Implementation of biotic interactions in niche analyses unravels the patterns underneath community composition in clownfishes

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BIOSKETCH

Alberto García is interested in Biogeography and Evolutionary Ecology of marine organisms. His interests rely on conducting empirical studies applied for conservation purposes as well as modelling and developing methods to improve the implementation of biotic interactions in evolutionary and ecological models.

Alberto García did his MSc in Behaviour, Evolution & Conservation at the University of Lausanne (Unil) and is now following up his master's project as a PhD student in prof. Nicolas Salamin's group at the Department of Computational Biology at Unil.

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SHORT RUNNING TITLE:

Host use shapes clownfish communities

ABSTRACT

Aim

Biotic interactions are key to understanding the ecology of species and communities. As such, integrating biotic interactions into ecological niche modelling methods has been a central topic of research for the last decade. Yet, the role of biotic interactions remains overlooked. Mutualistic systems constitute perfect study cases for analysing the effect of biotic interactions on species niches and communities' composition.

Location

Indo-Pacific Ocean

Time period

Current

Major taxa studied

Clownfish-sea anemone mutualistic system

Methods

We integrate mutualistic interactions into a niche quantification framework to analyse the effect of biotic interactions in the estimation of species niches, and competition patterns among clownfish communities.

Results

Implementing biotic interactions in ecological niche modelling can improve the reliability of niche estimations, especially in specialist species. Additionally, resource partitioning decreases niche overlap among clownfishes allowing coexistence in species-rich habitats.

Main conclusions

We provide a framework to estimate the effects of species interactions and demonstrate the importance of including biotic interaction to improve the estimation of species' ecological niches. Finally, we show how resource partitioning regulates competition and provides the ecological basis to explain why clownfishes have different sets of associations with sea anemones. The variety of mutualistic strategies serves to ecosystem sustainability, reducing the effect of saturation by species richness and competitive exclusion. Competition avoidance through resource partitioning may be the primary mechanism that shapes clownfish communities across the Indo-Pacific. These findings strongly support the importance of biotic interactions in shaping communities. Future studies could use the proposed analytical framework to serve multiple conservation purposes.

KEYWORDS

biotic interactions, clownfish, community composition, competition, mutualism, niche, species distribution, spatial ecology

INTRODUCTION

Ecological niche quantification and species distribution models have become important in ecological and evolutionary studies. There are currently two main approaches to estimating them: niche analysis in multivariate environmental space (i.e., ordinations, e.g., principal component analysis, PCA) and niche-based spatial modelling of species distributions (SDMs; see Guisan *et al*. 2014). A wide variety of SDM methods exist to predict species distributions (Valavi *et al.* 2021; Norberg *et al*. 2019), which can be used to assess the sensitivity of species to climate change or predict patterns of biodiversity at the community level (Franklin 2010; Guisan *et al*. 2013; Araujo *et al*. 2019). Similarly, numerous PCA-based methods have been proposed to quantify the realized environmental niche of species (Broennimann *et al*. 2012). However, most do not directly incorporate biotic interactions despite improving SDM predictions (Wisz *et al.* 2013; Early & Keith 2019; Kass *et al.* 2020; Jenkins *et al*. 2020). Thereby, the role of biotic interactions is still overlooked (Anderson 2017; Palacio & Girini 2018), leading to potential misinterpretations of ecological niches and species distributions (Zurell *et al.* 2020; Moullec *et al*. 2022). The development of SDMs integrating biotic interactions has been encouraged (see Soberón 2010; Boulangeat *et al.* 2012; de Araujo *et al.* 2013; Leach *et al*. 2016; D'Amen *et al*. 2018; but see Konig *et al.* 2021), but no study has yet accounted for biotic interactions in PCA-based niche quantification.

Among the diverse types of biotic interactions, mutualism is frequent and contributes to the increase of biodiversity (Bastolla *et al*. 2009). It favours ecosystem stability and facilitates species dispersal and resilience (Hale *et al.* 2020; Le Roux *et al*. 2020). Mutualism can drastically influence evolutionary processes, as seen in major evolutionary transitions such as the evolution of the eukaryotic cell or the colonization of land by symbiotic plants, and it can also influence species distributions (Pellissier *et al.* 2013; Schleuning *et al.* 2015; Marjakangas *et al.* 2020). In nature, we observe a gradient in the intensity of mutualism, from species that are less dependent on their multiple partnerships (generalists) to those that are highly dependent on a unique interaction (specialists; Bascompte & Jordano 2007; Sverdrup-Thygeson *et al*. 2017). These contrasting

mutualistic behaviours have a differential impact on the ecological and evolutionary dynamics of species (Gracia-Lázaro *et al*. 2018). This is typically the case in clownfishes for which the development of mutualistic associations with sea anemones triggered the rapid adaptive radiation, fostering a quick diversification into new ecological niches (Litsios *et al*. 2012).

Clownfishes are an emblematic group of reef fishes consisting of 30 species distributed in shallow waters along the Indo-Pacific Ocean. It is the only group of reef fishes with mutualistic associations with sea anemones, causing an important positive impact on clownfish survival (Lubbock 1980; Fautin 1991). While sea anemones are deadly poisonous and fierce predators (Hoepner *et al*. 2019), clownfishes have developed a mucus coat that prevents them from being stung by anemone's tentacles (Mebs 2009). The exchange of nutrients and improved reproductive success are among the benefits of this mutualism that constitutes a lifetime association for the clownfish. Clownfishes have a short dispersal time during the larval stage in which they find a single host to spend the rest of their lives (Laudet & Ravasi 2022). Consequently, clownfish distributions are anchored to the presence of their hosts. Each of the 30 species of clownfish developed specific associations with up to ten different sea anemone species, giving rise to both generalist and specialist species. Nevertheless, clownfish individuals from distinct species are rarely found cohabiting within the same sea anemone individual except in the Coral Triangle (Camp 2016), where clownfish richness peaks (Elliott & Mariscal 2001). The mechanisms underlying the association between a clownfish species and their specific host are not yet understood, nor are the macroecological patterns of the specificity of mutualistic associations and community composition.

We hypothesized that this heterogeneity of host usage plays a crucial role in the way clownfish communities are structured allowing resource partitioning and lowering competition. To test this hypothesis, we used a PCA-based approach to estimate the realized environmental niche of 28 out of the 30 clownfish species and study the effect of explicit mutualistic associations on these niche estimates. To capture the mutualistic dependence of clownfishes on sea anemones and their effects on species niches, we adapted the 'COUE' framework (Guisan *et al*. 2014) to provide new metrics to

estimate the effect of biotic interactions on niche quantification (Fig. 1). Further, we used the quantified niches to infer interspecific resource competition with the inclusion of spatially host-specific associations and resource partitioning. Our results provide a basis to better understand the patterns behind the clownfish community composition and illustrate the importance of host heterogeneity in the biogeography of this clade. Our study brings important new insights into this mutualistic system, with potential implications for future clownfish studies and conservation strategies, and extensions to other mutualistic systems.

MATERIAL and METHODS

Spatial data

The distribution of clownfish comprises the Indo-Pacific Ocean, from the East coast of Africa to Polynesia in the Pacific, and from the coast of Japan to the South of Australia. The distribution of sea anemones is not restricted to this area, and most have a worldwide distribution. We retrieved a total of 1,636 occurrences of the ten sea anemone species hosting clownfishes (mean: 163.6; min: 68; max: 335) and 4,258 occurrences for the 30 clownfish species (mean: 146.8; min: 2; max: 860) from the following online databases: RLS, GBIF, OBIS and Hexacoral (Atlas of Living Australia 2017; GBIF.org 2018; OBIS 2017; Fautin 2008 respectively). Datasets were filtered to remove duplicates, misplaced or misidentified occurrences, and redundant information. Two clownfish species had less than five occurrences and were excluded from further analyses.

Environmental data were obtained from GMED (Basher *et al*. 2018) and Bio-Oracle (Tyberghein *et al*. 2012; Assis et al. 2018) using the same resolution and extent for both datasets (0.083 x 0.083 cell size, representing approximately 9,2 km near the equator). A Total of 53 environmental variables classified into three categories representing physical, chemical, and biological factors were retrieved. Clownfishes inhabit only shallow reefs of the Indo-Pacific Ocean and we restricted the environmental data to locations corresponding to this habitat plus the epipelagic zone above 50m

depth using a map of the locations of warm waters coral reefs from UNEP-WCMC (UNEP-WCMC 2018).

Selecting environmental variables

We performed a first Principal Component Analysis (PCA) on the environmental data using R (R Core Team 2018) and the R package ade4 (Thioulouse *et al*. 1997) and selected the four variables with the highest proportion of variance explained for each PCA quadrant. We removed variables in which missing information increased overall data loss and discarded all but one of the highly correlated environmental variables (> 0.8). The environmental variables selected were: mean current velocity, mean salinity, mean temperature, mean nitrate concentration, nitrate concentration range, mean chlorophyll concentration, dissolved oxygen concentration range, and mean phytoplankton concentration.

Due to the restricted dispersal capacity of clownfishes (Jones *et al*. 2005; Almany *et al*. 2017), we might observe differential ecological dynamics regionally. We, therefore, analysed the data by regions by splitting the area of study into 27 provinces belonging to 5 marine realms - Western Indo-Pacific (7), Central Indo-Pacific (12), Eastern Indo-Pacific (5), Temperate Australasia (2), and Temperate Northern Pacific (1). The marine provinces and realm delimitations (Figure S1) were obtained from MEOW (Spalding *et al*. 2007).

Quantifying ecological niches

We created a global environmental space using the first two principal components of a second PCA based on the environmental variables previously selected (see above, first PCA). We then used the ecospat R package (Broennimann *et al*. 2012) to estimate the index of relative abundance o for both clownfishes and hosts occurrences in a two-dimensional grid of 100 by 100 cells:

(1) $$o = \delta(n) \,/\, max(n)$$

where $\delta(n)$ was the kernel density estimation of the number of occurrences on the environmental envelope defined by the PCA scores, and $max\,(n)$ was the maximum number of occurrences in any grid cell of the environmental space. The index o, which ranged from 0 for environments where the

species was not observed to 1 where it was most observed, estimated the distribution of clownfish environmental suitability in the environmental space, i.e., its ecological niche (a.k.a. realized environmental niche). To account for differential ecological dynamics regionally, we estimated species niches in each of the environmental space subsets representing each marine province.

Correction of the ecological niche using mutualistic interactions

We built a binary association matrix accounting for the species-specific mutualistic interactions between sea anemones and clownfishes using the literature (Fautin 1985, 1991; Godwin & Fautin 1992; Ollerton *et al*. 2007; Ricciardi *et al*. 2010; Litsios *et al*. 2012) and information available online (https://amphiprionology.wordpress.com, www.fishbase.org, https://reeflifesurvey.com). Only congruent information from all sources of information was considered reliable to create an association matrix *A* in which a focal clownfish species *s* had a vector of interactions (Fig. 1):

$$A_s = [(\alpha_1 \cdots \alpha_n)], \alpha \in \{0,1\}$$

with n being the number of sea anemone species (here 10 in total).

We assumed that due to the constitutive character of the mutualistic association, suitable environments for a clownfish would not be available if they were not suitable for its hosts. Environment availability would thus depend on i) the association between a host species present in the environment and the clownfish, given by *A,* and ii) the abundance of the sea anemone species in the environment. The host availability ω at a site was estimated as

(2) $$\omega_e = 1 - \prod_{k=1}^{n}(1 - o_{ek}\alpha_k)$$

where α_k was the association between a clownfish and its host k, while o_{ek} was the relative abundance index of k in a specific environment e. The value of ω ranged from 0 to 1 and represented the availability score that a suitable host was present at a site within a given environment. Then, the corrected relative abundance index o' of the focal species given the mutualistic associations was

(3) $$o' = \omega o$$

where o was the relative abundance index of the focal species, and ω was the host availability in each environment. This further constrained the environments that were not available due to the lack of hosts and kept those that could effectively be used, improving the estimation of the environmental niche. For spatial analyses we projected the relative abundance indexes of each estimated niche into the geographical space (see Supplementary Material & Methods).

Effect of mutualistic interactions on species niches and distributions

To understand the effect of implementing explicit mutualistic interactions on the estimation of clownfish niches, we compared the latter before and after adding the correction. We computed the Unavailable, Used, and Unoccupied proportions of the environmental space, adapting the 'COUE' framework (Guisan *et al.* 2014), as well as other metrics to quantify the niche shift caused by the correction (see Text Box 1 for metrics description). We classified species interacting with three or more available hosts as generalists and species with less than three available hosts as specialists following previous studies (Ollerton *et al*. 2007; Litsios *et al*. 2014). Comparisons between these two groups were done with a Kruskal-Wallis test while a multivariate nonparametric Cramer two-sample test was used to test differences between the environmental niches of species before and after the correction.

Effect of mutualistic interactions on species niche overlaps

We investigated the role played by the clownfish mutualistic interactions on the niche overlap among clownfishes. We used Schoener's D to compute species pairwise niche overlaps before and after the correction. We also split the niche correction for each host (skipping equation 2 and taking each host's relative abundance as ω). Then, computing the species pairwise niche overlaps for each host-specific corrected niche and averaging the obtained pairwise Schoener's D values to obtain the 'host-specific niche overlap' (Fig. S2). We tested for statistical differences among the different niche overlap estimates using a Wilcoxon paired signed-rank test. We tested for differences between species with different numbers of shared hosts (non-sharing, partially sharing, and sharing-all), and

mutualistic behaviour (generalist-generalist, generalist-specialist, and specialist-specialist) comparing niche overlaps between groups using a Kruskal-Wallis test.

Spatial patterns of clownfish interspecific niche overlap

We investigated whether environmental or host-specific niche overlap was linked to species richness and whether there is a geographic structure in the niche overlap patterns. We estimated species richness, as well as the intensity of environmental and host-specific niche overlap per site (i.e., the average overlap of all species occurring in a site). We tested for the effect of species richness on both estimates using a spatial generalized linear mixed model (spatial GLMM) using the spaMM r package (Rousset & Ferdy 2014) to correct for spatial autocorrelation. Finally, we created subsets of ecological and host-specific niche overlap for the three types of interaction: generalist-generalist, specialist-generalist, and specialist-specialist and estimated the number of species for each type of interaction. Then, carried out spatial GLMMs for each subset to see whether the obtained patterns of niche overlap varied depending on the type of interaction.

RESULTS

Effect of mutualistic interactions on species niches

Incorporating the mutualistic information led to a significant change in ecological niche estimates in 65 of the 108 regional niche subsets (60%; Table S1). We found that on average about a sixth of the species niche was not accessible due to the absence of hosts in those environments (Mean Unavailable = 0.179 ± 0.249). Similar proportions were unsuitable although available due to facilitation by their hosts (Mean Unoccupied = 0.178 ± 0.193). However, UUU proportions were highly variable among species (Fig. 2) and provinces (Fig. S3).

Comparisons between niche and spatial UUU proportions showed that suitable and accessible environments (i.e., that constitute the corrected niche) are geographically overrepresented and found in most locations in the provinces (V = 5,273, *p-value* < 0.001). Conversely, unavailable (V = 80,

p-value < 0.001) as well as available but unsuitable (V = 109, *p-value* < 0.001) environments tend to be marginal and geographically underrepresented (Fig. S4).

The UUU proportions differed significantly between specialists and generalists (Fig. 3 and Table S2). We found that the environmental niches of specialists showed higher Unavailable proportions (Kruskal-Wallis X^2 = 23.061, *p-value* < 0.001) and lower Used proportions (Kruskal-Wallis X^2 = 17.129, *p-value* < 0.001) compared to generalists, while no significant difference was found for the Unoccupied proportions (Kruskal-Wallis X^2 = 2.1735, *p-value* = 0.14). Ecological niches of specialists were more altered than those of generalists (Fig. S5), resulting in a higher niche dissimilarity (Kruskal-Wallis X^2 = 39.987, *p-value* < 0.001). Similarly, the centroid shift (Kruskal-Wallis X^2 = 20.681, *p-value* < 0.001) and environmental shift (Kruskal-Wallis X^2 = 17.704, *p-value* < 0.001) were significantly higher in specialists than in generalists. The same UUU patterns were found at the spatial level (Fig. S6)

Effect of mutualistic interactions on species niche overlaps

The levels of ecological and host-specific niche overlap among clownfishes were high (median D_{eco} = 0.741; IQR = 0.199; and median $D_{corrected}$ = 0.762; IQR = 0.220, respectively). Ecological niche overlap was significantly increased after correction for biotic interactions (V = 14,723, *p-value* = 0.015), while host-specific niche overlap (median $D_{host\text{-}specific}$ = 0.232; IQR = 0.304) was significantly lower than the two other measures (V_{eco} = 35,327 & $V_{corrected}$ = 33,650, *p-values* < 0.001; Fig. 4).

We found significant differences in niche overlap among the three types of interaction after the correction of the ecological niche (Kruskal-Wallis = 6.7509, p-value = 0.034), and host-specific niche overlap (Kruskal-Wallis = 71.623, p-value < 0.001) whereas no significant differences were found before the correction (Kruskal-Wallis = 4.193, p-value = 0.122). We found 15 specialist-specialist pairs that do not share any host among them, resulting in no host-specific niche overlap whereas the remaining 13 pairs showed high levels of host-specific niche overlap (median $D_{host\text{-}specific}$= 0.456; IQR = 0.374). On the other hand, the amount of overlap decreased significantly when implementing niche partitioning due to differential host use in all generalist-generalist (median $D_{host\text{-}specific}$= 0.351; IQR =

0.212) and generalist-specialist (median $D_{host\text{-}specific}$= 0.201; IQR = 0.172) interactions. The latter was the most predominant type of interaction among co-occurring clownfishes and showed the lowest levels of host-specific niche overlap (Fig. S7).

Geographically, the highest species richness and hence, the highest number of potential interactions were found in the Eastern and Western Coral Triangle provinces (Fig 5a). Important levels of environmental overlaps were found in provinces along the Pacific and Western and Central Indian Oceans (Fig 5b). In contrast, host-specific overlaps were higher in Tropical Northwestern Pacific and Somali/Arabian sea (Fig 5c). We observed host-specific overlaps to be generally lower than environmental overlaps (Fig 5d) with the highest differences in Temperate and Tropical Pacific provinces, Northeast Australian Shelf, the Coral Triangle, and the Western Indian Ocean.

Host-specific overlaps are positively correlated with ecological overlaps (Pearson's correlation = 0.800, *p-value* < 0.001) and negatively correlated with the number of species (Pearson's correlation = -0.287, *p-value* < 0.001). The overall spatial GLMM shows both the number of species (estimate = -0.018; 95% CI [-0.023,-0.013]) and ecological overlap (estimate = 0.558; 95% CI [0.516,0.600]) have a negative and positive effect, respectively, on the host-specific overlap. Yet, the combined effect of both species richness and environmental overlaps had no effect on host-specific overlaps (estimate = 0.02; 95% CI [-0.005,0.011]), Fig. S8a and Table S4a). When performing the spatial GLMM on each subset of interactions, generalist-generalist host-specific overlaps are positively affected by the number of generalists (estimate = 0.013; 95% CI [0.009,0.017]) and ecological overlap (estimate = 0.414; 95% CI [0.399,0.430]), whereas the other two interactions show similar effects as the overall model varying the intensity of the effect of ecological overlap (Table S4).

DISCUSSION

In this study, we developed a new approach to account for the effect of mutualistic interactions in the estimation of ecological niches. We used clownfishes to illustrate our method and investigated the influence that species-specific mutualistic interactions with sea anemones have on their ecological niche. Moreover, it allowed us to estimate the niche overlaps among clownfishes based

on resource use, providing new insights into the competition patterns in clownfish communities, and evaluating the importance of mutualistic behaviour and host-partitioning to regulate competition. Although we used our method on a strict mutualistic system, our framework could be extended to account for any type of interaction, either positive or negative (see supplementary Material & Methods for the proposed extension).

Effect of mutualistic interactions in clownfish species niches

We found consistent agreement between the ecological niches of clownfishes and their hosts as overall more than 60% of the clownfish niche is also part of its hosts' niche. This was expected as mutualistic partners must have resembling environmental suitability to co-occur. Nevertheless, the level of environmental agreement between mutualistic partners varied across clownfish species (Fig. 2). The comparison between the standard and corrected ecological niche showed that portions of the estimated niche can be inconsistent with the actual suitable and available environments due to the presence or absence of biotic interactions. This can lead to potential biases in spatial models in which biotic interactions are disregarded (Meineri *et al.* 2012), especially for species with strong biotic constraints such as specialists. Our implementation introduces explicit information about biotic interactions to correct the ecological niche, making the comparison of species niches more even. It also allows us to investigate in detail which environments are in disagreement between the clownfish and its hosts through the use of the UUU parameters. Used proportions of the ecological niches (i.e., the corrected niche) showed to maximize the spatial use of their environmental suitability. This means that suitable environments retained in the corrected niche are geographically predominant. Conversely, unavailable, and unoccupied environments are marginal and geographically underrepresented (Fig S2). This shows a strong agreement between clownfishes and their hosts in predominant environments, suggesting the clownfish-host system to be ecologically stable and likely to be a product of the evolutionary success of their interaction. Nevertheless, regions with a considerable number of unavailable environments due to the absence of hosts may represent ecologically unstable populations. These unstable populations may represent sink or

isolated populations that could foster new ecological adaptations (Holt *et al*. 2003; Peniston *et al.* 2019). On the other hand, unoccupied environments for the clownfish could be facilitated by their hosts, expanding the species' niche (Bruno *et al*. 2003; Bulleri *et al.* 2016). Hosts could create microenvironments, as exhibited by other cnidarians (see Arossa *et al*. 2021), facilitating the settlement of stranded clownfish larvae in harsh environments. These areas could potentially be areas of evolutionary interest, as these harsh conditions could accommodate new environmental adaptations for the species fostering range expansions (see examples in Chen *et al.* 2018; Álvarez *et al*. 2020). For instance, it could have facilitated the expansion of the clownfish clade towards the West Indian Ocean around 5 MY ago (Litsios *et al.* 2014) as sea anemones were long-established (Titus *et al*. 2019) providing an empty niche for environmentally adapted individuals.

Agreeing with previous studies (see Bascompte & Jordano 2007), our results show that the niches of generalist species were less altered by their biotic interactions whereas specialists were strongly affected (Fig. 3). The degree of ecological niche agreement between each clownfish and its hosts was higher in generalists than in specialist species, with the latter having higher proportions of unavailable environments. Specialists' niches are strongly nested within the niche of fewer hosts than generalists', and thus, niche estimations accounting for biotic interactions are more likely to diverge from environmental-only models (Bateman *et al*. 2012). Therefore, niche models of specialist species may be prone to overfitting when no biotic constraints are implemented, constituting a critical issue regarding ecological interpretations, especially in community analyses (Dormann *et al*. 2018). Conversely, shared proportions of niche between the clownfish and its hosts give biotic support to the model predictions in those environments as those predictions were supported for both clownfish and hosts from independent datasets.

Even though we consider our niche estimations reliable and realistic, we cannot disregard the possibility of introduced biases due to imbalanced occurrence data or wrongly assumed biotic associations. However, UUU parameters can also be used to draw the attention of those areas in need of a better sampling effort or expose potential misidentified associations such as the cases of

A. latezonatus, *A. chagosensis* and *A. sebae*, of which recent observations indicated that they can be associated with three, three and four more sea anemone species, respectively, than previously known (Titus *et al.* unpublished data). This could explain the levels of Unavailable proportions of the niche seen in those species. We consider this analysis a useful tool in conservation strategies as it can draw attention to specific areas or populations where stronger effort is needed. Used proportions could be used to identify ecologically stable environments that would accommodate source populations whereas Unavailable proportions could identify potential sink populations. Likewise, Unoccupied proportions could be useful to forecast scenarios of environmental adaptations, habitat displacement due to climate change, or other ecological pressures such as biological invasions.

Effect of mutualistic interactions on species niche overlaps

Our models provided useful information to investigate the effect of long-term dynamics of competition among clownfishes. Since competition can only occur when two or more species physically interact, the inference of species niches and distributions is crucial (Godsoe *et al.* 2015). The approach presented helped to infer more reliably the distribution of clownfishes that is nested within their hosts. More importantly, it allowed us to study the interactions among clownfishes while accounting for the partitioning of resources due to differential host use. Ecological niche overlaps were high regardless of the different sets of mutualistic associations and host use among species. As such, two clownfishes in the same region would have similar environmental suitability even though they are inhabiting different sea anemones. This is expected as tropical reef fishes typically inhabit a narrow set of environmental conditions (Brandl *et al.* 2020) leading to high ecological niche overlaps. On the other hand, host-specific niche overlaps did show to differ depending on the hosts that each species share and their mutualistic behaviour. Interestingly, host-specific overlap dropped significantly when the ecological overlap was high. Previous studies showed that associations with sea anemones have a fundamental impact on clownfish survival and reproduction (Lubbock 1980; Fautin 1991). However, the reason why each clownfish is associated

with certain species of sea anemones and not others is unresolved. Our results bring a potential explanation to this question, suggesting that the current species-specific set of interactions could be the result of long-term competition dynamics driving the host-specific niche toward reducing interspecific overlaps and facilitating species coexistence. The coexistence of competitors through resource partitioning has been empirically observed in different mutualistic systems (see examples in Palmer *et al.* 2003). To our understanding, the host-specific niche overlap could represent a realistic proxy of the interspecific levels of competition as it gives an accurate depiction of the resource overlap. Nonetheless, we cannot exclude other ecological elements that may regulate the spatiotemporal dynamics of clownfish interspecific competition.

Our study showed that interactions between generalists and specialists constitute the most abundant type of interaction (67 unique interactions), especially in species-rich environments. They also showed to have the lowest host-specific overlaps. This suggests that generalist-specialist interactions are favoured in saturated communities as it decreases competition, allowing species to coexist. Generalist-specialist interactions have been observed to be the most abundant type of interactions in plant-animal mutualistic systems and may play a crucial role in maintaining and promoting biodiversity (see Bascompte & Jordano 2007). Similarly, our results are congruent with the findings of Camp *et al*. 2016, where cohabitation was seen in areas where clownfish richness exceeded host richness. 42 unique interactions occurred throughout multiple provinces among generalists, and only four shared the complete set of hosts showing higher host-specific overlap than ecological overlap. There were 21 unique interactions among specialists of which ten did not share any host and only four in which specialists shared all the hosts, being host-specific overlap higher than the ecological overlap. Following the evolutionary dynamic observed in clownfishes (Litsios *et al.* 2014), showing a trade-off between the specialization in hosts or environment, species that share the same host would have either diverged in parapatry towards different environments or underwent a secondary contact coming from environmentally distant niches that had evolved into a common host. Indeed, we found coexisting species to be either sister species that recently diverged

in parapatry supporting the former explanation, or far-related species converging at the edge of their distributions supporting the latter. Interestingly, coexisting species show divergence of other traits such as colouration pattern, morphology, or distance from the host, in line with results in Camp *et al*. 2016, which could potentially explain local dynamics among those species.

The Coral Triangle gathers the highest number of co-occurring species, as well as being one of the areas with high ecological overlap. Nevertheless, it displays great differences between ecological and host-specific overlap, showing levels of host-specific overlap within values that support coexistence (Polechová & Storch 2019). This explains why the high clownfish richness can be sustained in this area as competition avoidance has been possible through resource partitioning by the co-occurring species. By contrast, the host-specific overlap is high in areas over the edge of species distributions such as Western Pacific provinces, the Somali/Arabian Peninsula, or the Central and Western Indian Ocean, which represent some of the most recently colonized areas (Litsios *et al.* 2014). This could imply that these areas have been colonised by environmental adaptation and following the results of Litsios *et al.* 2014, species could not specialise in different hosts to avoid competition.

Species richness and ecological overlap affect the levels of host-specific overlap. However, contra intuitively, the increase in the number of species drags down the host-specific overlap, especially when the ecological overlap is low. This can only be explained by differential host use, reducing competition in crowded environments. Remarkably, there are differences in those patterns across the different types of interactions (Fig. S9), showing that ecological overlap and the number of generalists increase host-specific overlap among generalists, reaching unsupported values for coexistence when the number of generalists and ecological overlap is high. This suggests that only communities composed of few generalists and moderate ecological overlap could coexist. Nevertheless, local dynamics may act strongly on generalists as hosts' switches are possible due to their generalist behaviour. Conversely, competition among specialists is decreased by the number of specialists although the effect is reduced when the ecological overlap is high. This shows a strong effect of the ecological niche and suggests that increasing the number of specialists in the same

environment is possible due to differential host use. Interestingly, specialist-generalist interactions find a balance between the previous two, supporting high species richness and high ecological overlap with low host-specific niche overlap.. This provides an immense advantage for species coexistence, and it may be the reason behind the high diversity of clownfish in the Coral Triangle, the most environmentally competitive area. It also explains why the clownfish clade has a balanced number of species representing both generalist and specialist behaviours, as both strategies complement each other maximising clownfish biodiversity.

CONCLUSION

Our study provides a framework to estimate the effects of species interactions and demonstrates the importance of including biotic interaction in the estimation of species' ecological niches. Our framework could be useful in the design of conservation strategies and provides a better understanding of the spatial patterns of mutualistic networks. Moreover, we used our framework to study interspecific competition in clownfishes, showing the importance of resource partitioning to regulate competition and the ecological basis to explain why clownfishes have different sets of associations with sea anemones. Our results aligned with previously supported hypotheses in other mutualistic systems upholding that the variety of mutualistic strategies serves ecosystem sustainability, reducing the effect of saturation by species richness and competitive exclusion. Competition avoidance through resource partitioning may be the primary mechanism that shapes clownfish communities across the Indo-Pacific. However, whether this mechanism is a product of evolutionary adaptations or dynamic responses to the composition of hosts remains to be investigated. Further studies in this direction may finally solve the evolutionary history and biogeography of clownfishes.

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Data accessibility statement

All data sets used and produced, figures and R scripts can be retrieved from the DRYAD repository (https://doi.org/10.5061/dryad.2bvq83bv8).

TEXT BOXES

Text Box 1. UUU parameters. The following developed metrics are adapted from the COUE framework (Guisan et al. 2014) to quantify and decompose species niche changes due to the implementation of biotic interactions.

Unavailable: Refers to the proportion of the species' environmental niche that is not available due to the absence of hosts.

Used: Proportion that refers to the area of the corrected niche over the area representing the union between environmental niche and environmental availability.

Unoccupied: Refers to the proportion of the environmental availability (multi-hosts "niche") not suitable for the focal species.

Centroid shift: Measures the shift in the niche position (centroid) between the environmental and corrected niches.

Environmental shift: Represents the change on the variables of importance that determine the position of the niche centroid.

Niche dissimilarity: Measures the amount of divergence between the environmental niche and the corrected niche computed as 1 – Schoener's D.

FIGURES

Figure 1.

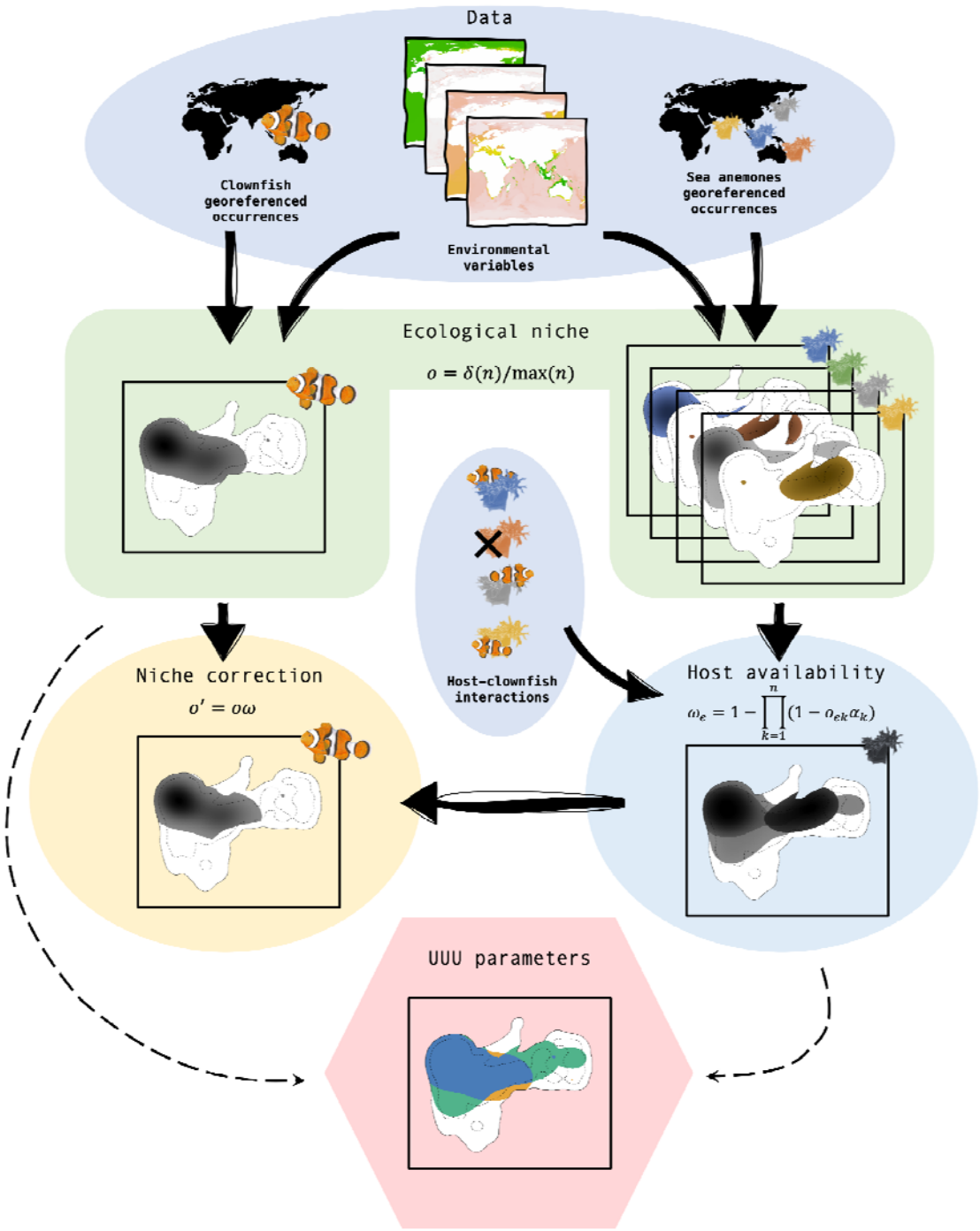


Figure 1. Framework scheme. For each clownfish species, georeferenced occurrences were collected, and the ecological niche was estimated from the environmental space created using the

selected environmental variables. Additionally, georeferenced occurrences of all sea anemones species were collected to infer their ecological niches following the same procedure as for the clownfish. Hosts' ecological niches were combined into a single multi-hosts “niche” using the interaction vector following the provided formula to create an envelope of host availability (). Finally, we constrained the clownfish ecological niche (o) by the host availability () to obtain a corrected ecological niche (o’). Comparisons between the host availability envelope and the estimated clownfish ecological niche (dashed lines) provided the UUU parameters, determining Unavailable environments (environmentally suitable but unavailable due to lack of host availability), Used environments as they were both suitable and available and Unoccupied environments as those that were available but not suitable for the clownfish.

Figure 2.

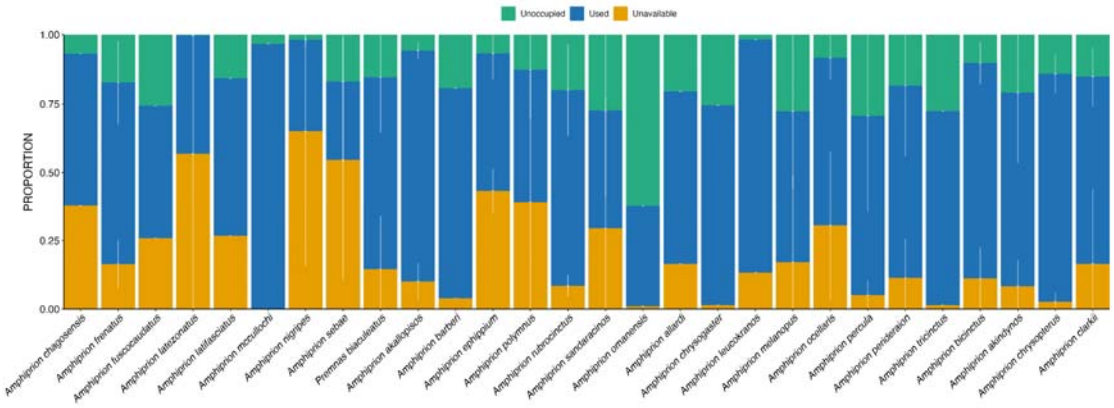


Figure 2. Stacked bar plot showing the averaged UUU proportions per clownfish species among ecoregions. Colours represent the different UUU parameters specified on the legend on top. White vertical lines represent the standard deviation across regions.

Figure 3.

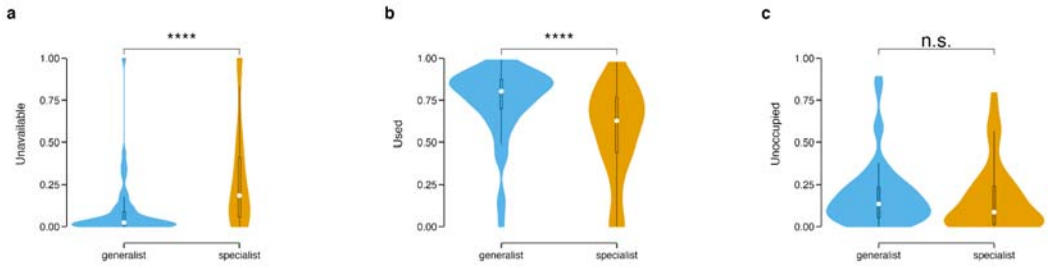


Figure 3. Comparisons between generalists and specialists on the proportions of Unavailable (a), Used (b), and Unoccupied (c) proportions of the niche, adapted from the 'COUE' framework (Guisan *et al*. 2014). Violin plots show the distribution of the data. Statistical significance is represented following the legend: no significant (n.s.); p.value < 0.05 (*); p.value < 0.01 (**); p.value < 0.001 (***); p.value < 0.0001 (****).

Figure 4.

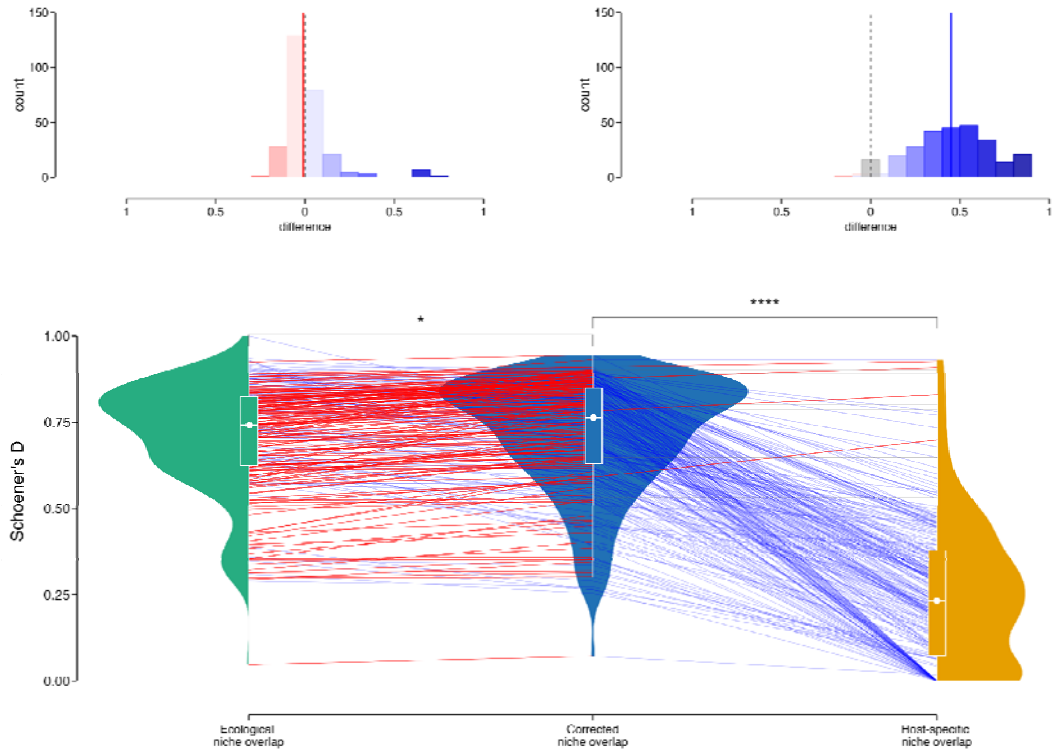


Figure 4. ecological niche, host-corrected niche, and host-specific niche pairwise species overlap. Top histograms show the distributions of differences between niche types of the bottom plot. Coloured bars follow the legend of the lines of the bottom plot. At the bottom, boxplots representing the overall intensity of niche overlap at each niche level are estimated. Crossing coloured lines represent each of the pairwise comparisons on each niche level. Blue lines show a decrease in intensity from one niche level to the next whereas red lines represent an increased intensity of competition. Violin plots show the distribution of the pairwise competition intensities of each niche level. Statistical significance is represented following the legend: no significant (n.s.); p.value < 0.05 (*); p.value < 0.01 (**); p.value < 0.001 (***); p.value < 0.0001 (****).

Figure 5.

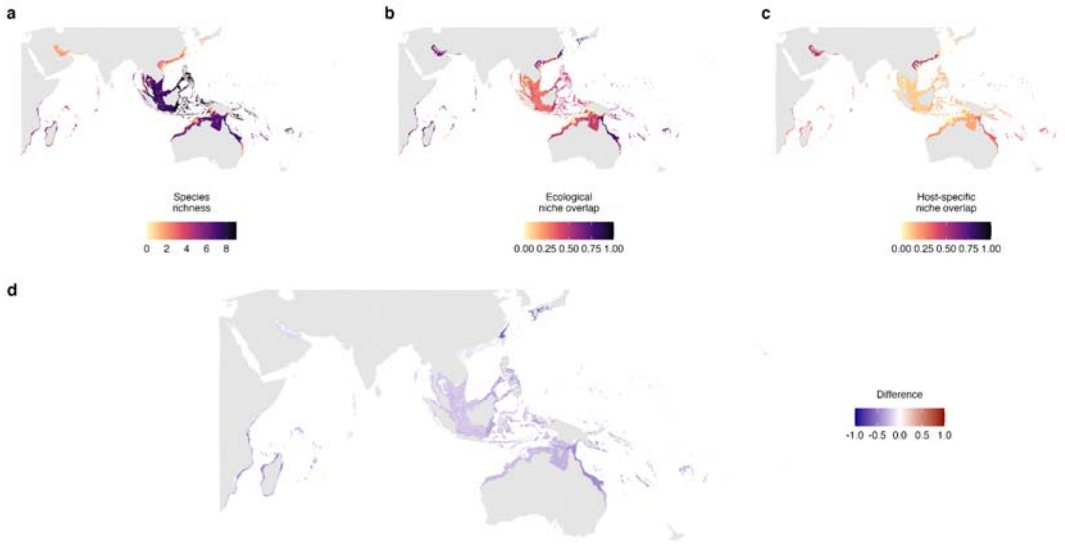
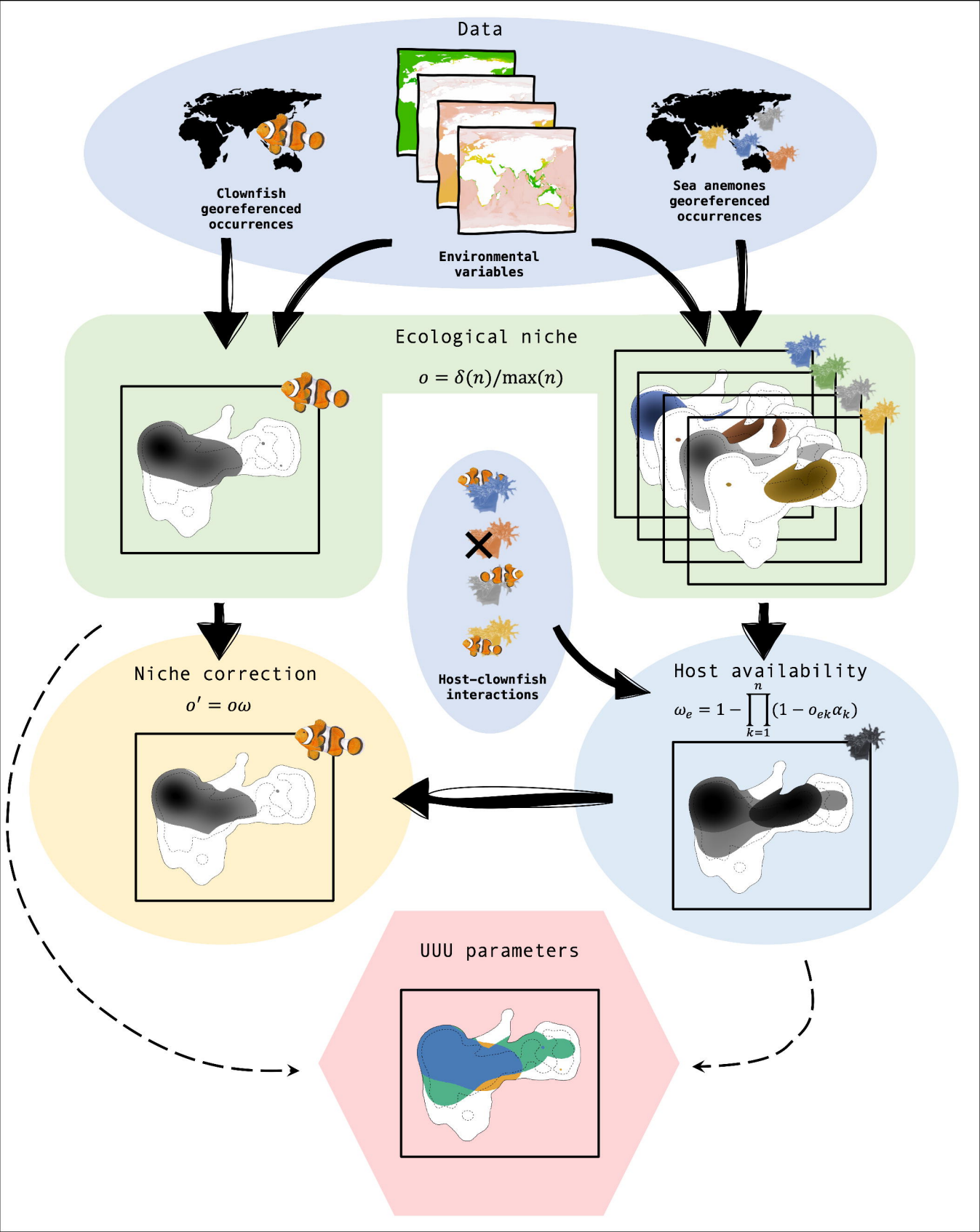
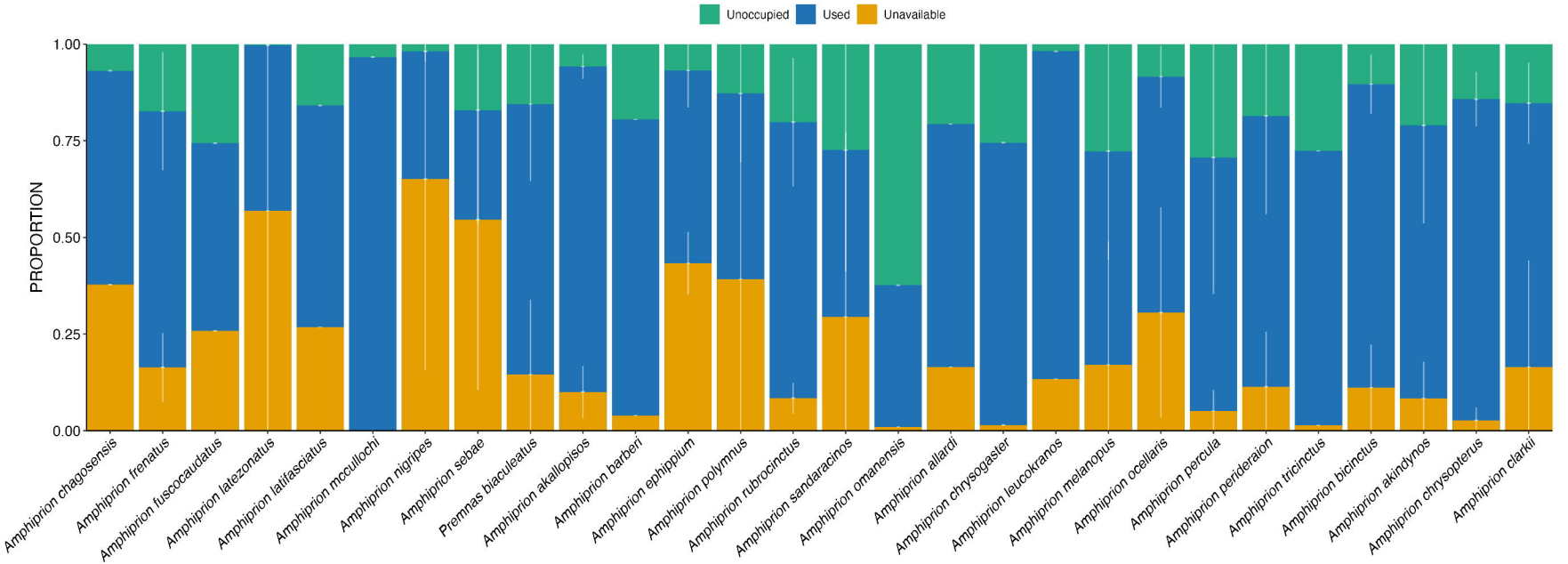
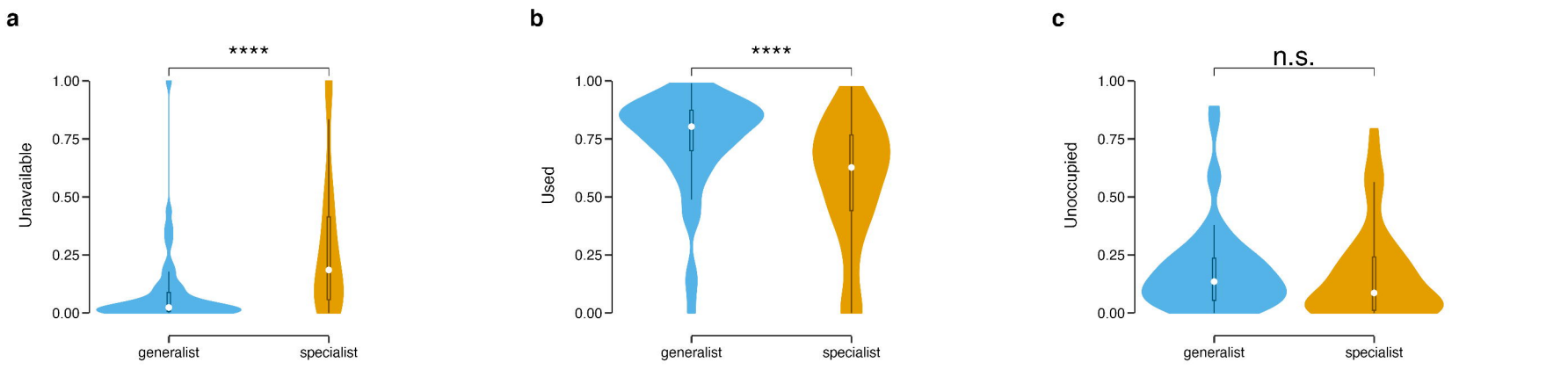
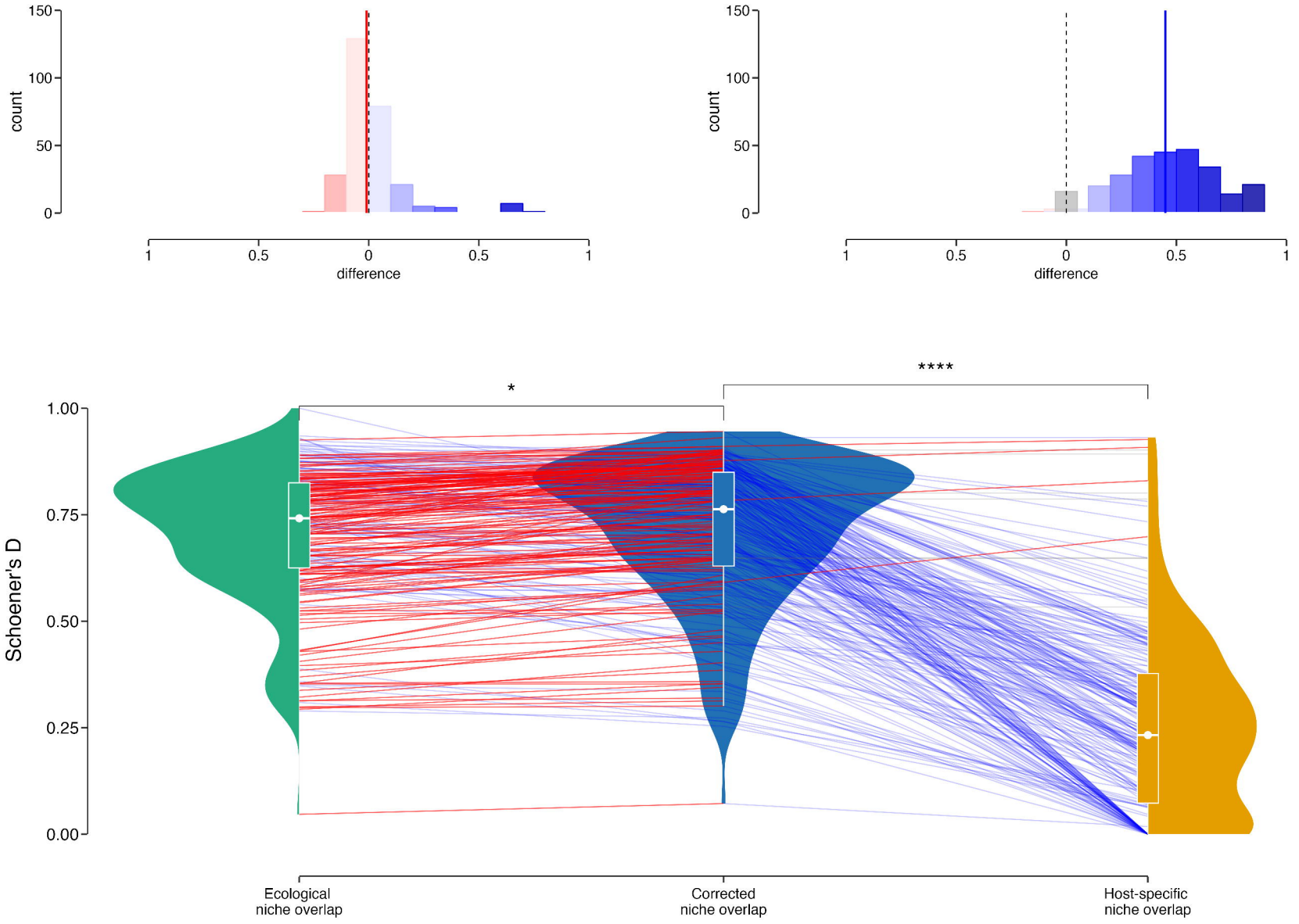


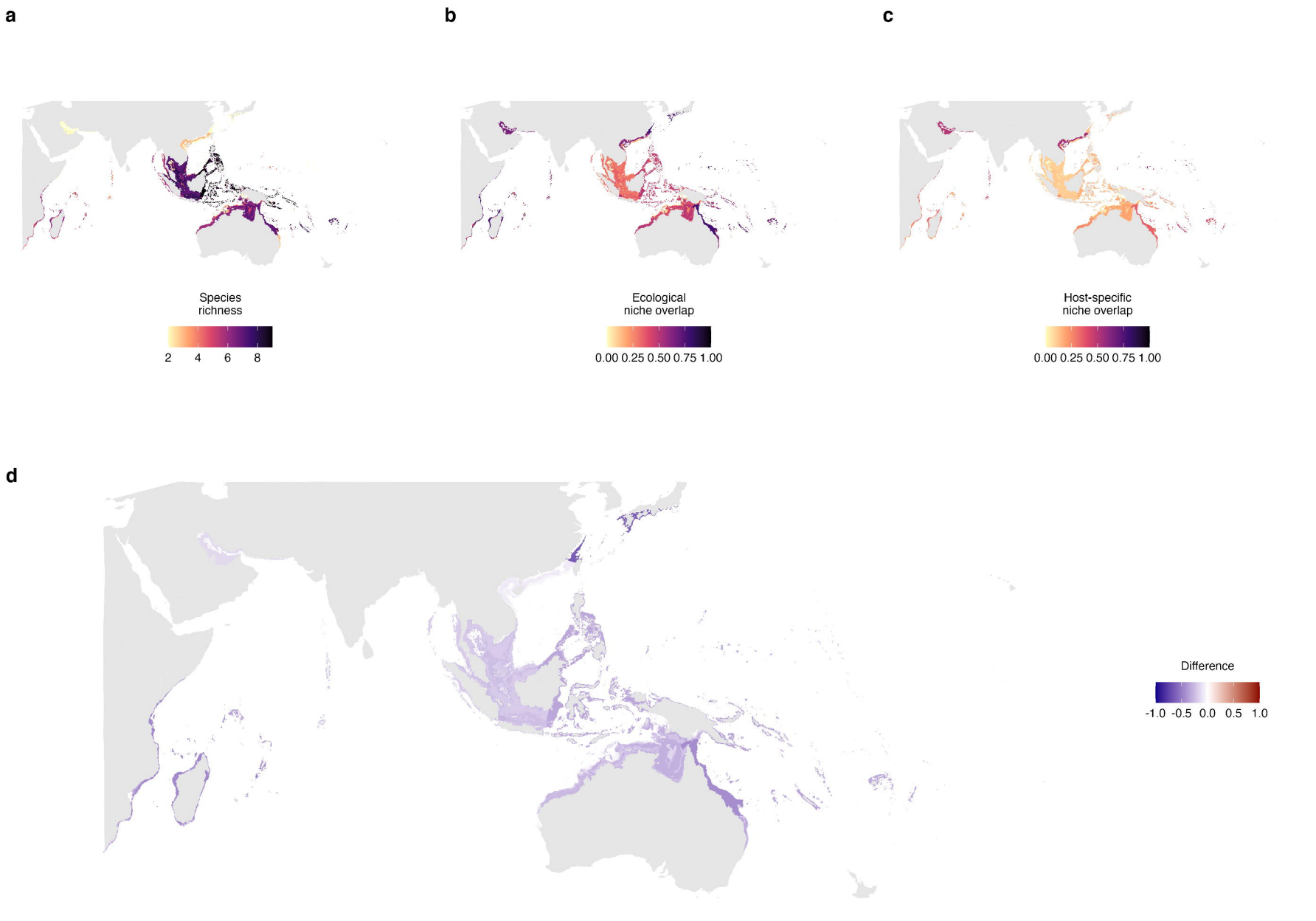
Figure 5. a) Estimated number of species occurring per location, b) Averaged ecological niche overlap among all co-occurring species per location. c) Average host-specific overlap intensity among of all co-occurring species per location. d) Difference between ecological niche overlap and host-specific overlap computed as $D_{host\text{-}specific}$ - D_{eco}. Negative values represent higher ecological niche overlap than host-specific niche overlap and positive values represent higher host-specific niche overlap than ecological niche overlap.


Data
Clownfish georeferenced occurrences
Environmental variables
Sea anemones georeferenced occurrences
Ecological niche
$o = \delta(n)/\max(n)$
Host-clownfish interactions
Niche correction
$o' = o\omega$
Host availability
$\omega_e = 1 - \prod_{k=1}^{n}(1 - o_{ek}\alpha_k)$
UUU parameters


Unoccupied
Used
Unavailable
PROPORTION
1.00
0.75
0.50
0.25
0.00
Amphiprion chagosensis
Amphiprion frenatus
Amphiprion fuscocaudatus
Amphiprion latezonatus
Amphiprion latifasciatus
Amphiprion mccullochi
Amphiprion nigripes
Amphiprion sebae
Premnas biaculeatus
Amphiprion akallopisos
Amphiprion barberi
Amphiprion ephippium
Amphiprion polymnus
Amphiprion rubrocinctus
Amphiprion sandaracinos
Amphiprion omanensis
Amphiprion allardi
Amphiprion chrysogaster
Amphiprion leucokranos
Amphiprion melanopus
Amphiprion ocellaris
Amphiprion percula
Amphiprion perideraion
Amphiprion tricinctus
Amphiprion bicinctus
Amphiprion akindynos
Amphiprion chrysopterus
Amphiprion clarkii


a
****
Unavailable
1.00
0.75
0.50
0.25
0.00
generalist
specialist
b
****
Used
1.00
0.75
0.50
0.25
0.00
generalist
specialist
c
n.s.
Unoccupied
1.00
0.75
0.50
0.25
0.00
generalist
specialist


count
150
100
50
0
1
0.5
0
0.5
1
difference
count
150
100
50
0
1
0.5
0
0.5
1
difference
*
****
Schoener's D
1.00
0.75
0.50
0.25
0.00
Ecological
niche overlap
Corrected
niche overlap
Host-specific
niche overlap


a
Species richness
2 4 6 8
b
Ecological niche overlap
0.00 0.25 0.50 0.75 1.00
c
Host-specific niche overlap
0.00 0.25 0.50 0.75 1.00
d
Difference
-1.0 -0.5 0.0 0.5 1.0