic demands (Dalponti et al. 2018, Dantas et al. 2019).

In fish food webs, climate may modulate the body size–trophic position relationship by a synergistic effect of temperature on energetic demands and the respiratory rates of aquatic ectothermic consumers, which are higher at warm temperatures, culminating on an increased absolute energy expenditure with body size (Kleiber 1932, Gillooly, 2001, Brown et al. 2004,

Forster et al. 2012, Dantas et al. 2019). Environmental conditions also modulate feeding strategies of organisms. Temperature can affect the digestibility of carbon-rich food resources, and as a consequence, plant material is more easily digestible in warmer temperatures (Behrens and Lafferty 2007), softening the necessity of larger fish to develop complex digestive systems that are needed to digest plant tissue in temperate climates (Lubchenco & Gaines 1981, Cronin et al. 1997). Therefore, large fish in warmer climates may supply their higher energetic demands by feeding on food items at lower trophic levels, which are usually more carbon-rich and are not accessible by large fish in temperate climates due to digestibility constraints (Sterner and Elsen 2002, Floeter et al. 2005, Clements et al. 2009, Boersma et al. 2016). Indeed, herbivory and omnivory are more common in fish inhabiting warm climates (Lowe-McConnell 1987, Winemiller 1995, Jepsen & Winemiller 2002, González-Bergonzoni et al. 2012). On the other hand, carnivory tends to be more common in cold temperatures, since lower carbon-to-nutrient ratio demands increase the efficiency of protein absorption making a carnivorous diet more profitable for growth (Boersma et al. 2016, Moody et al. 2019).

In addition, the size-related environmental differences between freshwater and marine ecosystems, which are irrespective of each climate, may affect the resource heterogeneity (i.e. quality) entering the aquatic food webs, the disturbance regime and the water temperature climate-dependency (Tanentzap et al. 2014, Bakker et al. 2016), which may indicate that ecosystem type can mediate the effects of climate on body size-trophic position relationship (Dantas et al. 2019). For example, freshwater systems are smaller than marine ones. Consequently, freshwaters have a high perimeter-to-volume ratio than marine ecosystems, which determines that freshwaters receive greater loads of allochthonous plant material, therefore increasing the contribution of carbon-rich plant tissues as detritus to the diet of freshwater

consumers (Lowe-McConnel 1987, Bayley 1973, Winemiller 1995, Ou et al. 2017). As a consequence of such characteristics, the body size-trophic position relationship has been found to be steeper in cold temperate climates and marine environments when compared to their tropical or freshwater counterparts (Pyke et al. 1997, Dantas et al 2019).

The trophic position of consumers in different climates and environments, therefore, may emerge from the combination of morphophysiological characteristics, energetic demands, behavior and the environmental availability of food items (Violle et al. 2007, Díaz et al 2013, Stuart-Smith et al 2013, Carvalho et al 2015, Gravel et al. 2016). I hypothesize that only species that present an optimal body size - trophic position relationship are able to colonize or thrive in different climates and environments, and the occurrence of species which don't present an optimal body size - trophic position relationship for a given environment, e.g. large herbivorous fish in cold climates may be constrained as the environmental conditions may pose ecological filters to these traits (Arim et al. 2007, Dantas et al. 2019). Despite the evidence for distinct body size-trophic position relationships between tropical and temperate climates (Dantas et al 2019), little attention has been devoted to unraveling possible evolutionary dynamics that lead to a correlated pattern of these attributes. Throughout evolutionary time, climate may influence evolutionary dynamics such as evolutionary rates and evolutionary correlation of the traits that are affected by temperature, driving stabilizing selection in a coordinated manner, modulating the evolutionary correlation between these traits and resulting in evolutionary integration (Armbruster & Schwaegerle 1996, Walker 2007, Collar et al. 2008, Revell & Collar 2009, Armbruster et al. 2014, Caetano & Harmon 2019). I use the term integration in this work as the pattern of phenotypic correlations among traits (Pigliucci 2003) which may change in magnitude and direction among traits due to environmental conditions (Felsenstein 1988, Young

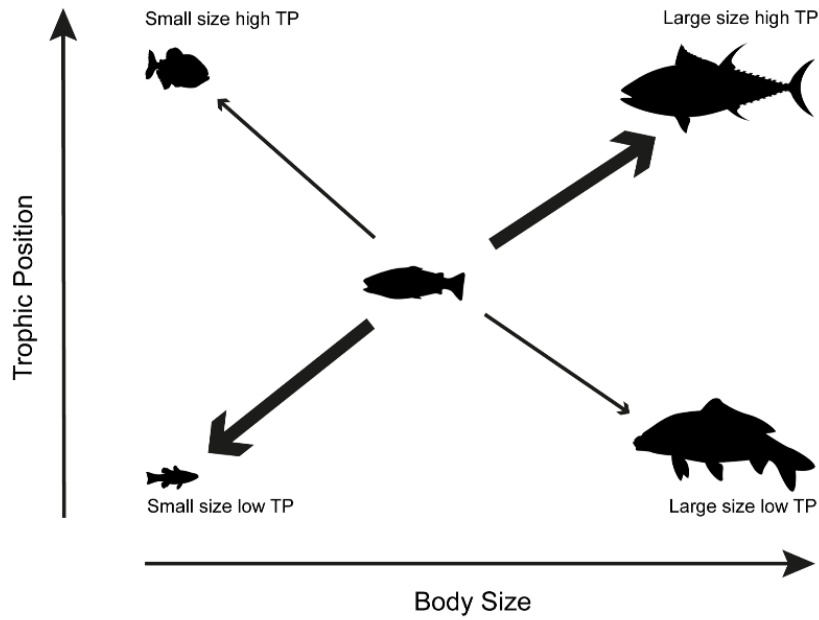
& Hallgrímsson 2005, Hallgrímsson et al 2009, Monteiro & Nogueira 2010, Claverie & Patek 2013), leading to a correlated evolution of multiple traits.

The contrasting body size-trophic position relationship in fish food webs observed on warm and cold climates, or in marine and freshwater habitats, may then be a result of divergent patterns of evolutionary integration between body size and trophic position of fish in each climate or environment, lineages in warm climates, for example, might show a trend of negative correlation, as the evolution of larger body sizes might be correlated with the evolution of herbivory and omnivory (Arim et al. 2010, Romanuk et al 2011) while the evolution of larger body sizes at cold-water lineages will be correlated with strict carnivory and higher trophic levels (Arim et al. 2010, Romanuk et al 2011). It is pivotal, therefore, to investigate the role of climate on the correlated evolution between body size and trophic position in order to highlight possible evolutionary constraints on the body size-trophic position relationship (Arim et al. 2010, González-Bergonzoni et al. 2012, Dantas et al. 2019).

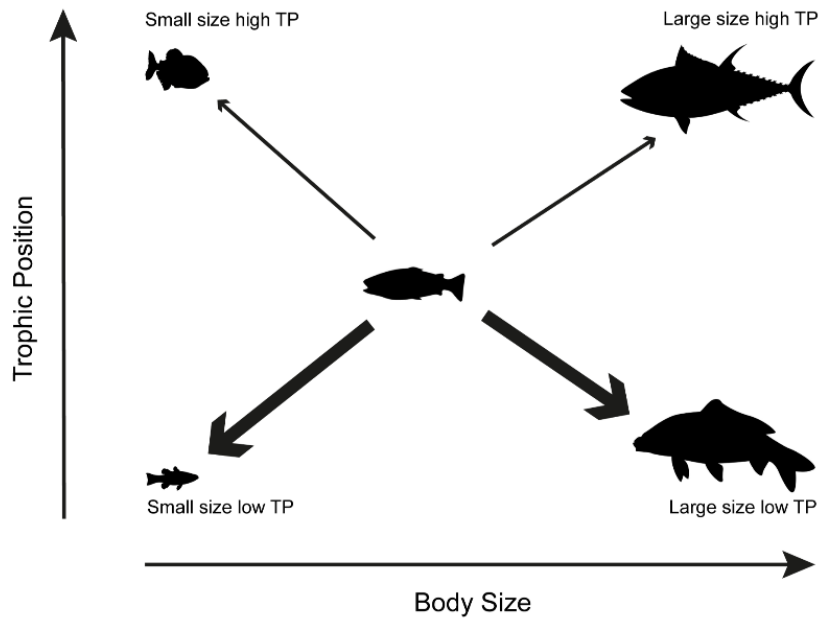
The objective in this study was thus to investigate the body size – trophic position relationship and to compare the evolutionary rates and evolutionary integration of these traits in tropical and temperate fish species of marine and freshwater environments. I hypothesize that the pattern of evolutionary integration between body size and trophic position in fish food webs is less pronounced in the tropical climate than in the temperate climate due to the likelihood of large bodied species that forage low in the food web in the tropics(Figure 1), I also hypothesize that, within climates, the relationship would be stronger in the marine environments than in freshwater environments, resulting in distinct shapes of the body size–trophic position relationship of extant species among climates and environments (Reznick & Ghalambor 2001, Hendry et al. 2008, Condamine et al. 2013, Burin et al. 2016).

Figure 1 - Hypothesis for the likelihood of evolutionary transition rates for body size and trophic position of fish in (a) tropical and (b) temperate climates from a medium sized omnivorous ancestor. The coupled effect of environment and climate may lead to different likelihoods of transitions due to the following factors: higher respiratory rate and consequent demand for carbon may lead to the selection of large species that forage on low trophic levels in both environments on the tropical climate while environmental availability of detritus and the quality of low trophic level resources may lead to an even accentuated likelihood of low body sized - trophic position relationships on freshwater tropical environments, leading to low evolutionary correlations. On the other hand need for higher Nutrient/Carbon ratios on cold climates may lead to a selection of more carnivorous diets in both marine and freshwater environments leading to more likely transitions for large body size coupled with high trophic position on temperate climates suggesting a higher evolutionary correlation between these traits.

Temperate Climate



Tropical Climate



Methods:

Sampling data: To test this work's hypothesis, I used freshwater and marine ray-finned fishes occurring on tropical or temperate areas for which the information of the most recent phylogenetic tree for fishes was available, comprising 1992 species (Betancur-R et al. 2017). For these species, I obtained data for maximum body size and trophic position on FishBase (www.fishbase.org) (Froese & Pauly 2014). Maximum species' body length - represented by the standard length of the largest individual recorded - is the most available metric of species body size in FishBase (only a few species have size at maturity and mean size available). I only considered species for which trophic position was estimated based on trophic studies. Trophic Position was based on diet studies as adding the value of one (corresponding to the base producer trophic position) to the mean trophic position weighted by the relative abundance of all food items consumed by a given species (Froese et al. 2014). For a given consumer i , the trophic position is defined as: $Troph_i = 1 + \sum_{j=1}^S DC_{ij} \times Troph_j$, where $Troph_j$ is the fractional trophic level of prey j , DC_{ij} is the proportion of prey i in the diet of a consumer (j), and (S) is the total number of prey species. I used species from all trophic guilds which occur in freshwater or marine environments in temperate or tropical areas only. I excluded from the dataset species which are distributed over tropical and temperate ecosystems for they would hinder the power to detect changes related to the climate as they have evolved to occupy both climates. Subtropical, anadromous and brackish species were also excluded as they were underrepresented on the data set and I could not fit models that accomplished these species due to sampling constraints. I also excluded those species whose preferred upper depth is below 200m as their environment is cold independent of their climatic zone (Dantas et al, 2019). The final dataset used in this study was composed by 1,111 species for which reliable information was achieved after disregarding species whose information did not meet the study criteria (Supplementary online material - Table

S1). During preliminary analysis I found out a very low representation of herbivore species in the temperate climate, hence, in order to uncover the influence of herbivores on the results, I did all the analysis using the complete dataset and a dataset without herbivores.

Statistical analyses: To uncover the influence of climate and environment on the relationship between body size and trophic position on extant species I performed regression models using Phylogenetic Independent Contrasts of body size and trophic position for each possible combination of climate and environment (Felsenstein 1985, Symonds & Blomberg 2014). I also explored the distribution of the species in the trait-space using a reconstruction of the phylogeny in the coordinates formed by the correlation between body size and trophic position in all combinations of climate and environment using the *phylogenetic morphospace* function in R package *phytools* (figure 3)

To incorporate the influence of climate and environments on character evolutionary rates and rates of correlated evolution between characters I reconstructed the evolution of climate and environment use along the phylogenetic tree using a reversible Markov model with all four possible combinations of climate and environment (marine tropical, marine temperate, freshwater tropical and freshwater temperate) with stochastic character mapping using an “all rates different” (ARD) Markov model, meaning that the transitions from and to any of the possible climate/environment combinations occur at different rates (O’meara et al. 2006, Beaulieu et al. 2013), rates of transitions from physically disconnected environments were disallowed on the model. The implementation of this model was performed using the function “*asr_mk_model*” from the R package “*castor*” (Louca et al. 2017). To test for patterns of the transition rates, I used Akaike Information Criterion (AIC) to compare the transition rates given by the ARD model with models where the transition rates between two given regimes were set

to be equal, in this case higher values of AIC for models with equal rates indicate that the performance of the model is better with ARD. Results of the reconstructed climate and environment use reconstructed evolutionary tree are presented in appendix 1.

To access the pattern of evolutionary integration between body size and trophic position under the two climate regimes I estimated the rates of evolution for both traits and their evolutionary covariation using a Bayesian estimate of the evolutionary rate matrix fitted to the evolutionary tree with estimated mapped characters and trait data using Markov-Chain Monte Carlo under a Brownian motion model implemented using the “*Ratematrix*” R package and function “*ratematrixMCMC*” (Revell & Harmon 2008, Caetano & Harmon 2017). I tested whether traits followed a Brownian Motion or Ornstein Uhlenbeck model to determine whether I could use the Ratematrix approach to modeling divergence I found support for an OU model over BM by AIC (AIC BM for body size = 4996.70 AIC OU for body size = 4914.52 AIC BM for Trophic position = -1017 AIC BM for Trophic position = -1196), however estimated relatively long phylogenetic half-lives (46.4 my tp and 71.9 my for body size). These are lower bounds for the rate, as biological and measurement error are predicted to result in higher levels of phylogenetic half-life. Both of these estimates are substantial fractions of the total tree height, indicating that deviations from Brownian Motion are likely not severe, allowing the usage of ratematrix for the calculation of evolutionary rates and rates of correlated evolution. The evolutionary rate matrix determines the evolution of individual characters in the diagonal elements and the proportion of coevolution between characters in the off-diagonal (Revell & Harmon 2008). All analyses were performed in the statistical environment R (R development core team 2019).

Results:

The phylogenetic-corrected body size-trophic position relationship is shown in figure 2. I found that it was positive and significant for the following environment-climate combinations using independent contrasts: marine temperate (slope = 0.043, R-squared = 0.16, $p < 0.001$), freshwater temperate (slope = 0.07, R-squared = 0.13, $p < 0.001$), and marine tropical (slope = 0.0017, R-squared = 0.0084, $p < 0.001$). For the combination of freshwater environment and tropical climate there was no relationship between body size and trophic position (slope = 0.0004, R-squared = 0.0012, $p = 0.24$). For the dataset without the herbivore species I found out that the body-size relationship is positive and significant for all combinations of environment and climate reinforcing the notion that herbivory is an important driver of the pattern of a shallower body size – trophic position relationship in the tropical climate (Freshwater Tropical slope = 0.0008, R-squared = 0.09, $p < 0.05$; Marine Tropical slope = 0.0019, R-squared = 0.17, $p < 0.05$; Freshwater Temperate slope = 0.063, R-squared = 0.22, $p < 0.05$, Marine Temperate slope = 0.043, R-squared = 0.17, $p < 0.05$)(figure 3).

The phylomorphospace reconstruction showed higher dispersion for both marine and freshwater environments on the tropical climate, indicating a lower correlation between body size and trophic position meaning that there are small and large species occupying high or low trophic positions in tropical regions (figure 4), in the phylomorphospace constructed without herbivores the dispersion of species in the trait-space presents the same form for both tropical and temperate species (figure 5).

Figure 2 - Phylogenetic independent contrasts (PIC) without herbivores between body mass and trophic position for freshwater tropical regime (n = 266), marine tropical (n = 517), freshwater temperate (n = 103) and marine temperate (n = 194).

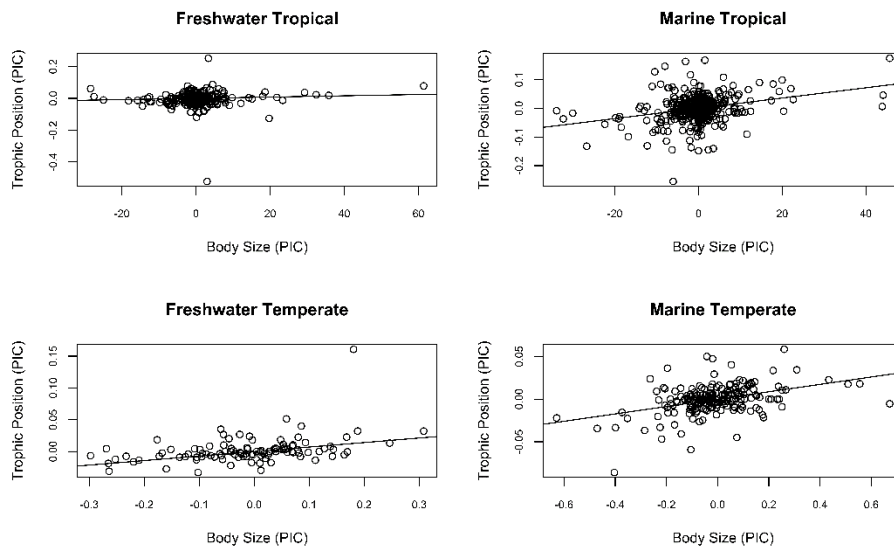


Figure 3 - Phylogenetic independent contrasts (PIC) between body mass and trophic position for freshwater tropical regime (n = 296), marine tropical (n = 460), freshwater temperate (n = 101) and marine temperate (n = 193).

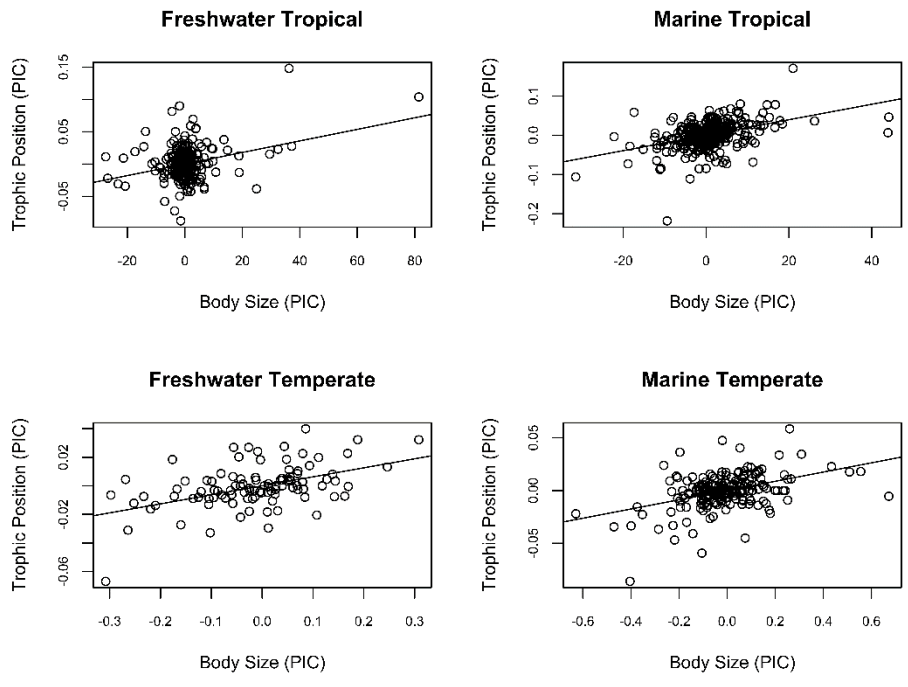


Figure 4 Phylomorphospace for the relationship between body size and trophic position under different climates and environments, colors represent feeding guilds (green = herbivores, blue = omnivores, red = carnivores).

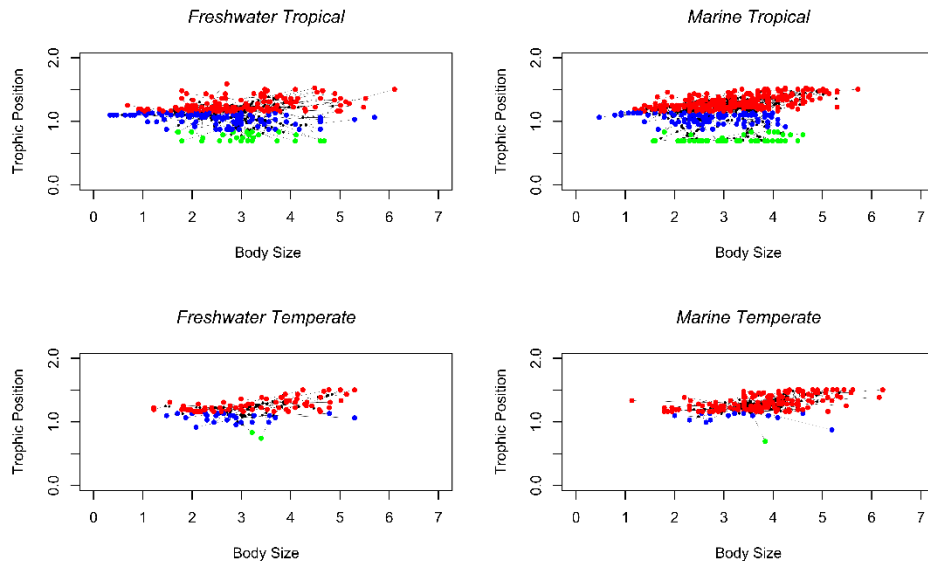
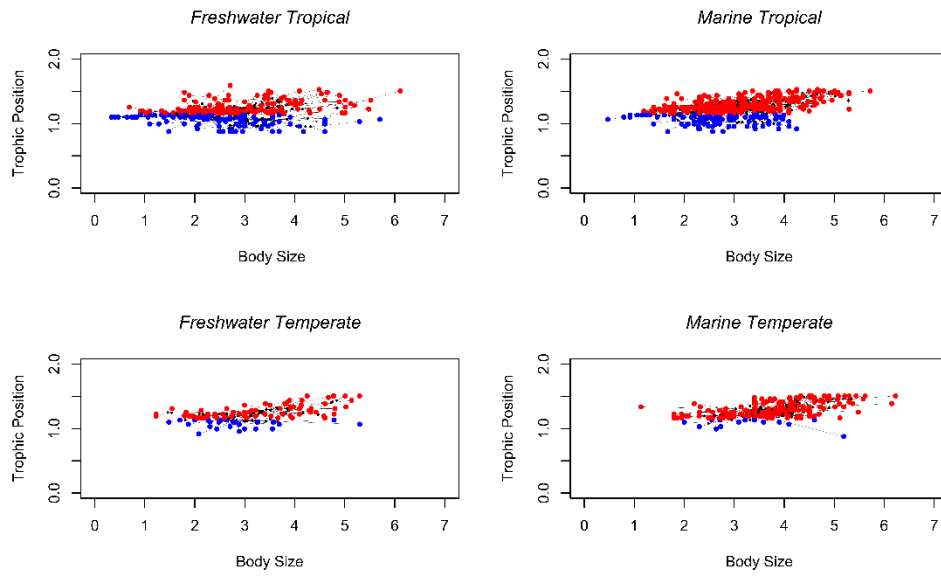


Figure 5 Phylomorphospace without herbivores for the relationship between body size and trophic position under different climates and environments, colors represent feeding guilds.



Evolutionary rates for trophic position showed high overlap for all combinations of environment and climate (figure 6 panel A), for body size evolutionary rates were similar for all combinations of environment and climate except for the combination of marine environment and temperate climate, which showed higher evolutionary rates (figure 4 panel D). Evolutionary correlations between body size and trophic position were similar in freshwater and marine environments within the same climate but were significantly different among climates, being higher in temperate climates (figure 6 panels B and C). Without the herbivores evolutionary rates for trophic position were higher for freshwater tropical species in relation to marine tropical species and marine temperate species while marine tropical, marine temperate and freshwater temperate showed high overlap as well as there was high overlap between tropical freshwater and temperate freshwater (figure 7 panel A), body size evolutionary rates and did not change in relation to the dataset with all the species (figure 7 panel B), evolutionary covariance was lower for marine tropical in relation to the marine temperate while overlapping for all other combinations of environment and climate. Evolutionary correlation showed to be lower for tropical marine and higher for freshwater temperate (figure 7 panel C).

Figure 6 – Posterior density distribution of the of evolutionary rates for trophic position (panel A) body size (panel D) and rates of correlated evolution (Panels B and C) between the traits for environmental-climatic regimes: freshwater tropical = green; marine tropical = red; freshwater temperate = black; marine temperate = blue.

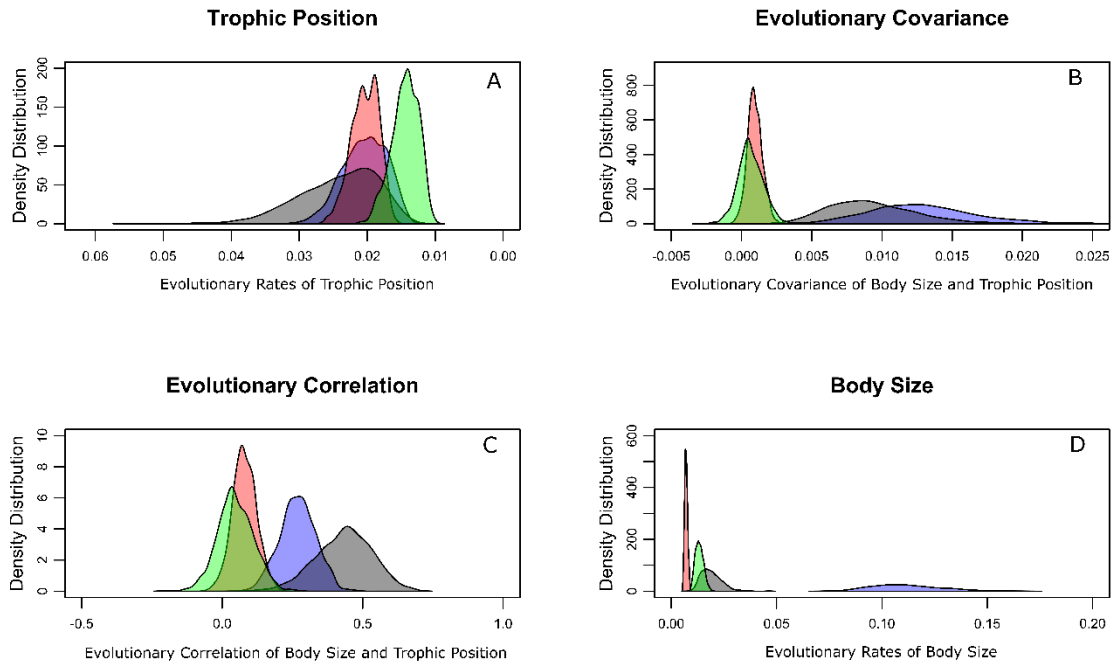
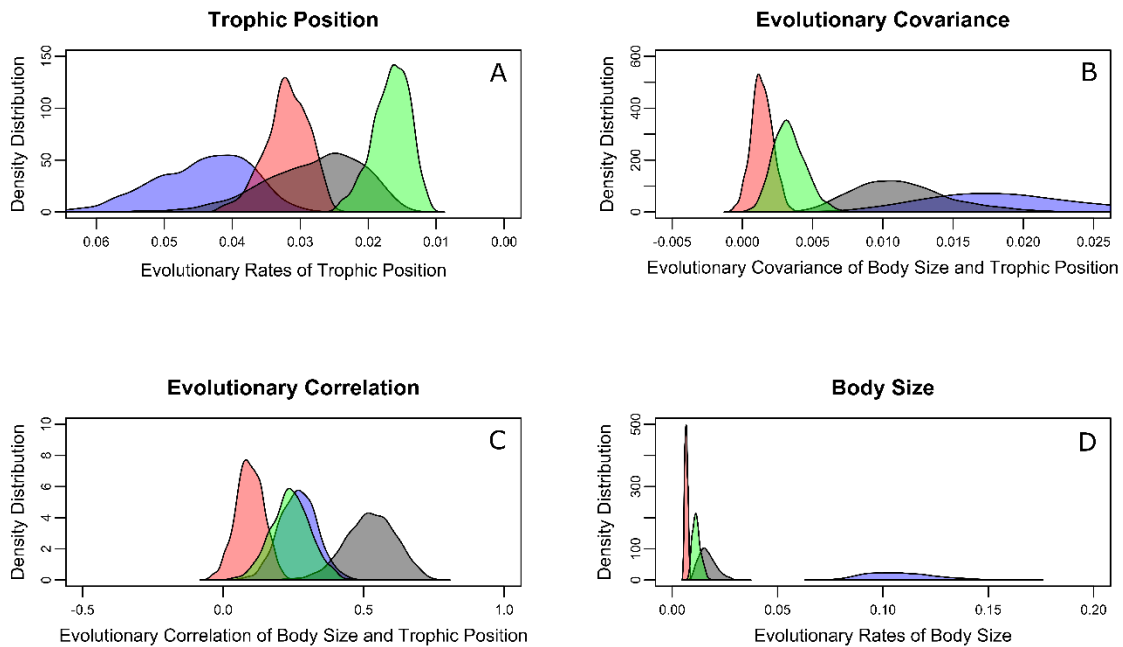


Figure 7 – Posterior density distribution without herbivore of the of evolutionary rates for trophic position (panel A) body size (panel D) and rates of correlated evolution (Panels B and C) between the traits for environmental-climatic regimes: freshwater tropical = green; marine tropical = red; freshwater temperate = black; marine temperate = blue.



Discussion:

The positive relationship between body size and trophic position for the fish food webs in marine environments on both climate regimes corroborates the notion that this is a common pattern observed across systems and taxa (Arim et al. 2010, Romanuk et al. 2011), and the lower slope of this relationship on the tropics reflects that distinct evolutionary divergence mechanisms, which affect the dietary patterns of fish, are operating among climate regimes (Layman et al. 2005, Arim et al. 2010, Ou et al. 2017, Dantas et al. 2019). The weak and non-significant body size - trophic position relationship on freshwater tropical environments, as observed here, reinforces the idea that environmental conditions can be a strong driver of the body size - trophic position relationship (Dantas et al. 2019). Which highlights that the availability of resources is an important driver of the body size – trophic position relationship in aquatic consumers. These results are likely to be related to the higher proportion of herbivores in the tropical climate as if, these are excluded from the analysis, no clear difference for the body size – trophic position relationship between tropical and temperate climates can be found.

The trait-space comprising both trophic position and body size coordinates can be more completely filled in the tropical climates both for marine and freshwater environments as indicated by the reconstruction of the phylomorphospace (figure, 3) , comparison with the phylomorphospace generated by the dataset without herbivores (figure 4) showed that the presence of large herbivores and omnivores found in the tropics filling a trait space area that is not occupied in the temperate climate is the main driver of this pattern as was expected for tropical species as demonstrated in Figure 1 where large species with low trophic position are expected mostly for the tropical climate, empirical examples for fish lineages that reinforce this pattern are lineages that occur over a large latitudinal gradient, as is the case of Perciformes which comprise large herbivorous and large predators representatives in warm climates while

only omnivorous or carnivorous representatives in cold climates (Gaines and Lubchenko 1981, Horn 1989, Harmelin-Vivien 2002, Floeter et al. 2005, Clements et al. 2009). Some tropical freshwater fish species even exhibit an inverse pattern of the body size-trophic position relationship like several Cyprinids, that undergo ontogenetic diet shifts towards a detritivore diet at maturity (Persson & Crowder 1998, Burress et al. 2016), and the Serrasalminae subfamily where the largest species are highly frugivorous whereas the smallest are carnivorous (Werner & Gilliam 1984, Romanuk et al. 2011).

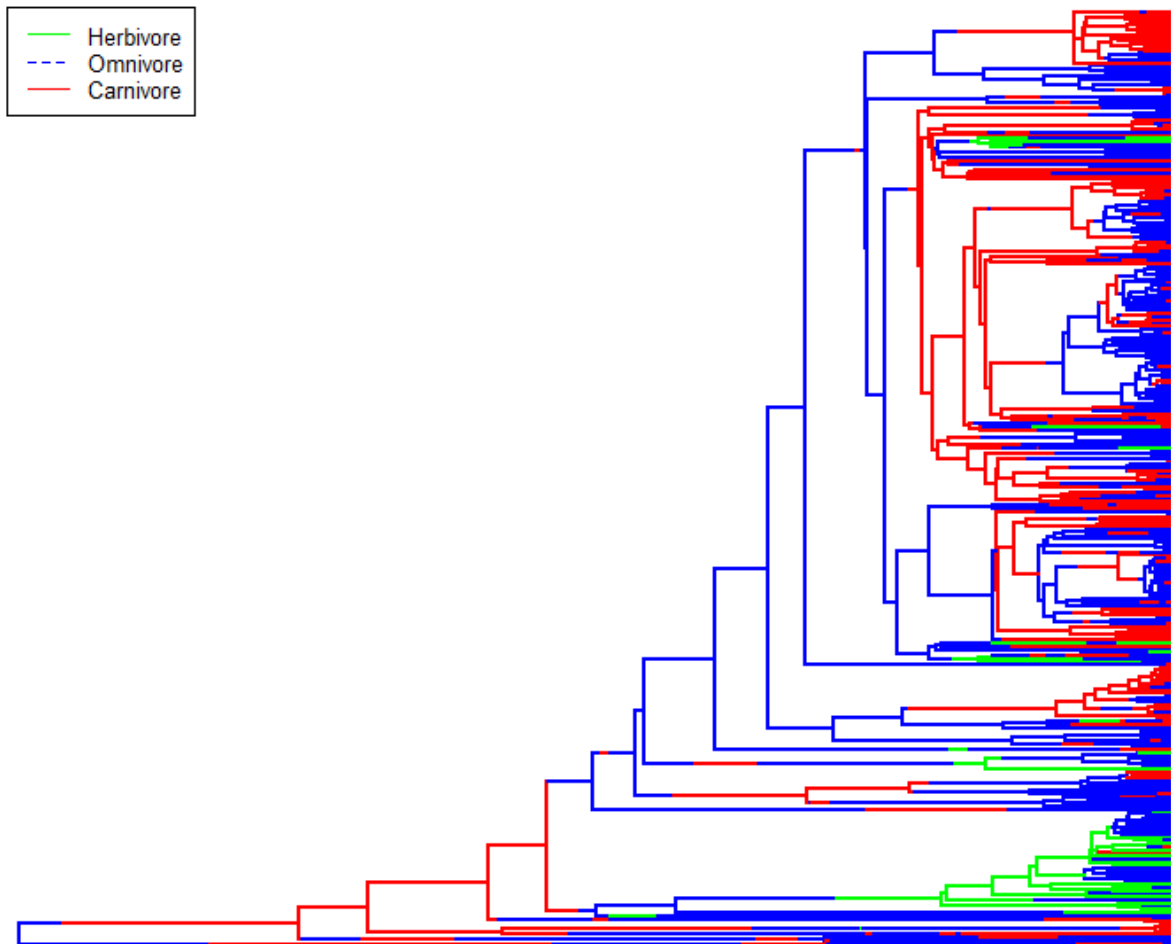
Higher evolutionary rates for body size on the marine temperate regime does not support the notion that character evolutionary rates are higher under warm climates (Allen et al. 2006, Allen et al. 2007, Lin et al 2019), However this pattern can be the result of faster speciation rates of marine fish at high latitudes (Rabosky et al. 2018) as phenotypic evolution has been found to follow species diversification (Folk et al. 2018) and rates of speciation and trait evolution have been found to be correlated in teleost fishes (Rabosky 2013). The lower evolutionary correlation between trophic position and body size in both freshwater and marine environments, observed in the tropical climate, corroborates the hypothesis that the less steep body size - trophic position relationship for the tropics may result from a divergent pattern of evolutionary integration between temperate and tropical climates, for omnivore and carnivore species this pattern holds when comparing tropical marine species against temperate freshwater species showing that the prevalence of herbivory in the tropics is an important driver of the overall low evolutionary integration between body size and trophic position but even in the absence of herbivores freshwater temperate species still show a tighter evolutionary integration between body size and trophic position. Several mechanisms have been proposed to explain a possible temperature-sensitive influence on the body size - trophic position relationship. One mechanism is related to

higher respiratory rates on the tropics (Peters & Peters 1986, Gillooly et al. 2001, Brown et al. 2004), that lead tropical species to forage on more carbon-rich resources (Boersma et al. 2016), therefore lowering their trophic position in relation to temperate species (Arim et al. 2010, Cross et al. 2015). The environmental availability of detritus, that comprise most of the organic matter in tropical lakes and rivers (Winemiller 1990, Jepsen & Winemiller 2002, Tanentzap et al. 2014, Jardine 2016), and the lower macrophytes C:N ratio (Bakker et al 2016), may reduce trophic position of large fish due to the combination of energetic demands and the environmental availability and quality of food items, in tropical freshwater environments (Violle et al. 2007, Díaz et al 2013, Stuart-Smith et al 2013, Carvalho et al 2015, Gravel et al. 2016). Therefore, the increase in the prevalence of omnivory and herbivory in freshwater tropical environments may represent an important mechanism driving the body size-trophic position relationship, indeed a recent investigation of the main predictors of trophic position in freshwater and estuarine environments in tropical and sub-tropical environments have demonstrated that traits related to feeding strategies are better predictors of trophic position than body size in these environments (Kepeller et al. 2020). On the other hand, in temperate areas the rate of energy transfer throughout the food web may be higher, as less energy is lost due to respiratory rates (Gillooly et al. 2001). In addition, conversion of food on body mass has shown to be more efficient if omnivorous species feed on animal matter at low temperatures (Behrens & Lafferty 2007), leading to a tighter, and more conserved, relationship between large sizes and carnivorous habits in the temperate regions. In contrast, especially for large tropical species, they may overcome the energetic constraint posed by higher metabolic rates under warm environmental conditions by consuming food items at lower trophic levels, which are more abundant and have higher carbon-

to-nutrient ratios (Arnold 1992, Wootton & Oemke 1992, Floeter et al. 2005, Boersma et al. 2016).

In summary, I found that after accounting for phylogenetic relatedness, there is a positive relationship between body size and trophic position for a wide array of body sizes for extant species. However, the slope of this relationship is significantly lower for organisms in the tropics and is not significant for tropical freshwater species when herbivores are present, indicating a synergistic effect between environment and climate possibly driven by the occurrence of large herbivores in the tropics. This result corroborates the notion that tropical fish species occupy lower trophic positions compared to similarly sized fish in the temperate region (Dantas et al. 2019). I found evidence that this pattern is consistent with a divergent evolutionary integration between body size and trophic position on distinct climates and that herbivory in the tropics is an important factor driving the patterns of body size – trophic position relationship specially because large herbivores that are more common in the tropics lower the correlation between these traits. Demonstrating why and how historical factors may play a role on fish trophic structure may become an important inquiry for understanding the variation of the body size– trophic position relationship across climates (Ou et al. 2017). Further studies focusing on trait-dependent diversification of species, especially concerned with fish dietary guilds, are particularly needed to unravel the role of the temperature on fish extinction and diversification rates within specific trophic guilds, determining the ultimate causes of the divergence on fish trophic structure among climate regimes.

Appendix A: Phylogenetic tree with mapped characters for environment and climate use.



Chapter 3

Evolutionary roots for the prevalence of low trophic levels in tropical fish species

Abstract:

Herbivorous fishes are far more common in the tropics when compared to the fish assemblages in the temperate regions, this pattern may be generated by conditions related to climate e.g. availability and predictability of algae and vegetal matter as well as by metabolic effects of temperature on ectotherms, such conditions and constraints may affect macroevolutionary dynamics, in this work I investigated how speciation, extinction and diversification of the trophic guilds of herbivores, omnivores and carnivores are affected by the climatic region in which fishes occur using State-Dependent Speciation and Extinction models that allow for multiple states of traits (MuSSE models). I observed that both globally and in the tropical regions speciation of herbivores and omnivores is higher than that of carnivores, global extinction rates are slightly higher for carnivores and overlapping for all trophic guilds in the tropics while in the temperate regions speciation of omnivores is higher and extinction of herbivores is slightly higher although net diversification is highly overlapping for all trophic guilds. These results show that the higher proportion of herbivores in the tropics when compared to the temperate regions may be related to faster evolutionary rates of herbivores in the tropics.

Introduction:

A remarkable pattern in fish communities is the higher proportion of species that feed low in the food web e.g. herbivores, detritivores and omnivores in the tropics in relation to the temperate regions (Lowe and MacConnell 1987, Winemiller 1995, Jepsen and Winemiller 2002, Ferrera et al. 2004), those differences in the distribution of species may be the result of uneven diversification of trophic guilds throughout the tree of life due to the influence of biotic and abiotic factors driven by differences in climate (Benton 2009, Alfaro et al. 2009, Maliet et al. 2019, Pontarp et al. 2019, Siqueira et al. 2020), the development of novel traits and environmental changes, for example, can burst diversification of certain clades through specialization and ecological opportunities (Konow et al 2008, Alfaro et al 2009, Yoder et al. 2010, Helmstetter et al. 2016, Foster and Piller 2018), as well as trophic guilds may influence macroevolutionary dynamics, increasing or decreasing speciation and extinction or presenting different evolutionary transitions from one guild to another (Price et al 2012, Siqueira et al. 2020) in this context, trophic and habitat specialization are the most commonly studied drivers of adaptive radiation since they influence fundamental aspects of the species' life histories and may influence macroevolutionary patterns (Chakrabarty 2005, Burin et al 2015, Foster and Piller 2018).

A specific geographic location can function as a cradle where species are evolving faster than in other areas or a museum where higher diversity is rather generated by lower extinction rates followed by species accumulation,(Mittelbach et al., 2007; Rohde, 1992; Schluter & Pennell, 2017) (Rohde 1992, Mittelbach et al. 2007, Brown 2014, Schluter and Pennell 2017) these processes are not exclusive and a region may show both higher speciation and higher extinction at the same time and these dynamics may be divergent for species that present different sets of traits, generating unevenness with certain clades more diverse than others

(Stebbins 2013, Mittelbach et al 2007, Siqueira et al 2016). In general, for fish species, mixed evidence for the role of climate on evolutionary dynamics exist, with evidence of higher speciation in colder areas for marine fishes (Rabosky et al. 2018) and evidence of higher speciation of tropical reef fish, which correspond to the most speciose lineages of marine species (Siqueira et al. 2016), the higher proportion of herbivore and omnivore species may, therefore be a reflex of the mechanisms that lead to: higher diversification rates in the tropics making tropical regions “evolutionary cradles” for herbivores and omnivores or higher extinction rates for these guilds making the temperate region an “evolutionary sink”.

The type of climate can influence on evolutionary dynamics through its influence on speciation and extinction rates, speciation on clades that occupy low trophic positions in the tropical climate may be more likely due to the increase in the energetic expenditure and metabolic rates with temperature (Gillooly et al. 2001, Brown et al. 2004) increasing the need for carbon to sustain activities, which is more abundant low in the food web (Forster et al. 2012, Boersma et al. 2016), possibly leading to higher diversification rates for herbivores and omnivores are negative. On the other hand, in the temperate climate, lineage extinction may be higher for herbivores and omnivores as in colder climates slower digestion may render the consumption of resources with a low Nutrient/Carbon ratio insufficient to supply enough nutrients to sustain growth (Boersma et al. 2016, Moody et al. 2019).

My goals in this work are to investigate evolutionary dynamics of bony fish linking climate and the evolution of trophic guilds body fish, I hypothesize that on the tropical climate diversification to low trophic levels (herbivory and omnivory) will be higher due to higher metabolic rates leading to a higher carbon consumption. For the temperate climate I hypothesize higher diversification for carnivorous species led by higher foraging efficiency if the largest prey

available if consumed and digestive constraints of less nutritious food resources would they feed low into the food web. To my knowledge this is a first attempt to investigate trait-dependent diversification conditioned by climate in bony fish.

Methods:

Data collection was conducted as described in chapter 2, I also used the same phylogeny to conduct phylogenetic analysis, I assigned species to three trophic guilds based on the mean trophic position following Stergiou and Karpouzi (2001), species with mean trophic position ranging from 2 to 2.2 feed exclusively on producers and were very rare on the dataset, especially in the temperate climate, species with trophic position varying from 2.3 to 2.8 feed mostly on producers but also include filter feeders and detritivores that occasionally consume other consumers such as sponges, polychaetes and zooplankton therefore, species on the trophic position range from 2.0 to 2.8 were assigned on a guild that encompasses herbivores and detritivores hereafter I call this guild herbivores for short, species with trophic position ranging from 2.9 to 3.7 are omnivores that can feed on both producers and other consumers and species with trophic position > 3.7 are specialized carnivores, according to the authors Stergiou and Karpouzi (2001).

To estimate speciation rates and extinction rates related to each trophic guild I conducted Multi State Speciation and Extinction (MuSSE) with trophic guilds of herbivores, omnivores and carnivores for the global dataset with both tropical and climate species together and with tropical and temperate species separately in order to uncover differences in the diversification dynamics between climates. SSE models allow for the estimation of speciation rates (λ), extinction rates (μ) and overall diversification ($\lambda - \mu$) related to multi-state characters throughout a phylogeny.

After conducting the MuSSE models I fitted the likelihood of the models in a Bayesian Markov Chain Monte Carlo (MCMC) framework to account for uncertainties in rate values and used the posterior distribution values to infer the differences in the parameters irrespective to each climate. Convergence of the parameters was obtained with 10000 steps (sampling every 100th step). To assess significance of the models I compared the likelihood models with rates and transitions varying freely for each character state to null models where all rates and transitions were constrained to be equal through Akaike Information Criterion for model selection and with ANOVA Analysis with a χ^2 test. All analyses were performed in the statistical environment R (R development core team 2019).

Results:

For all species and for tropical and also for the temperate climate separately, the proportion of herbivores was higher in the tropical climate (24% of all tropical species compared to 6% in the temperates), confirming the trend of the prevalence of species that feed low in the food web, for omnivorous species with preferentially carnivorous habits the proportion was that of 53% in the tropics and 59% in the temperate climate, strictly carnivorous species represented 21% of tropical species and 33% of temperate species, showing that the proportion of carnivores is higher in the temperate climate (Figs 1, 2 and 3).

Fig 1 Number of species in each trophic guild of extant species in both tropical and temperate climates (green = herbivores, blue= omnivores, red = carnivores).

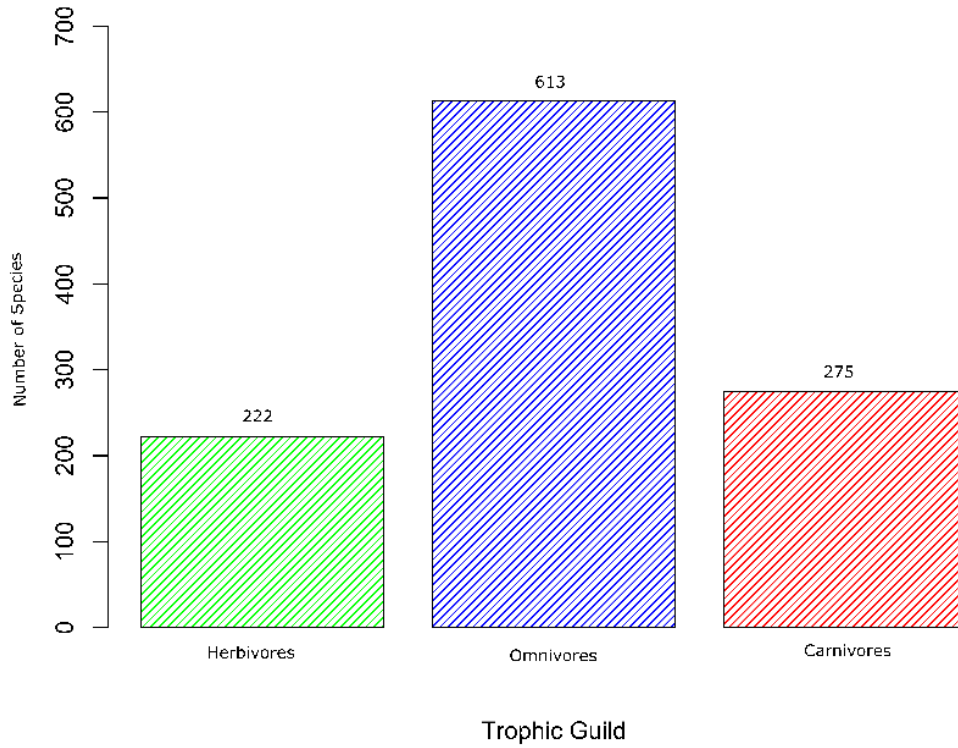
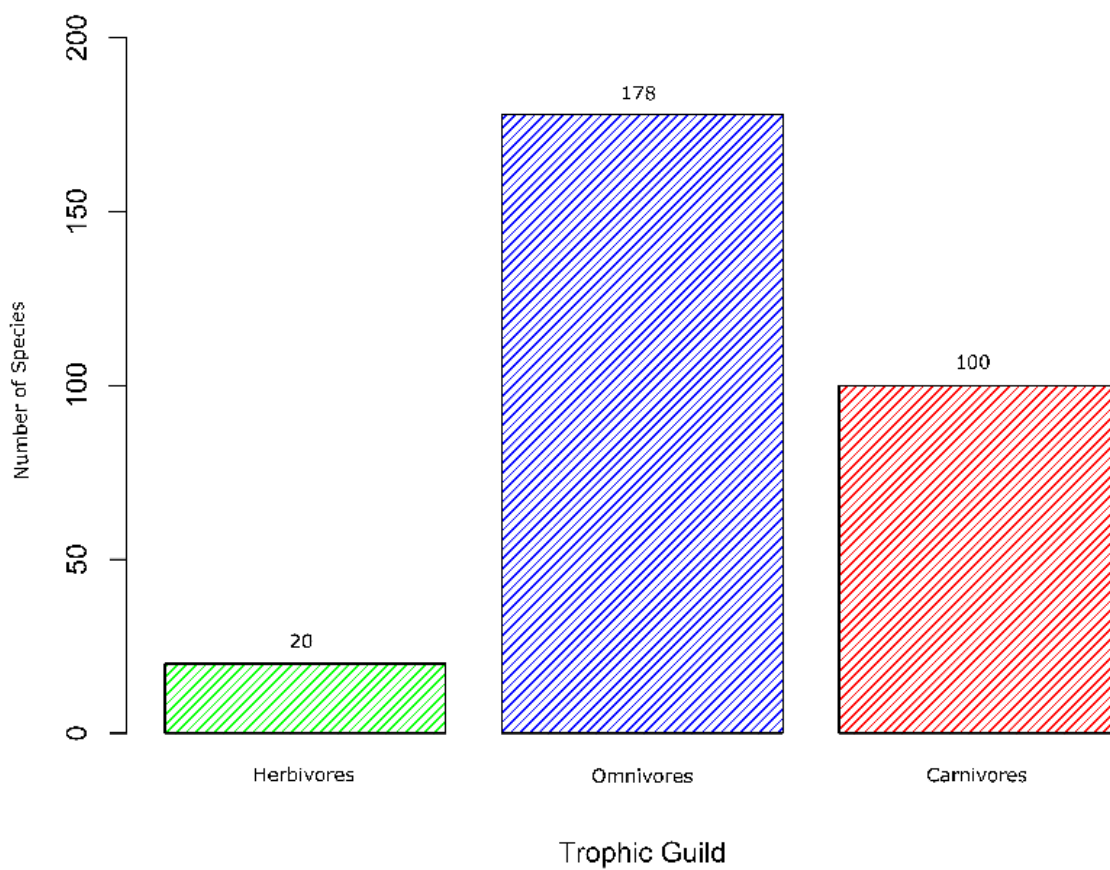


Fig 2 Number of species in each trophic guild of extant species in the tropical climate
(green = herbivores, blue= omnivores, red = carnivores).



Fig 3 Number of species in each trophic guild of extant species in the temperate climate (green = herbivores, blue= omnivores, red = carnivores).



All MuSSE models that incorporated variation in the speciation, extinction and transition rates had lower AIC values than the null models and had significant P-values for the χ^2 tests (all species model: χ^2 151.23, $p < 0.001$; tropical species model: χ^2 92.79, $p < 0.001$; temperate species model: χ^2 83.053, $p < 0.001$). For the tropical climate, speciation rates were higher for herbivore and omnivore species with overlapping 95% confidence intervals between these trophic guilds and speciation rates were lower for carnivorous species, extinction rates were similar for all trophic guilds and as a consequence, diversification rates followed the same pattern as speciation rates in the tropical climate. For the temperate environment, speciation rates were different between carnivores and omnivores being higher for omnivores and lower for carnivores with very wide confidence intervals of the estimate for herbivores overlapping the two other guilds. Extinction rates were overlapping for all trophic guilds and diversification rates also followed the same pattern found for speciation rates in the temperate climate (Appendix 1 and figures 4 through 6).

Transition rates among trophic guilds for all species showed a tendency to go from herbivores to omnivores and then carnivores with higher transitions “forwards” than “backwards”, transitions directly from herbivores to carnivores and from carnivores to herbivores were equally low (figure 7). For tropical species, all transition rates were within the same order of magnitude except for transition rates from herbivores towards omnivores that were one order of magnitude higher (figure 8). For temperate species the higher transition rates occurred from the herbivores guild towards the guild of carnivores, transition rates from herbivores towards omnivores and from carnivores to omnivores were one order of magnitude than from omnivores towards the other guilds (figure 9).

Fig 4 Posterior distributions of the speciation, extinction and diversification rates of species in the trophic guilds for all species (green = herbivores, blue= omnivores, red = carnivores).

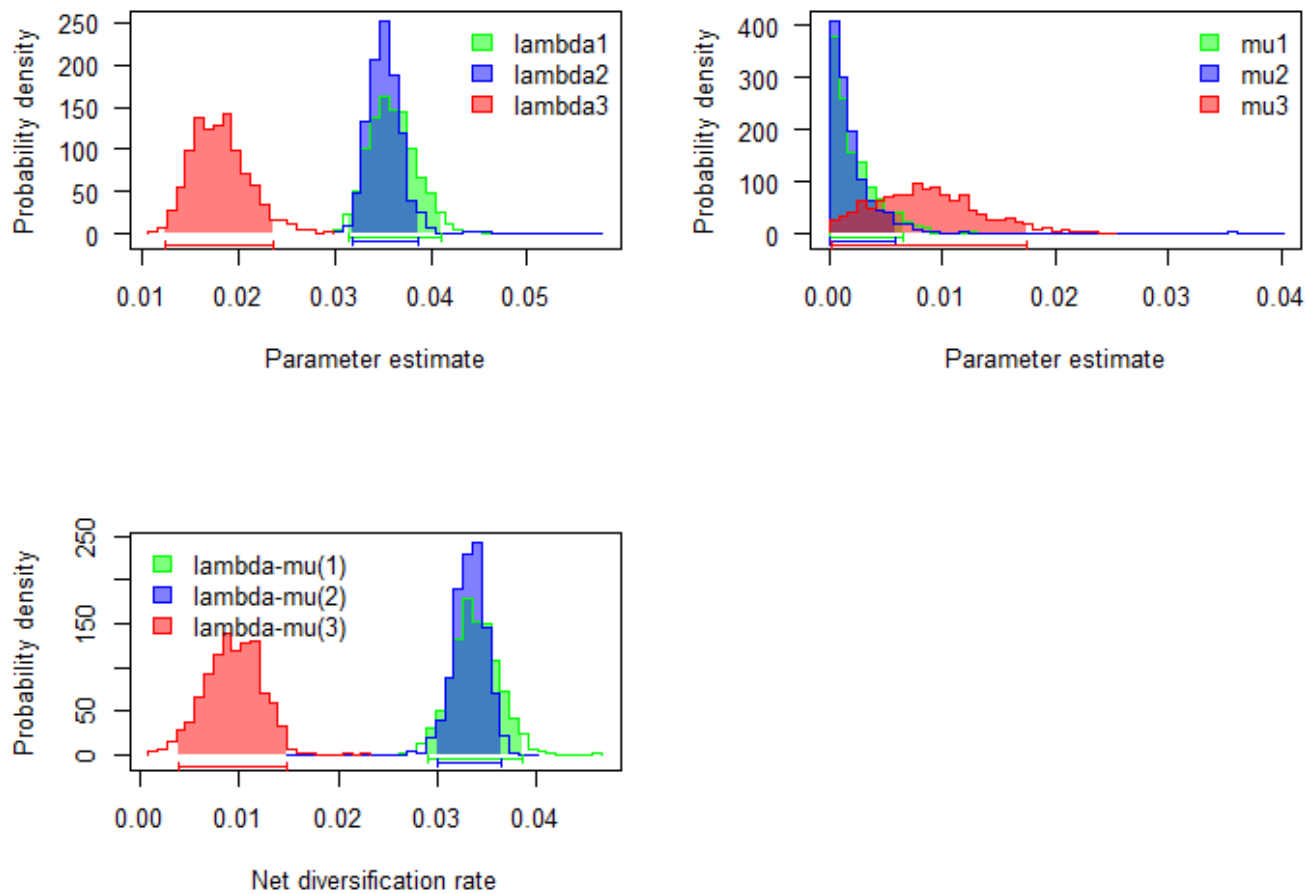


Fig 5 Posterior distributions of the speciation, extinction and diversification rates of species in the trophic guilds in the topical climate (green = herbivores, blue= omnivores, red = carnivores).

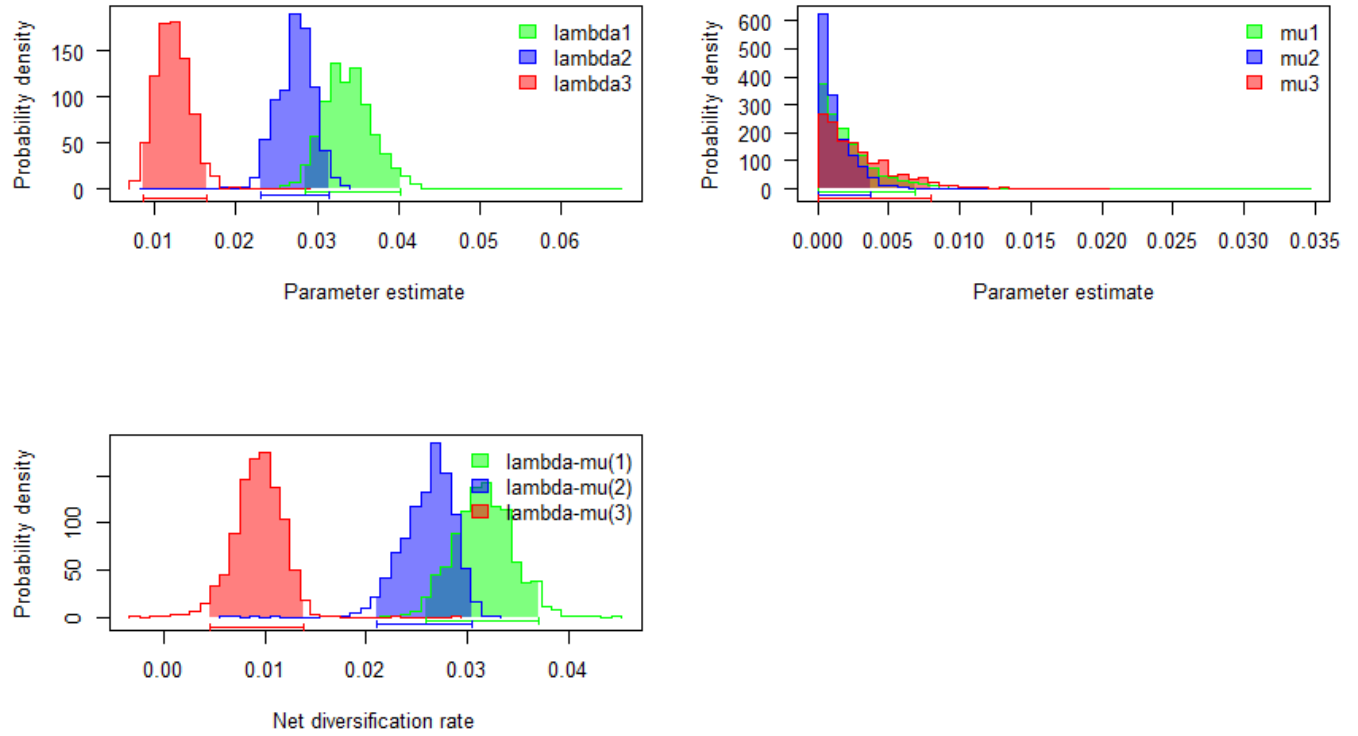


Fig 6 Posterior distributions of the speciation, extinction and diversification rates of species in the trophic guilds in the temperate climate (green = herbivores, blue= omnivores, red = carnivores).

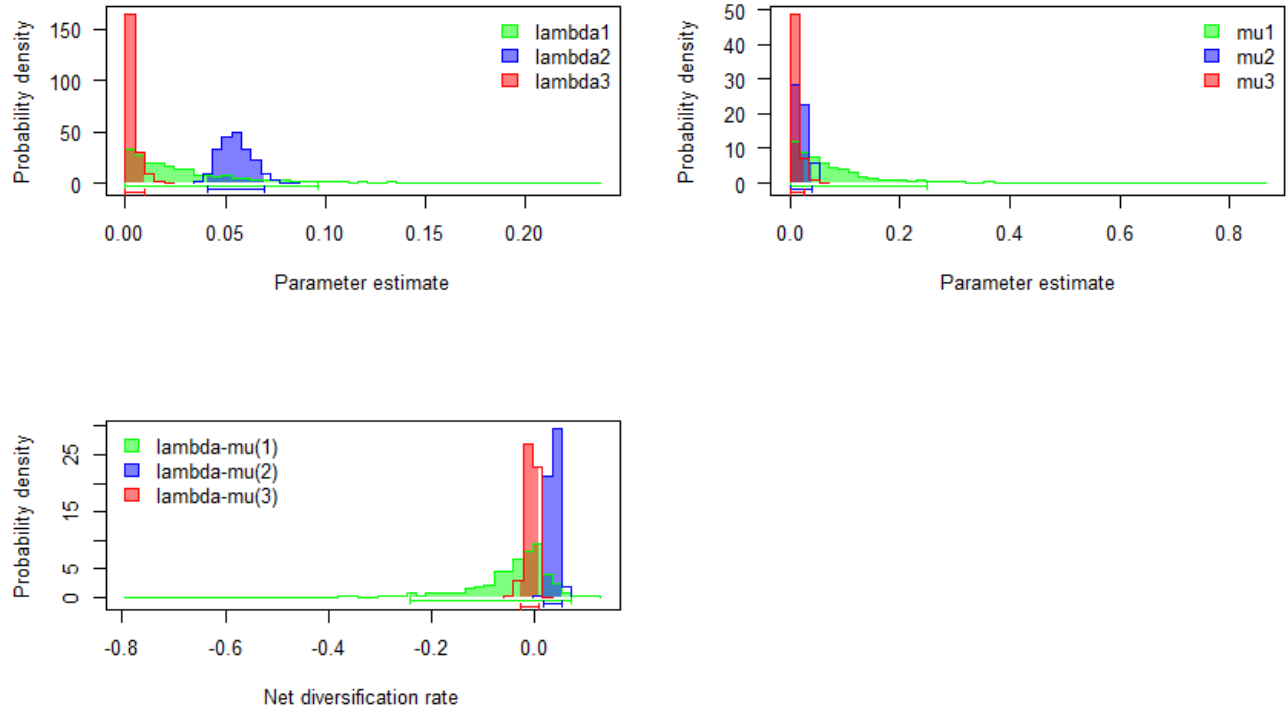


Figure 7 Transition rates among trophic guilds for both tropical and temperate species.

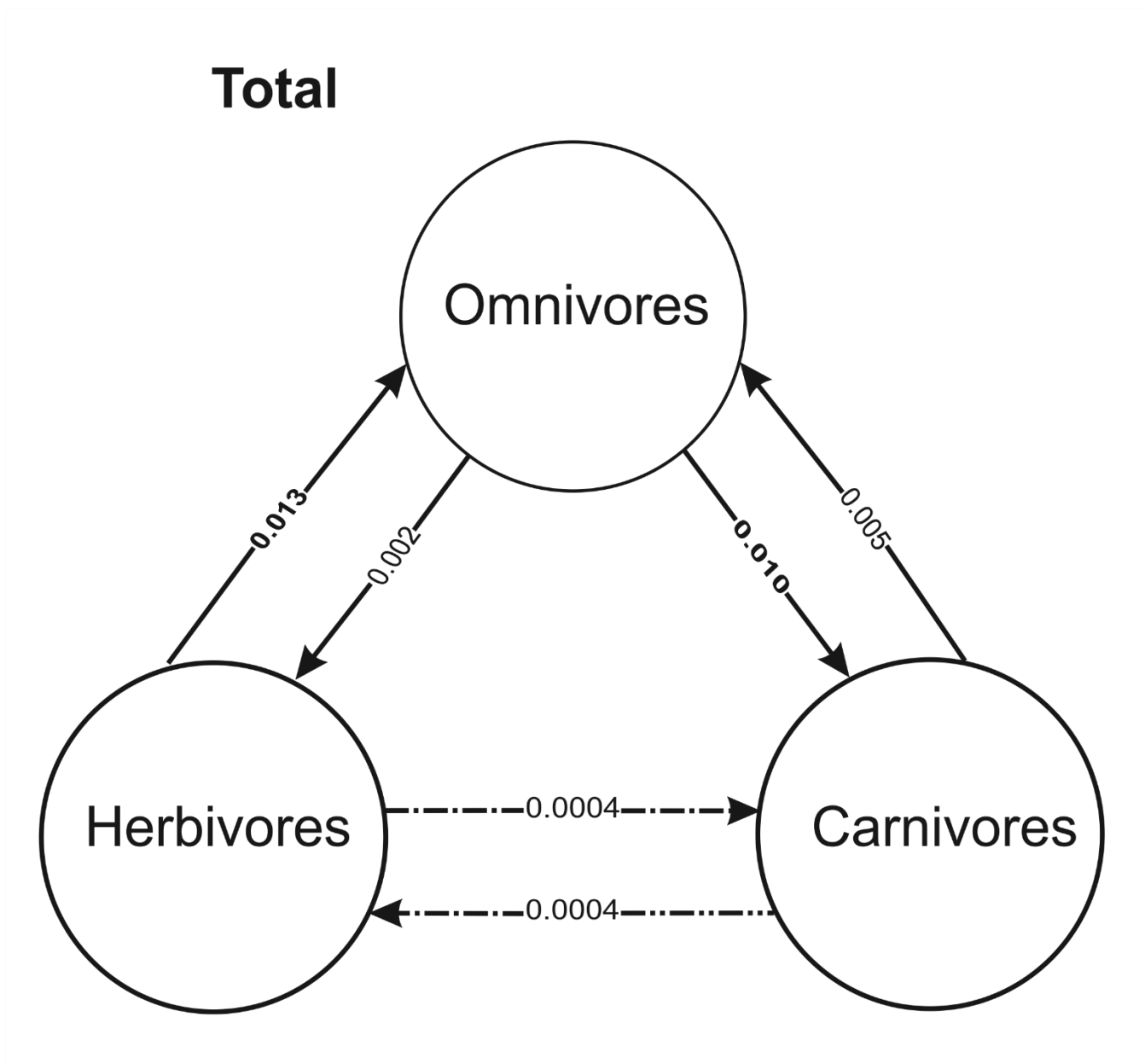


Figure 8 Transition rates among trophic guilds for tropical species.

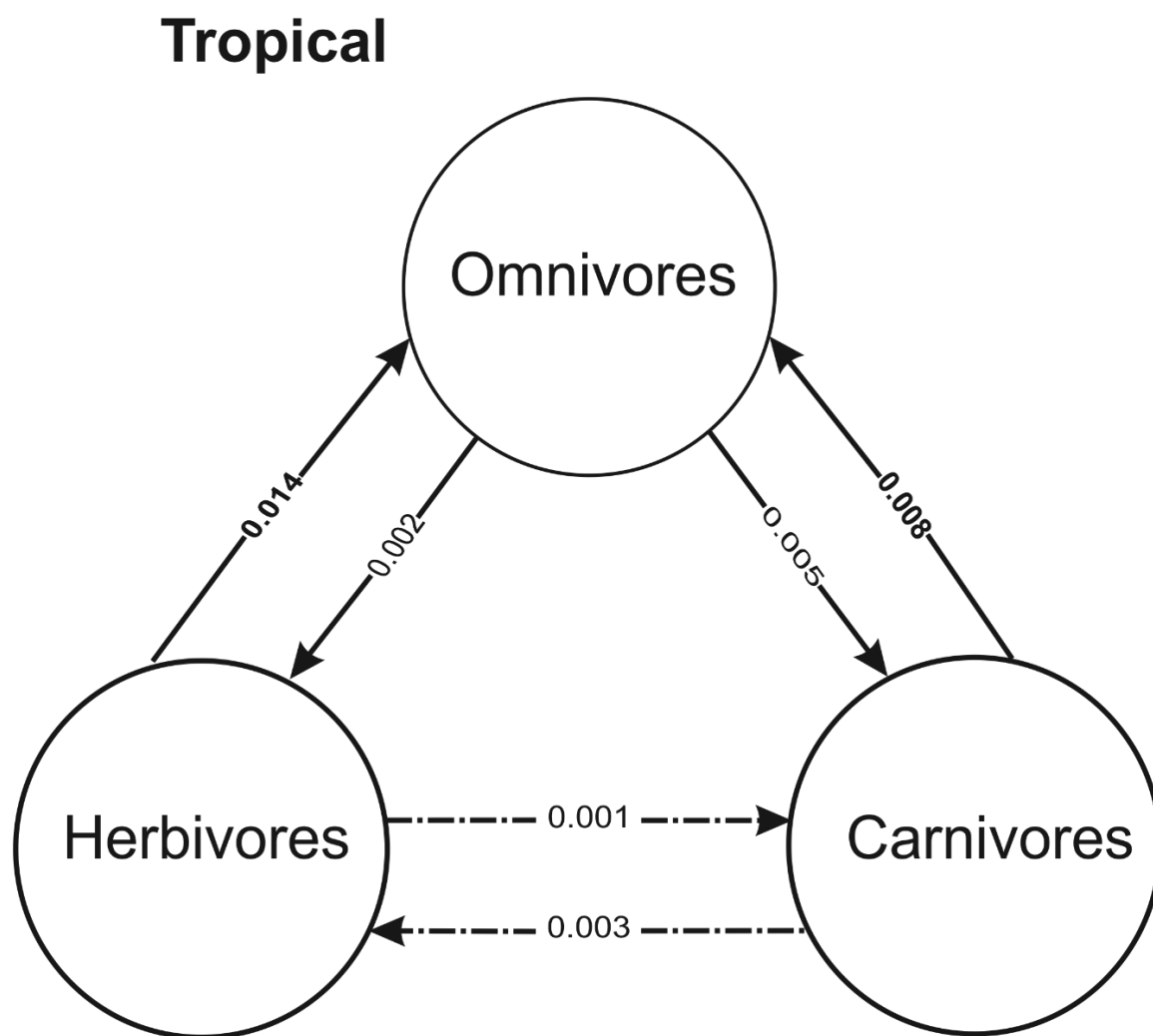
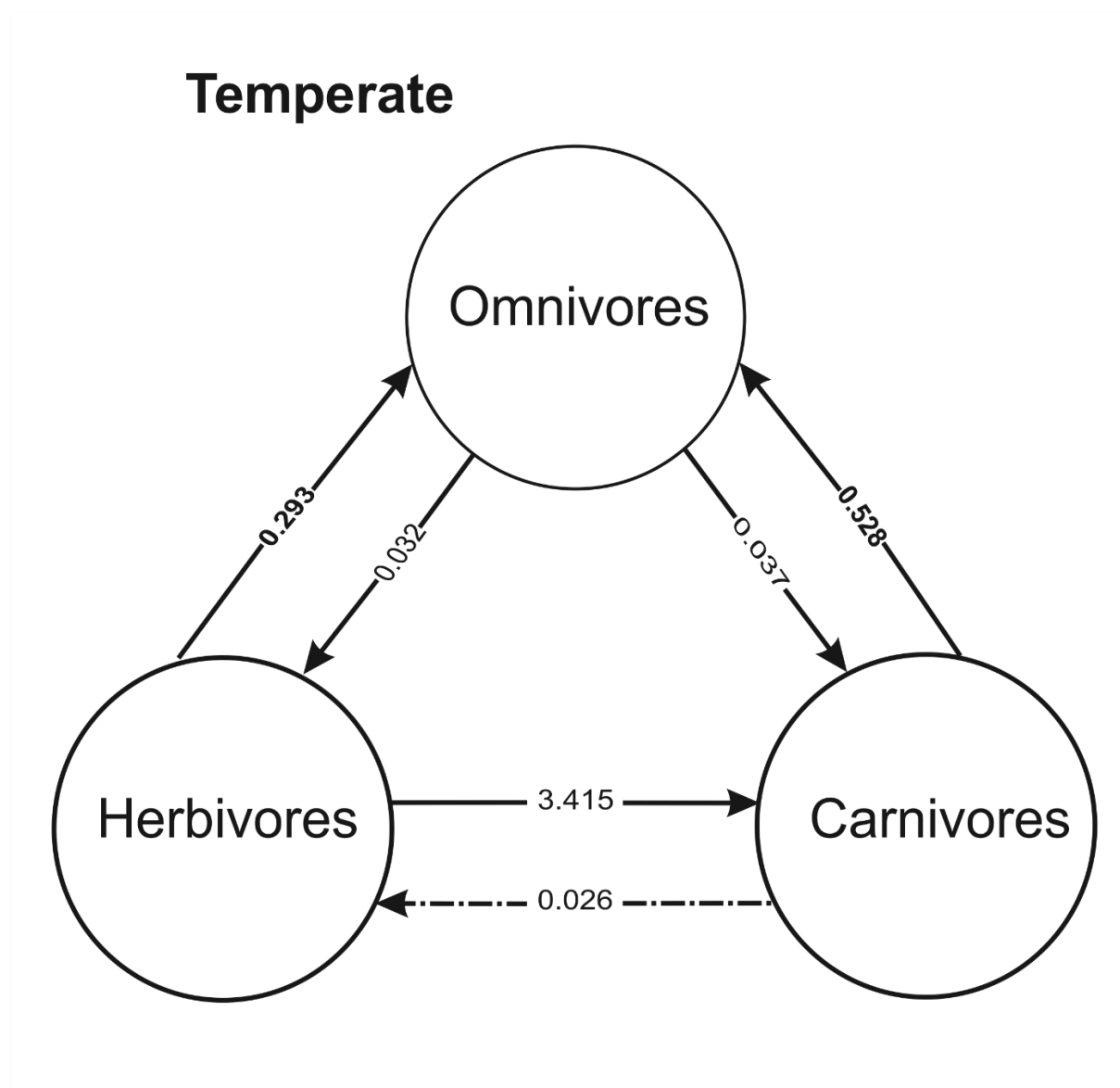


Figure 9 Transition rates among trophic guilds for temperate species.



Discussion:

I found out that omnivores are the most common guild both in the tropical and the temperate climate, a possible driver for this pattern is the tendency of fish species to undergo ontogenetic niche shifts with young small individuals within a species occupying low trophic positions and older large individuals feeding high in the food web (Dalponti et al 2018), due to the data collection methodology ((Froese et al., 2014)Froese et al. 2014), trophic position for a species is a measurement of items consumed by different individuals within populations including both young and adults, therefore the representation of trophic position tends to be the mean of trophic positions occupied by the individuals so, in size-structured populations, median trophic positions, which fall within the omnivore range tend to be more common, despite these caveats mean trophic position can still be used as an indicative of the trophic guild occupied by a species as mean trophic position and maximum trophic position are strongly correlated (Stergiou and Kapouzi 2001, Dalponti et al. 2018). The most striking difference between the tropics and the temperate regions lay, therefore when I consider the guilds of herbivores and carnivores, as expected I found a bigger proportion of herbivores in the tropics and that of carnivores in the temperate regions, which is an indicative that climate is an important driver of the feeding ecology in fish species, possibly due to ecological opportunities in warmer regions and metabolic constraints in colder regions (Ferrera et al. 2004).

The results show that dietary guild has a strong effect on diversification rates, with the diversification models indicating that speciation is lower for carnivores in relation to herbivores and omnivores while extinction rates are similar for all trophic guilds leading to lower diversification rates for carnivores, a pattern that is followed in the tropical regions, in the temperate region omnivores have higher speciation rates than carnivores and similar extinction rates leading to slightly higher diversification for omnivores in relation to carnivores with

estimated diversification rates for herbivores overlapping those of the two other guilds. The higher commonness of herbivores and omnivores in the tropical climate when compared with the temperate climate may therefore, be linked to overall higher speciation rates within the guilds that consume resources lower in the food web while in the temperate climate these guilds show higher extinction when compared to their tropical counterparts, these findings are in agreement of recent models of reef fish evolution which show higher evolutionary rates for large herbivores (Siqueira et al 2020), showing that this pattern also holds when considering non-reef fish species.

When both the global and the tropical regions diversification dynamics are considered we note that the speciation rates for carnivores is lower than that for omnivores and herbivores but still there is a considerable proportion of carnivores even in the tropics which may seem intriguing as there is a tendency for lineages with low evolutionary rates to disappear or have a reduced diversity due to species sorting in a deep-time scale (Leibold et al. 2004, Jablonski 2006), we might hypothesize that when considering that extinction rates do not vary among trophic guilds we can argue that diversification is stable hence there's no trend towards a change in the proportion of trophic guilds with a reduced diversity of carnivores with time as all guilds have positive net diversification rates (Burin et al. 2015).

Regarding the results of the transition rates, I found overall above average transitions towards omnivores in all case scenarios, omnivores have been found to be an “evolutionary sink” for birds (Burin et al 2015) with higher transition towards omnivores coupled with higher extinction and negative net diversification. In this study I found out that diversification for omnivores were positive therefore not compatible with a pattern of “evolutionary sink”, analyzing the results for the dataset with all species we observe that transitions follow a linear

pattern from herbivores to carnivores through omnivores, in this case the guild of omnivores can be viewed as a intermediate guild.

Considering the dynamics of speciation, extinction and diversification along with transition rates for trophic guilds among tropical and temperate regions I argue that the proportion of species occupying different trophic positions is determined by macroevolutionary dynamics irrespective to the climatic region in which species are diversifying, possibly driven by both environmental conditions and metabolic effects of climate. Evolution towards low trophic positions appears to be more likely to occur in the tropical regions possibly due to the availability of vegetal matter, easier digestibility of algae and plant materials (Violle et al. 2007, Díaz et al 2013, Stuart-Smith et al 2013, Carvalho et al 2015, Bakker et al. 2016, Gravel et al. 2016). and the higher metabolic rates associated with warmer temperatures (Gillooly et al. 2001, Brown et al. 2004), driving fish species to feed on food resources richer in carbon (Forster et al. 2012, Boersma et al. 2016), reversibly these same effects would cause extinction rates for herbivores in the temperate regions to increase, as feeding on producers in these regions would be difficult due to smaller availability of resources and even when possible, require digestive adaptations to cope with slower digestion related to colder climates (Ferrera et al. 2014, Boersma et al. 2016, Moody et al. 2019).

In summary, the usage of state-dependent speciation and extinction models of species diversification helped us shed light on the evolutionary roots for the prevalence of herbivory in the tropics

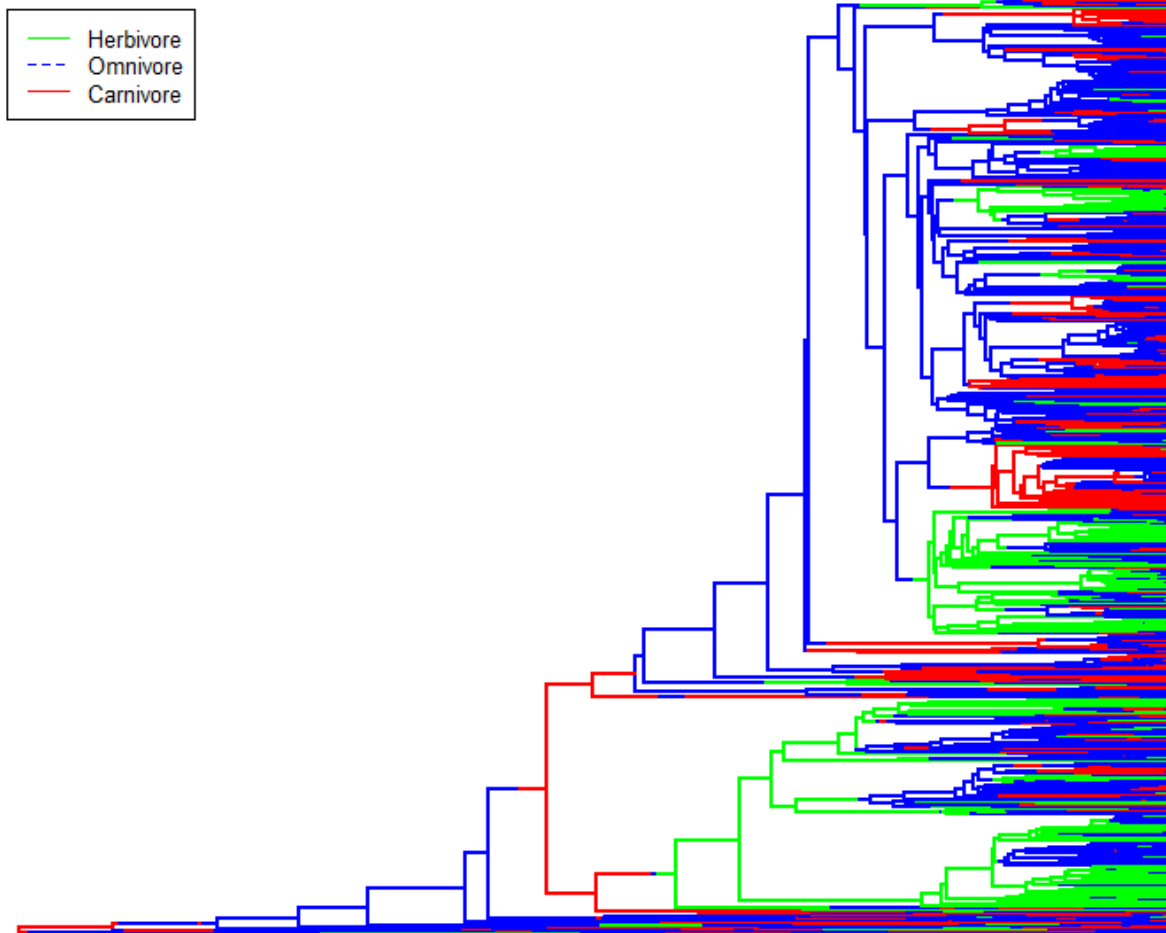
Appendix 1:

Speciation, Extinction and Diversification of trophic guilds in the tropical and temperate climates.

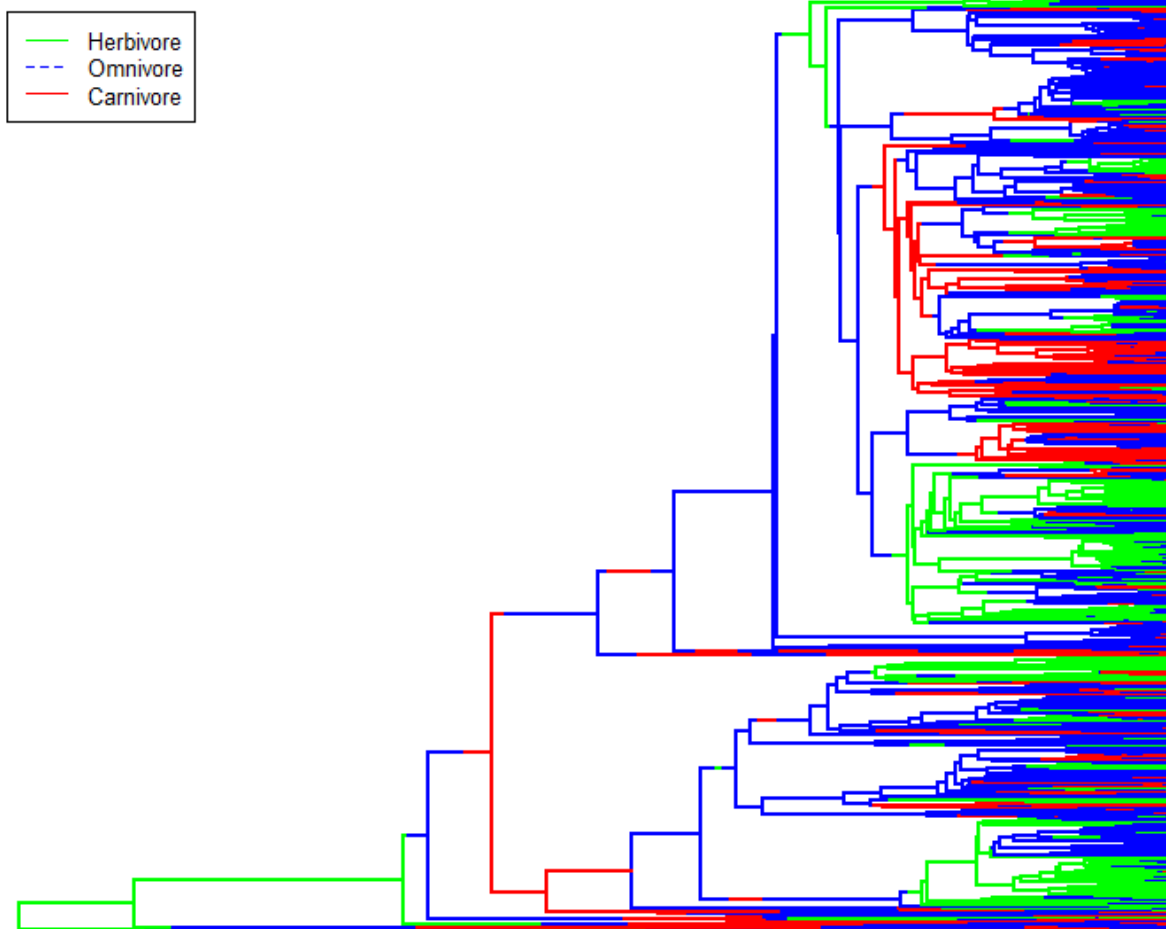
Climate	Trophic Guild	Speciation (λ)	Extinction (μ)	Diversification ($\lambda-\mu$)
Total	Herbivore	mean=0.036 sd=0.002	mean=0.002 sd=0.002	mean=0.033 sd=0.002
	Omnivore	mean=0.036 sd=0.002	mean=0.002sd=0.003	mean=0.033sd=0.001
	Carnivore	mean=0.018 sd=0.002	mean=0.008 sd=0.004	mean=0.009 sd=0.002
Tropical	Herbivore	mean=0.033 sd=0.003	mean=0.002 sd=0.002	mean=0.031 sd=0.002
	Omnivore	mean=0.027 sd=0.002	mean=0.001 sd=0.001	mean=0.026 sd=0.002
	Carnivore	mean=0.012 sd=0.002	mean=0.002 sd=0.002	mean=0.009 sd=0.002
Temperate	Herbivore	mean=0.03 sd=0.031	mean=0.081 sd=0.102	mean=-0.05 sd=0.102
	Omnivore	mean=0.055 sd=0.007	mean=0.018 sd=0.012	mean=0.036 sd=0.008
	Carnivore	mean=0.003 sd=0.003	mean=0.009 sd=0.008	mean=-0.006 sd=0.008

Appendix 2

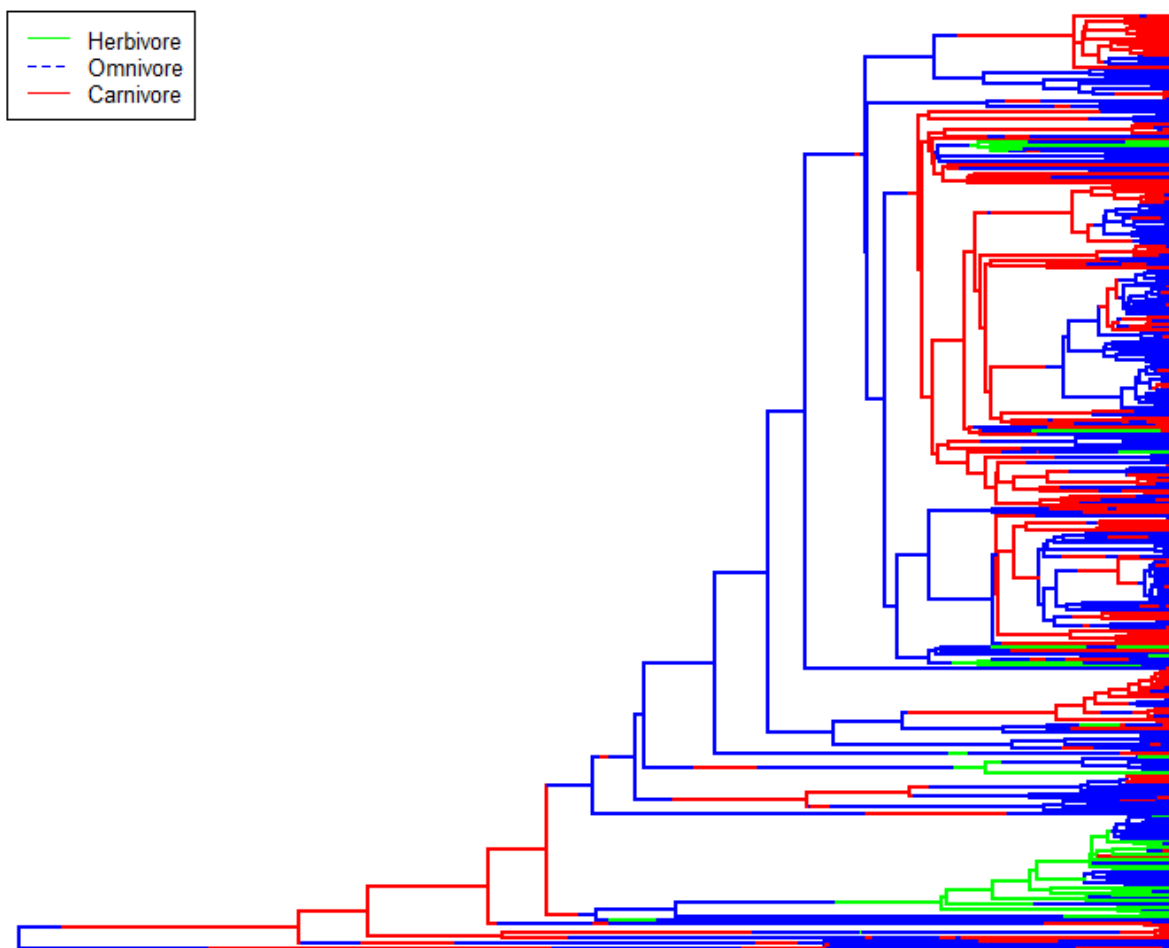
A - phylogenetic evolutionary tree with mapped transitions of feeding guilds for all species.



B - phylogenetic evolutionary tree with mapped transitions of feeding guilds for tropical species.



C - phylogenetic evolutionary tree with mapped transitions of feeding guilds for temperate species.



General Conclusions:

In the three chapters of this thesis I addressed important drivers of the trophic position of fishes, in the first chapter I found an overall positive association between body size and trophic position for fish species as well as for individual fishes in the temperate region reinforcing the idea that fishes undergo ontogenetic trophic niche shifts and higher trophic position amplitude observed for large fish species is driven by the ample variance of sizes these species go through from birth to complete development. In the second chapter I looked at the evolutionary roots for the positive body size- trophic position relationship adding the effect of climate and environment, I concluded that in the temperate regions and marine environments the evolutionary correlation of body size and trophic position is stronger and that this pattern is possibly caused by the higher proportion of herbivores in the tropics. In the third chapter I investigated the evolutionary dynamics that lead to the occurrence of a larger number of herbivores in the tropics in comparison to the temperate regions, drawing the conclusion that higher speciation of herbivores in the tropics and higher extinction of herbivores in the temperate regions are strong candidate drivers on this pattern.

These ideas reinforce that metabolic, climatic and environmental conditions are all important determinants of the trophic position of fishes, as seen in the first chapter body size constitutes a good predictor of the trophic position in most cases for temperate fish, species and individual wise but as seem in some species, behavior may also play a strong role, omnivorous territorial species, for example, may have their trophic position determined by the availability of resources within the plot they live in as demonstrated by the correlations between body size and trophic position for flatfish species in which I found individuals of the same size that presented very different trophic positions, this divergence of trophic positions for individuals of the same size seems to be more evident for larger individuals as small individuals are constrained by

physical limitations that prevent them from preying on big preys and consequently occupying higher trophic positions, therefore even as I find a strong body size – trophic position relationship for most species, meaning that I can reasonably say that bigger fish species occupy higher trophic positions as well as bigger individuals within species there are also many attributes to be considered and the study of fish biology and behavior is fundamental to make guided assumptions about trophic ecology of fishes as functional attributes that are not related to body size may also drive the trophic positions of fishes e.g. mouth morphology and specialized gut flora. In summary I argue that, for temperate fishes, a size-structured food web is a reasonable model for trophic ecology, although there are exceptions most of them seem to be related to ecological opportunities and resource availability, the main trend and the best strategy for temperate fish stills seems to be feeding on the largest prey possible, consequently on the immediate trophic level below them.

When considering the effects of climate and environment on the body size - trophic position relationship I found out that this relationship is stronger in the temperate regions and marine environments, with no relationship at all in the freshwater environments of tropical regions, this pattern seems to be related to an evolutionary correlation between body size and trophic position as I found out that these traits usually evolve in a correlated direction in temperate climates and not in the tropics, a good way to picture this evolutionary correlation is considering that if a fish clade tends to evolve to bigger sizes it also tends to evolve to higher trophic positions in the temperate regions while if a clade is in the tropics it has similar chances to evolve higher or lower trophic positions, I also found out that an important driver of this pattern is the higher number of herbivores in the tropics, especially large body-sized ones, which are absent in the temperate regions. As seen in the third chapter this pattern of a higher number

of herbivores in comparison to carnivores in the tropics might be caused by higher speciation rates and net diversification of herbivorous lineages in these regions, possible drivers of these macroevolutionary dynamics are ecological opportunities for herbivorous species in the tropics and metabolic rates that drive carbon consumption making diversification of lineages that feed low in the food web more common, differently than in the temperate regions where the consumption of nutrient-rich resources is preferred and herbivory might slow diversification.

I believe that the results presented in this thesis, as well as the discussions of its implications and possible underlying mechanisms of the patterns I have found might be interesting for researchers on trophic ecology of fishes as well as the broad public interested in macroecology and macroevolution, helping better understand the complex body size – trophic position relationship of fishes as well as highlighting the importance of climate and environment on the trophic positions occupied by fish species.

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