



Community Assembly Processes as a Mechanistic Explanation of the Predator-Prey Diversity Relationship in Marine Microbes

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Predator and prey α -diversities are often positively associated; yet, understandings of the underlying mechanisms require manipulative experiments and thus remain unclear. We attempt to address this issue by deciphering how α -diversity of predator and prey influences each other's community assembly processes, which subsequently determine their α -diversity. The occurrence of assembly processes was indicated by the mean pairwise taxonomic index within a community (α MPTI), assuming assembly processes left traceable imprints on species' phylogeny. Specifically, α MPTI quantifies deviations of observed phylogenetic distances from that of random, so that it can be used to hint at the occurrence of non-random/deterministic assembly processes. Larger α MPTI of a community implies the occurrence of weaker homogenizing deterministic assembly processes, which suggests that this community might be comprised of less similar species and thus has higher α -diversity. We hypothesize that higher predator and prey α -diversity would be positively associated with each other's α MPTI, which would then be positively associated with their α -diversity. To test the hypothesis, we calculated Shannon diversity and α MPTI for heterotrophic nanoflagellates (HNF; predator) and bacteria (prey) communities in the East China Sea (ECS). The HNF Shannon diversity was found to be positively associated with α MPTI of bacteria, which was then positively associated with bacterial Shannon diversity. In contrast, bacterial Shannon diversity did not correlate with HNF's α MPTI. We argue that top-down control is one of the explanations to the positive α -diversity association among trophic levels in microbes of the ECS.

Keywords: biodiversity, community assembly processes, homogeneous versus heterogeneous selection, predator-prey diversity relationship, phylogeny

INTRODUCTION

The α -diversities of predator and prey communities are often found to be positively associated in natural systems (Haddad et al., 2009). To explain this positive association, studies have been conducted, including observational (Yang et al., 2018) and experimental (Haddad et al., 2009) studies as well as meta-analyses (Castagneyrol et al., 2012). The mechanisms proposed by these studies can be classified into three categories. The first one is that predator and prey α -diversities respond to the same external forces in the same direction so that they are positively correlated (e.g., Hawkins and Porter, 2003; Axmacher et al., 2009). The other two are related to trophic interactions between the predators and prey (Hunter and Price, 1992; Power, 1992) and can be further categorized into top-down or bottom-up control mechanisms. The top-down control mechanisms occur when predators either directly suppress the dominant prey and prevent competitive exclusion (Leibold, 1996; Proulx and Mazumder, 1998) or indirectly create an environment that fosters the diversity of prey (Borer et al., 2014). In contrast, bottom-up control mechanisms take place, while more diverse prey community provides greater diversity (Hutchinson, 1959; Southwood et al., 1979) or greater amount (Siemann, 1998; Srivastava and Lawton, 1998) of resources to promote predator diversity. These three mechanisms are not easy to disentangle because they can act jointly to determine diversity associations between predator and prey in nature.

To unveil the causes underlying the positive association between predator and prey α -diversities, manipulative experiments that include multiple trophic levels are often required (e.g., Scherber et al., 2010; Hertzog et al., 2016). Conducting this kind of complex and long-term experiments often costs large amount of labor and resources. Consequently, despite many efforts, identifying and disentangling the mechanisms remains challenging.

To address this issue, we propose an analytical framework that quantifies community assembly processes of predators and prey to decipher the bi-trophic diversity association. The community assembly processes are inferred from the degree of relatedness among species, i.e., phylogenetic similarity, within a community (Webb et al., 2002; Cavender-Bares et al., 2009) because phylogenetic similarity is considered as an imprint left by evolutionary and ecological processes (Mouquet et al., 2012; Gerhold et al., 2015). These community assembly processes have been synthesized in Vellend's conceptual synthesis of community ecology (Vellend, 2010; Götzenberger et al., 2012), including four fundamental processes – ecological drift, selection, speciation, and dispersal. We propose to use phylogenetic similarity within a community as a hint of the occurrence of these processes that collectively determine the species composition and thus the diversity of a community (Logares et al., 2018).

Specifically, the analytical framework, we proposed here consists of two steps (Figure 1) to investigate mechanisms underlying the α -diversity association between predator and prey. First, we investigate how predator's (or prey's) α -diversity affects assembly processes of the other community. Then, we examine how the assembly processes of prey (or predator) community are associated with their own α -diversity.

When we find significant effect of predator's α -diversity on prey's assembly processes, which are then significantly associated with the α -diversity of prey, we infer that top-down control mechanisms are likely to be responsible for the bi-trophic diversity association. On the other hand, significant association of prey's α -diversity and predator's assembly processes along with significant association between predator's assembly processes and α -diversity would evidence bottom-up control mechanisms. When none of the above is found, the predator-prey diversity association may be a result of their congruent responses to the same external forces.

The first step of the analytical framework is to investigate the roles of predator and prey α -diversities in each other's assembly processes. Here, we mainly focus on the two unambiguously deterministic processes, i.e., selection and speciation. We chose to make inferences based on deterministic processes because they result from species' different responses given a set of biotic and/or abiotic environment, including predator-prey interactions (Vellend et al., 2014). The deterministic processes could thus be used to represent how those biotic and/or abiotic environments affect each other's community diversity. In contrast, ecological drift is not our focus because it represents the random/stochastic events governing the presence of species in a community rather than predator-prey interactions (Hubbell, 2001). We also restrict ourselves from making inferences based on dispersal because dispersal could be deterministic or stochastic depending on whether species differ in dispersal ability or respond idiosyncratically to dispersal force (Nemergut et al., 2013; Lowe and McPeck, 2014). Consequently, in this study, we only investigate how the deterministic assembly processes of predator and prey community are affected by each other's α -diversity.

After clarifying the effects of predator and prey α -diversity on each other's deterministic assembly processes, we proceed to examine how the deterministic processes are associated with their own community diversity. Deterministic processes are positively or negatively associated with community diversity because those processes can weakly or strongly homogenize the community, respectively (MacArthur and Wilson, 1967; Zhou and Ning, 2017). When the deterministic processes weakly homogenize the community *via* selecting for different species and/or promoting speciation, species that are less similar to each other comprise a community. Such weak homogenizing deterministic processes should be positively associated with community diversity. On the other hand, when the deterministic processes impose consistent selection pressure to select for similar species or prevent speciation in a community (e.g., Dini-Andreote et al., 2015), species that are more similar to each other comprise a community. Such strong homogenizing processes should be negatively associated with community diversity. This second step in our analytical framework examines how the deterministic assembly processes (i.e., weak or strong homogenizing the community) is associated with community diversity. This framework can be used to deconstruct the positive α -diversity association in order to discern whether the positive association stems from the top-down control mechanisms or the bottom-up control mechanisms (Figure 1).

We apply this two-step analytical framework to deconstruct the α -diversity association between heterotrophic nanoflagellates

(HNF) as the predators and bacteria as prey in the marine planktonic system of southern East China Sea (ECS). A previous study in the ECS has found a positive association between the α -diversity of HNF and bacteria, even after accounting for confounding environmental factors (Yang et al., 2018). According to our analytical framework, the positive α -diversity can result from the occurrence of either top-down control or bottom-up control, or both, mechanisms. When either mechanism occurs, the diversity of one trophic level is expected to make the deterministic processes weakly homogenizing the other community and thus lead to higher diversity of the other community. We thus hypothesize that the positive α -diversity association between bacteria and HNF results from the occurrence of either top-down control or bottom-up control, or both mechanisms.

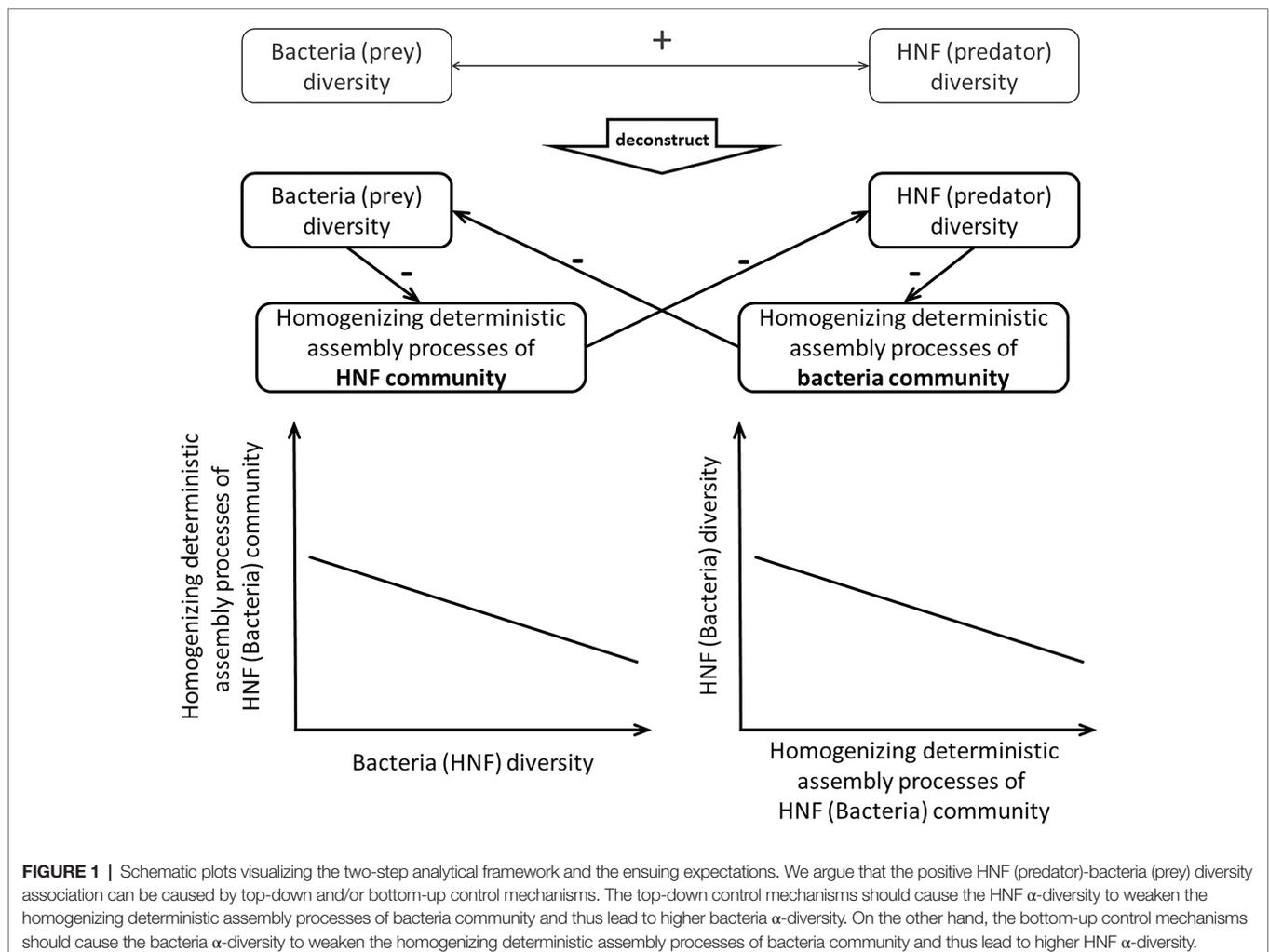
MATERIALS AND METHODS

Microbial Samples and Environmental Variables

Heterotrophic nanoflagellate and bacterial communities were revealed by using sequence data collected in the southern ECS

from 14 cruises in the period of April 2014 to July 2017. In each sampling cruise, we visited the same six stations along a transect in the southern ECS (**Supplementary Figure 1**). Thus, a total of 84 samples each for HNF and bacteria were included in analysis. At each sampling, GoFlo bottles (General Oceanics) mounted on a conductivity, temperature, and depth profiler (CTD profiler, Sea-Bird Electronics, Bellevue, WA, United States) were used to collect 20 L of seawater from 5 m beneath surface. The seawater was first pre-filtered through a screen mesh with 20 μm openings to remove large organisms like zooplankton. The pre-filtered seawater was sequentially filtered onto 1.2 μm -pore-size filters (Millipore Isopore™ hydrophilic polycarbonate membrane) to collect nanoflagellates and then onto 0.2 μm -pore-size filters (Millipore Isopore™ hydrophilic polycarbonate membrane) to collect bacteria (Yang et al., 2018). After filtration, both the 0.2 and 1.2 μm -pore size filters were stored in liquid nitrogen and then at -20°C until molecular analysis (Yang et al., 2018).

Environmental variables, including temperature, salinity, and photosynthetic active radiation, were recorded by the CTD profiler. In addition, seawater samples for chlorophyll-a concentration as well as nutrient variables, including nitrite,



nitrate, and phosphate concentrations, were collected and measured according to the standard methods developed by Gong et al. (2003).

DNA Extraction, Sequencing and Sequence Processing

We briefly introduced how we extracted DNA and analyzed sequences in this section (detailed methods are explained in **Supplementary Material 1**). Total DNA was extracted separately from the 0.2 and 1.2 μm -pore size filters with the PowerWater DNA Extraction Kit (PowerWater, Qiagen) according to the manufacturer's instructions. DNA extracts from the 0.2 to 1.2- μm -pore size filters were used as templates of PCR to amplify the 16S rRNA gene for prey and 18S rRNA gene for predators, respectively. PCR was performed in two steps to gain better reproducibility and consistent results (Berry et al., 2011); see **Supplementary Material 1** for details of the two-step PCR procedures. After obtaining 16S and 18S rRNA gene sequences, the DADA2 pipeline was used for quality filtering and assembling sequences into amplicon sequence variant (ASV; Callahan et al., 2016a; see **Supplementary Material 1.2** for sequence merging procedures). Taxonomy assignment was performed on ASVs to recognize and select for predators from 18S rRNA gene and prey from 16S rRNA gene. From 18S rRNA gene, the Protist Ribosomal Reference database (PR2) database (Guillou et al., 2012; Vaultot and Guillou, 2019) was used to recognize taxonomy. Those belonging to the HNF taxonomy were further selected as the predators (see **Supplementary Table 1** from Yang et al. (2018) for the list of HNF taxonomy). From 16S rRNA gene, the Silva 132 database (Quast et al., 2013) was used and only those classified under the bacteria kingdom were selected as prey. Finally, in order to obtain the phylogeny, we used maximum likelihood method (with negative edges length = 0; Callahan et al., 2016a) to build phylogenetic trees for bacteria and HNF from 16S rRNA gene and 18S rRNA gene of all cruises, respectively.

Quantifying Diversity of Predator (HNF) and Prey (Bacteria)

Before calculating the Shannon diversity index of HNF (predators) and bacteria (prey), each community was resampled once to achieve the same number of reads among stations, which were 331 for HNF and 13,129 for bacterial communities. The rarefaction yielded 93.76 ± 3.81 and $97.91 \pm 0.69\%$ sample coverage for HNF and bacterial communities, respectively (**Supplementary Figure 2**). Although this procedure addresses the disparity issue, i.e., unequal reads among stations, it is not appropriate when comparing the relative abundance of AVSs across stations (McMurdie and Holmes, 2014). Therefore, in order to have a fair among-station comparison, we applied method of Chao et al. (2014) to rarefy and estimate the expected Shannon diversity index of both HNF and bacteria communities for the following analyses (Chao and Chiu, 2016; Hsieh et al., 2016).

Inferring Community Assembly Processes

To hint the community assembly processes experienced by each HNF and bacteria community, we calculated the α mean pairwise taxonomic index (αMPTI). The αMPTI is akin to

Webb's net relatedness index (NRI; Webb, 2000; Webb et al., 2002), which quantifies the deviation of the observed mean pairwise phylogenetic distance (MPD_{obs}) from a null distribution of mean pairwise phylogenetic distance (MPD). The MPD_{obs} was the mean branch length among all pairs of species within each community. The null distribution of MPD was generated by random processes so that the distribution represented the values of MPD if a community is assembled by completely random processes, e.g., ecological drift. The deviation of MPD_{obs} from the null thus represents the non-random/deterministic processes by which a community is assembled. To generate a null distribution of MPD by random processes, we first randomly shuffled the phylogeny (i.e., shuffled the tips of the phylogenetic tree) of all species within a community (i.e., each cruise-station). With the randomized phylogeny, we calculated MPD of each community. Repeating this randomization technique 999 times, we generated the null distribution of MPD . Finally, $\alpha\text{MPTI} = (MPD_{\text{obs}} - \text{mean}MPD_{\text{null}}) / \text{sd}MPD_{\text{null}}$, where $\text{mean}MPD_{\text{null}}$ represents the mean of the null distribution of MPD , and $\text{sd}MPD_{\text{null}}$ represents the SD of the null distribution of MPD .

When calculating αMPTI , we did not multiply -1 as in the NRI calculation (Webb, 2000; Webb et al., 2002). Therefore, the sign of αMPTI should more intuitively represent whether the observed phylogenetic distance is more different or less different from random. A positive value of αMPTI of a community means that species are phylogenetically more different than expected by random. Accordingly, positive αMPTI hints the occurrence of weak homogenizing assembly processes following the same logic, negative αMPTI hints the occurrence of strong homogenizing assembly processes.

α -Diversity Association and Impacts of Community Assembly Processes

Before testing our hypotheses, we first conducted univariate regression modeling to show that HNF and bacteria α -diversity were positively associated. To do so, we performed generalized linear mixed effect model (GLMM) to regress the HNF Shannon diversity on bacteria Shannon diversity, with cruise as the random effect. Here, making cruise as a random effect should account for the temporal autocorrelations among cruises. After confirming the positive association, we proceed to test the hypothesis that HNF and bacteria α -diversity negatively affects each other's deterministic assembly processes and in turn increases each other's α -diversity (**Figure 1**). To do so, we performed two sets of univariate GLMMs to separately test for top-down control mechanisms and bottom-up control mechanisms. Each set of univariate GLMM consisted of two steps corresponding to the two steps of our analytical framework. First, we regressed the αMPTI of bacteria (or HNF) community on the Shannon diversity of HNF (or bacteria) to test how the Shannon diversity of predator (or prey) influenced prey's (or predator's) αMPTI , i.e., community assembly processes. We then regressed the Shannon diversity of bacteria (or HNF) on its own αMPTI to test how the community assembly processes of bacteria (or HNF) determined its Shannon diversity.

The objective of this study is to detect the effects of ecological interactions by statistically accounting for other potential

confounding environmental factors. Therefore, when conducting the two sets of GLMMs, we used backward selections to identify the variables that also have significant effects but did not attempt to make inference from those variables. To conduct backward selection, we first included all available environmental variables in the GLMMs and then step-wisely removed variables that are not significant based on p -values. The environmental variables include temperature, salinity, total dissolved inorganic nitrogen (TN), total dissolved inorganic phosphorous (TP), chlorophyll a (Chla), and photosynthetically active radiation (PAR). In addition, we built Moran's Eigenvector Maps (MEM; Dray et al., 2006, 2012) that are orthogonal vectors to account for the spatial autocorrelations among stations. These spatial eigen-vectors were always included in the backward selection processes in order to account for the effects of dispersal because bacteria and HNF are passive dispersers (Declerck et al., 2013). In all above GLMM analyses, cruise was set as a random effect to avoid spurious correlations simply due to seasonal variation among cruises.

Computation

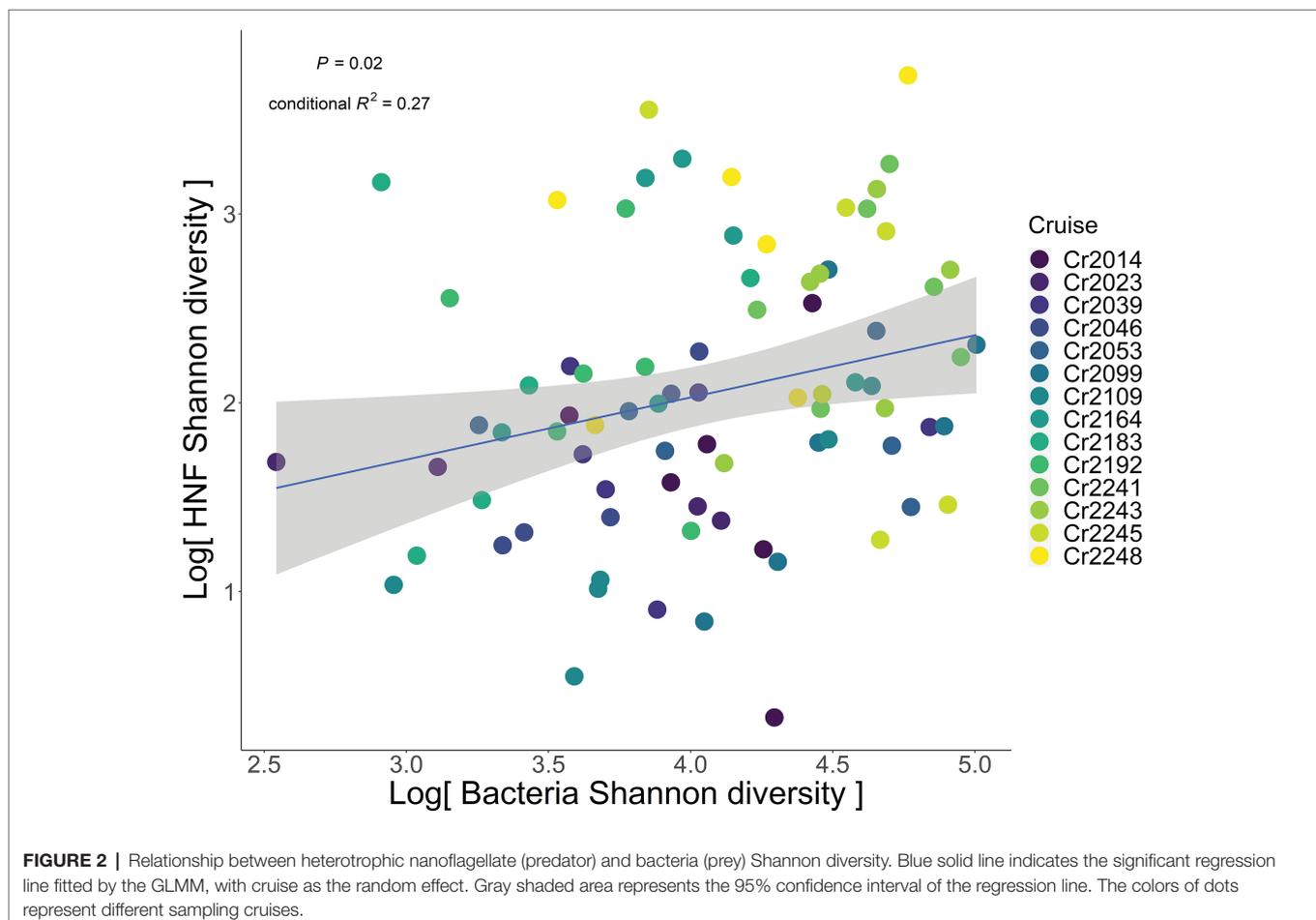
We used the “phyloseq” package to perform sequence subsampling to achieve parity in total number of reads (McMurdie and Holmes, 2013), the “iNEXT” package to perform rarefaction and calculate the Shannon diversity index (Hsieh et al., 2016), the “phangorn” package to build phylogenetic trees (Callahan et al., 2016b), the

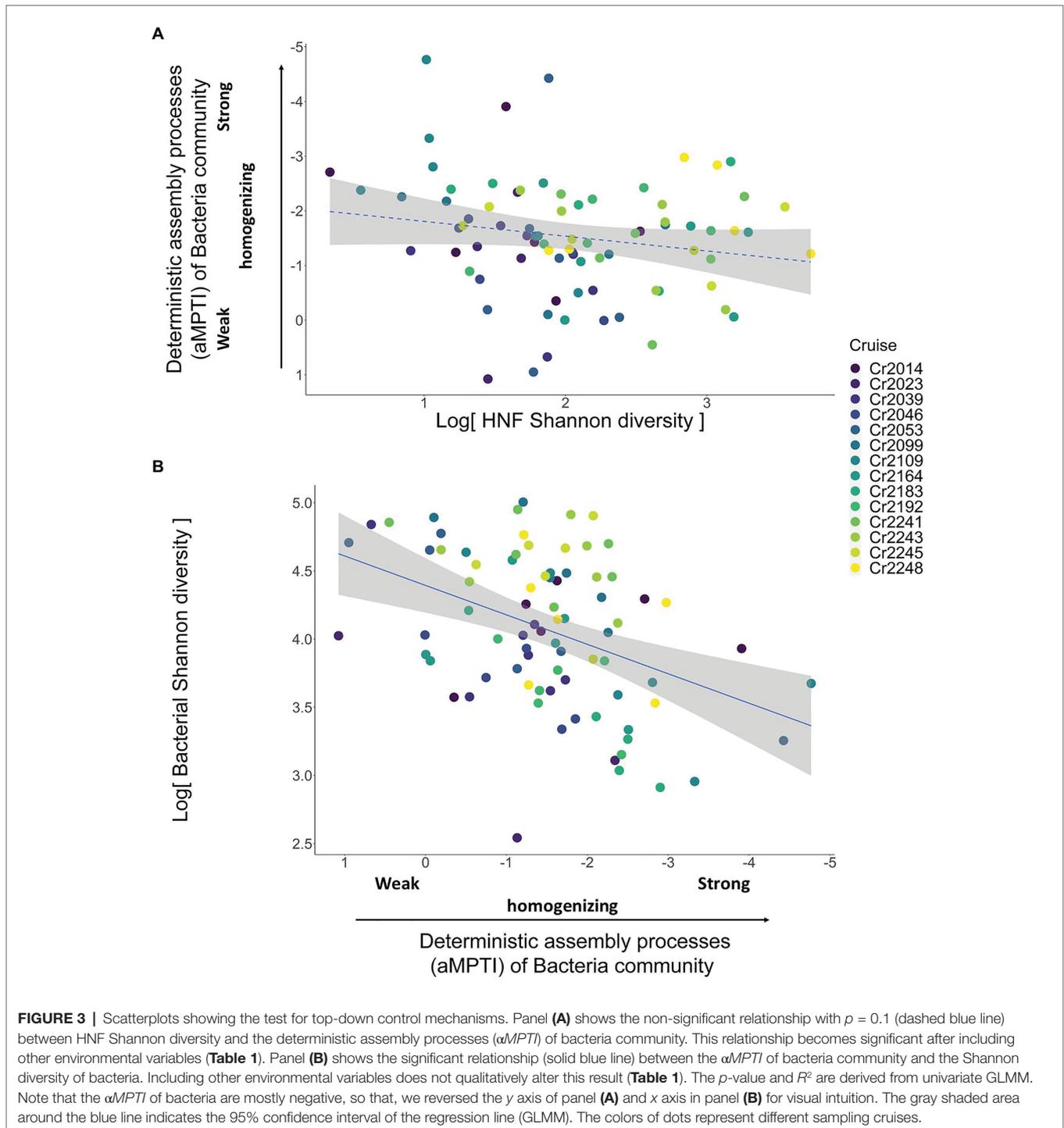
“picante” package to calculate phylogenetic distances to derive α MPTI (Kembel et al., 2010) and the “nlme” package to perform GLMMs (Pinheiro et al., 2019). All packages were built and computation was carried out in R version 4.0.4 (R Core Team, 2020).

RESULTS

Hydrology, HNF (Predator) and Bacteria (Prey) α -Diversities in Southern East China Sea

In the southern East China Sea, temperature and salinity were significantly lower at the most nearshore station than other stations, especially in the spring time ($p < 0.01$; **Supplementary Figure 3**). This reflects the influences of river runoff from the Min River. The river runoff caused the concentrations of total dissolved inorganic nitrogen and phosphorous as well as chlorophyll a to be significantly higher at the most nearshore station than others ($p < 0.01$; **Supplementary Figure 3**), except for the station northeast of Taiwan (station 9; **Supplementary Figure 3**). The region northeast of Taiwan has long been reported to be influenced by the upwelling of subsurface Kuroshio waters that provide a large amount of nutrients to the East China Sea (Wong et al., 2000). Although the hydrology varied in the southern East China Sea,





the HNF ($p = 0.8$) and bacteria ($p = 0.08$) α -diversity did not exhibit such clear spatial variation (Supplementary Figure 3). Rather, we found a negative, but weak ($R^2 = 0.08$), association between HNF Shannon diversity and chlorophyll a concentration (Supplementary Figure 4). This finding suggests that HNF communities might not be strongly affected by abiotic environmental factors (Yang et al., 2018). On the other hand, bacteria Shannon diversity was positively associated with salinity

(Supplementary Figure 4), which is consistent with a previous study (Fuhrman et al., 2008).

α -Diversity Association Between HNF (Predator) and Bacteria (Prey) Community

After accounting for the aforementioned hydrological processes, we found a positive association between the Shannon diversity of HNF and bacteria in the southern ECS (Figure 2). The positive

TABLE 1 | Results of generalized linear mixed effect model (GLMM) after backward selection to test for top-down control mechanisms.

Independent variable	Regression coefficient	Standard error	p-value
Step 1: Bacteria αMPTI as dependent variable			
HNF Shannon	0.34	0.16	0.04
Log (PAR)	0.04	0.02	0.02
Step 2: Bacteria Shannon as dependent variable			
Bacteria α MPTI	0.23	0.04	<0.01

These results indicate that heterotrophic nanoflagellate (HNF) Shannon diversity positively affects the α mean pairwise taxonomic index (α MPTI) of bacteria community after accounting for other confounding environmental factors. α MPTI of bacteria community in turn increases the bacteria Shannon diversity.

TABLE 2 | Results of generalized linear mixed effect model (GLMM) after backward selection to test for top-down control mechanisms.

Independent variable	Regression coefficient	Standard error	p-value
Step 1: HNF αMPTI as dependent variable			
Bacteria Shannon	-0.11	0.29	0.71
Spatial autocorrelation	0.3	0.14	0.03
Step 2: HNF Shannon as dependent variable			
HNF α MPTI	-0.09	0.06	0.13

These results indicate that bacteria Shannon diversity does not influence the α MPTI of HNF community, which also does not determine its Shannon diversity. This conclusion is qualitatively the same as that drawn from the univariate GLMM.

association was still significant after either setting station as a random effect ($p = 0.02$), or setting station as a random effect nested within cruise to account for spatial autocorrelation ($p = 0.02$).

In order to reveal whether the underlying mechanisms are top-down control and/or bottom-up control, we then applied the two-step analytical framework to deconstruct this positive association. From the top-down control perspective, we found that the α MPTI of bacteria community was not significantly associated with the Shannon diversity of HNF community with $p = 0.1$ (univariate regression coefficient = 0.27; **Figure 3A**). However, after accounting for other environmental variables via backward selections (**Supplementary Tables 1 and 2**), the α MPTI of bacteria community became significantly less negative with the increase of HNF Shannon diversity (**Table 1**). Less negative α MPTI of bacteria community was in turn associated with higher bacterial Shannon diversity (univariate regression coefficient = 0.23; $p < 0.01$; **Figure 3B**). These findings suggest that, after statistically accounting for the environmental factors, the α -diversity of HNF community possibly made the deterministic processes weakly homogenizing the bacteria community, which then led to higher diversity of bacteria community.

From the bottom-up control perspective, we first found that of HNF community was independent of the bacteria Shannon diversity (univariate regression $p = 0.29$; **Figure 4A**). Subsequently, we found that the HNF community did not significantly affect its Shannon diversity ($p = 0.09$; **Figure 4B**). Including other environmental variables did not alter these findings (**Table 2**). These results suggest that the bacteria α -diversity did not influence the assembly processes of HNF community, and these

assembly processes did not determine the α -diversity of HNF community.

DISCUSSION

In the southern ECS, the diversity of HNF (predator) and bacteria (prey) community are positively associated (**Figure 2**), which is consistent with a previous study that included data from the whole ECS (Yang et al., 2018). Positive association between predator and prey diversity is also observed in other aquatic systems (Aranguren-Riaño et al., 2011). More importantly, our novel analytical framework allows us to decipher how this positive association likely results from the associations between predator α -diversity and weak homogenizing deterministic assembly processes of prey community, which are then associated with higher prey α -diversity (**Figure 3**). Our findings echo the argument that top-down control mechanisms determine the α -diversity of prey community (Lovejoy et al., 2000; Vázquez-Domínguez et al., 2005a; Longnecker et al., 2010) and may propagate to affect energy flows in marine ecosystem (Vázquez-Domínguez et al., 2005b; Pradeep Ram et al., 2015).

The importance of top-down control mechanisms revealed in this study contradicts with many studies that emphasize the impacts of bottom-up control mechanisms (e.g., Scherber et al., 2010; Hertzog et al., 2016; Otero et al., 2020). One possible explanation to this disagreement is the fact that our data come from an aquatic system, whereas the majority studies demonstrating bottom-up control mechanisms is conducted in terrestrial systems (as reviewed in Haddad et al., 2009). In aquatic systems, predators have been demonstrated to impose larger impacts on prey than in terrestrial systems (Shurin and Borer, 2002; Shurin et al., 2006). Stronger predation pressures may act as a weak homogenizing deterministic processes for prey community, i.e., make the α MPTI of prey community less negative, and thus increase prey α -diversity. However, more detailed analyses are required to test this conjecture.

The prevalence of top-down control in aquatic systems implies that HNF community might also be controlled by their predators (Gasol, 1994; Segovia et al., 2014). Top-down control on HNF community is reportedly more prominent in productive regions because productive regions can sustain more diverse top predators, such as ciliates or other microzooplankton (Gasol et al., 2002; Pernthaler, 2005). Since the productivity in the southern East China Sea is not particularly low (Gong et al., 2000; Chen et al., 2004), it is possible that HNF diversity could be controlled by their predators instead of bacteria. Besides, lack of evidence for bottom-up control on HNF diversity could result from the fact that HNF have alternative food resources other than bacteria. It has been shown that HNF feed on picoeukaryotes with similar rate as that on prokaryotes (Parslow et al., 1986; Christaki et al., 2005). The α -diversity of HNF community could be affected not only by the diversity of bacteria but also picoeukaryotes. These speculations require empirical feeding experiments to be verified; these create some possibilities for future work.

The other possible explanation why the bottom-up control mechanisms are non-significant in our study is that the

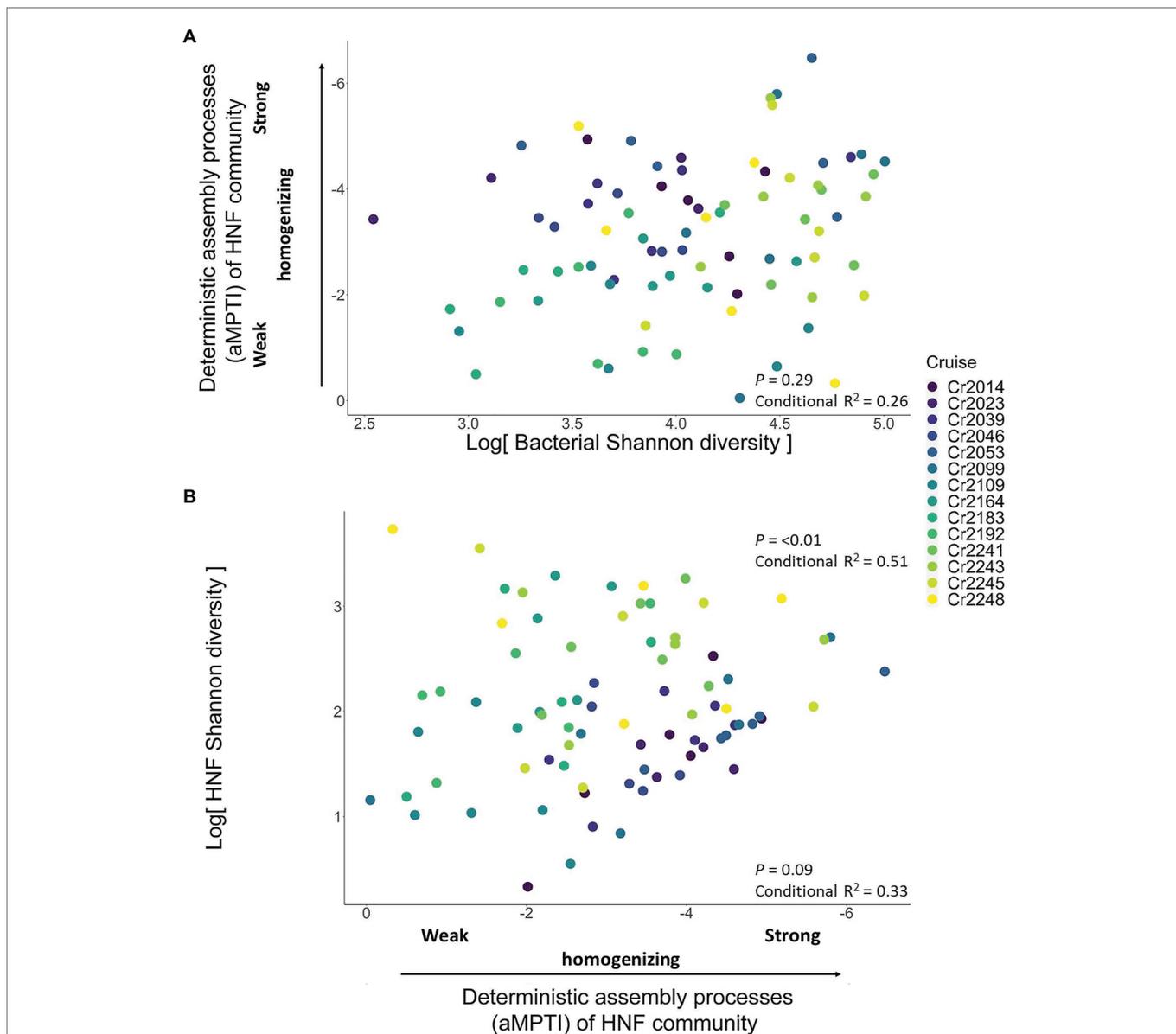


FIGURE 4 | Scatterplots showing the test for bottom-up controlled mechanisms. Panel (A) shows the non-significant relationship (dashed blue line) between bacteria Shannon diversity and the deterministic assembly processes (α MPTI) of HNF community. Panel (B) shows the non-significant relationship (dashed blue line) between the α MPTI of HNF community and the Shannon diversity of HNF. The p -value and R^2 are derived from univariate GLMM, whereas including other environmental variables does not qualitatively alter the conclusions (Table 1). Note that the α MPTI of bacteria are mostly negative, so that, we reversed the y axis of panel (A) and x axis in panel (B) for visual intuition. The gray shaded area around the blue line indicates the 95% confidence interval of the regression line (GLMM). The colors of dots represent different sampling cruises.

phylogeny of HNF in the southern ECS might not faithfully represents their ecological niche. Faithfully approximating species' ecological niche using their phylogeny is a critical assumption that underpins the inferences based on species' phylogeny (Losos, 2008). We did find significant phylogenetic signals, i.e., significant correlations phylogeny and habitat preferences, for both the HNF and bacteria community (Supplementary Figure 5). However, the phylogenetic signals of the HNF community were much weaker than that of bacteria (Supplementary Figure 5). For the HNF, the phylogenetic signal was only significant in

a narrow range of phylogenetic distance (panel B of Supplementary Figure 5), meaning that the index based on phylogenetic distance (here, the α MPTI) might not completely represent the ecological processes experienced by the HNF community. Consequently, we do not completely rule out possible the occurrence of bottom-up control mechanisms in mediating bi-trophic diversity associations in the southern ECS.

We demonstrated that the top-down control mechanisms likely explain the positive association of predator and prey diversities; nevertheless, top-down control processes encompass

a variety of detailed mechanisms (Hillebrand and Shurin, 2005). HNF have been shown to exhibit selective feeding behavior that can promote the diversity of their prey, including bacteria (Montagnes et al., 2008; Gereá et al., 2013). HNF have also been demonstrated to suppress dominant prey species and promote prey diversity, i.e., the kill the winner hypothesis (Winter et al., 2010). In addition, HNF, as predators, can indirectly increase prey diversity through regenerating resources (Attayde and Hansson, 1999), maintaining the diversity of resources for prey (Abrams, 2001), and/or trait-mediated indirect interactions (Werner and Peacor, 2003). For example, in a tri-trophic food web consisted of a basal resource (an isopod *Jaera nordmanni*), an intermediate consumer (an amphipod *Echinogammarus marinus*), and a top-predator fish (*Lipophrys pholis*), the presence of top-predator can reduce the feeding rate of an intermediate consumer (Alexander et al., 2013). Furthermore, both bacteria and HNF communities interact with other trophic groups, including marine viruses, phytoplankton, and zooplankton (Needham et al., 2017; Zeldis and Décima, 2020; Zimmerman et al., 2020). We cannot rule out the impacts from those organisms in this analysis. By including those trophic groups in the analysis could potentially resolve the puzzles. Clarifying the above mechanisms is a venue beyond the scope of this study but will render fruitful results.

One major concern of our analytical framework is that interpretations of α MPTI, or phylogenetic similarity in general, are controversial. Using phylogenetic similarity to approximate species' ecological difference is an assumption commonly made in the field of microbial ecology (Webb, 2000; Webb et al., 2002). Ever since Webb developed the net related index (NTI) and nearest taxon index (NRI), species' phylogenetic similarity has been used to indicate whether a community is subject to environmental filtering (e.g., Horner-Devine and Bohannan, 2006) or competition (e.g., Cooper et al., 2008). More recently, species' phylogeny has been used to decipher the structure or underlying processes of a meta-community (Stegen et al., 2013, 2015; Dini-Andreote et al., 2015; Wu et al., 2018). Based on this assumption of using phylogenetic similarity to approximate species' ecological difference, we developed the analytical framework with the attempt to decipher the positive association between predator and prey diversity. However, as suggested in several studies, phylogenetic similarity is an imperfect proxy of species' ecological difference because ecological interactions, e.g., trophic interactions, might not leave traceable footprints on species' evolutionary history. Species' phylogenetic similarity thus may not be used to faithfully represent community assembly processes (Mayfield and Levine, 2010; Pavoine and Bonsall, 2011). We are fully aware of this controversy and believe that quantifying ecological interactions, e.g., feeding rates, is the most direct way to decipher predator and prey diversity associations. However, without resorting to manipulative experiments, here, we assume that phylogeny could approximate species' ecological niche. Verifying this assumption requires further investigations so that we mindfully regard the α MPTI as an implication of the occurrence of certain community assembly processes. Through our analyses, we offer a possible explanation to the diversity association but our findings critically hinge on the fidelity of phylogeny to ecological niche.

In spite of some caveats, we still provide a useful analytical framework to better decipher why the diversity of predator and prey are associated. This analytical framework can be an alternative to manipulative experiments that are often required to understand the mechanisms underpinning the association between the diversity of predator and prey (e.g., Scherber et al., 2010; Hertzog et al., 2016). Besides being costly and labor intensive, manipulative experiments could suffer from unsatisfying spatial or temporal scale (Briggs and Borer, 2005). Our analytical framework can potentially provide an alternative approach that can be applied in any predator-prey system.

In summary, our analyses support top-down control as the underlying mechanisms of positive α -diversity association between HNF and bacteria in the southern ECS. We showed a positive association between predator α -diversity and weak homogenizing deterministic assembly processes of prey community, which then are positively associated with the α -diversity of prey community. These results suggest that predators are likely the driver of the positive association between predator and prey α -diversity in the southern ECS microbes.

DATA AVAILABILITY STATEMENT

The datasets generated and analyzed for this study can be found in the NCBI Sequence Read Archive (SRA) under the accession numbers: PRJNA662424 (<https://www.ncbi.nlm.nih.gov/sra/?term=PRJNA662424>).

AUTHOR CONTRIBUTIONS

F-HC and C-hH developed the hypothesis, conducted the analyses, and composed the manuscript. All other authors contributed equally to collect data and help polish the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2021.651565/full#supplementary-material>

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