



## Microhabitat distributions and species interactions of ectoparasites on the gills of cichlid fish in Lake Victoria, Tanzania



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### ABSTRACT

Heterogeneous exposure to parasites may contribute to host species differentiation. Hosts often harbour multiple parasite species which may interact and thus modify each other's effects on host fitness. Antagonistic or synergistic interactions between parasites may be detectable as niche segregation within hosts. Consequently, the within-host distribution of different parasite taxa may constitute an important axis of infection variation among host populations and species. We investigated the microhabitat distributions and species interactions of gill parasites (four genera) infecting 14 sympatric cichlid species in Lake Victoria, Tanzania. We found that the two most abundant ectoparasite genera (the monogenean *Cichlidogyrus* spp. and the copepod *Lamproglana monodi*) were non-randomly distributed across the host gills and their spatial distribution differed between host species. This may indicate microhabitat selection by the parasites and cryptic differences in the host–parasite interaction among host species. Relationships among ectoparasite genera were synergistic: the abundances of *Cichlidogyrus* spp. and the copepods *L. monodi* and *Ergasilus lamellifer* tended to be positively correlated. In contrast, relationships among morphospecies of *Cichlidogyrus* were antagonistic: the abundances of morphospecies were negatively correlated. Together with niche overlap, this suggests competition among morphospecies of *Cichlidogyrus*. We also assessed the reproductive activity of the copepod species (the proportion of individuals carrying egg clutches), as it may be affected by the presence of other parasites and provide another indicator of the species specificity of the host–parasite relationship. Copepod reproductive activity did not differ between host species and was not associated with the presence or abundance of other parasites, suggesting that these are generalist parasites, thriving in all cichlid species examined from Lake Victoria.

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### 1. Introduction

Parasites can be important agents of selection on host populations, affecting host fitness through effects on e.g. host growth, reproduction and survival (Agnew et al., 2000; Lafferty and Kuris, 2009; Segar et al., 2018). They engage with their hosts in

coevolutionary arms races of adaptation and counter-adaptation (Decaestecker et al., 2007). Host species occupying different ecological niches are exposed to different parasites, potentially resulting in different infection profiles (here defined as the combination of parasite species diversity and abundance in a given host population (Knudsen et al., 2004; Pegg et al., 2015; Hablützel et al., 2017; Hayward et al., 2017)). Differences in exposure may lead to genetic divergence in immunity among host populations and species, possibly contributing to host reproductive isolation (Hamilton and Zuk, 1982; Landry et al., 2001; Nosil et al., 2005; Maan et al., 2008; Eizaguirre et al., 2011; Karvonen and Seehausen, 2012).

Several studies have reported differences in infection (in terms of parasite species identity and numbers) between closely related

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host species (Morand et al., 2015). If parasites impose a fitness cost, such differences may contribute to host divergence in resistance or tolerance, promoting reproductive isolation and perhaps speciation (Karvonen and Seehausen, 2012). Most studies of parasite-mediated divergent selection are based on parasite counts: differences between host populations in the prevalence, abundance, and intensity of various parasite taxa (e.g. Forbes et al., 1999; Medel, 2000; Maan et al., 2008; Konijnendijk et al., 2013). This approach presents two limitations. First, the parasite count approach ignores possible differences between host species in the spatial distribution of parasites. Some parasitic groups, for example monogeneans, are not only specialised to host species, but also to specific microhabitats within the host (Šimková and Morand, 2015). This may be driven by spatial variation in competition intensity, attachment opportunities, resource quality or access to mates (Rohde, 1994), or host spatial variation in defence mechanisms. We hypothesize that host species that are infected by the same parasite species in similar numbers may actually differ in how these parasites are spatially distributed. We suppose that this variation could result from the specific host morphology, without involving specific adaptations by the parasite. Alternatively, we may expect that differences in host characteristics (morphology, behaviour, physiology) could give rise to adaptation of the parasites, generating host species-specific parasite 'ecotypes', occupying different niches in different hosts. Such patterns can be detected only by investigating the within-host spatial distribution of parasites. Here, we expand on our previous studies of parasite-mediated divergence in African cichlid fish (Maan et al., 2008; Karvonen et al., 2018; Gobbin et al., 2020), by exploring parasite microhabitat segregation in a species assemblage of cichlids from Lake Victoria, Tanzania.

Second, parasite count measures are based on the assumption that parasites are independent of each other. However, hosts very frequently carry several parasite species at the same time (López-Villavicencio et al., 2007; Poulin, 2007; Taerum et al., 2010; Griffiths et al., 2011; Schmid-Hempel, 2013). These parasites may interact, with consequences for both host–parasite and parasite–parasite dynamics (Poulin, 2001; Mideo, 2009; Alizon et al., 2013). In the presence of competitors, parasite infection sites may change, thereby reducing interference (Holmes, 1973; Poulin, 2001). If parasite–parasite competition is strong and consistent over evolutionary time, then such niche segregation may become genetically fixed, resulting in a permanent change in the fundamental ecological niche (Holmes, 1973; for ecological character displacement see Brown and Wilson, 1956; Schluter, 2000). Competition-driven niche segregation has been observed in gastrointestinal helminths of fish (Vidal-Martínez and Kennedy, 2000; Karvonen et al., 2006) and birds (Bush and Holmes, 1986), in arthropod ectoparasites of birds (Choe and Kim, 1988, 1989) and in oxyurid nematodes infecting cockroaches (Adamson and Noble, 1992). In other host–parasite systems, this phenomenon was not observed, such as in 23 metazoan species of marine fish (Mouillot et al., 2003) and nine monogenean species in roach (Šimková et al., 2000).

Positive (synergistic) and negative (antagonistic) interactions among parasites modify each other's effects on host individuals (Graham, 2008; Thumbi et al., 2013), with possible consequences at the host population level (Rohani et al., 2003; Graham, 2008; Telfer et al., 2008; Mideo, 2009). For example, simultaneous and subsequent co-infections may facilitate parasite infection through mechanical damage (Bandilla et al., 2006) or through immunosuppression of the host (immunity-mediated facilitation (Jokela et al., 2000; Graham, 2008; Ezenwa et al., 2010; Karvonen et al., 2012)). Such positive interactions are relatively common (Lotz and Font, 1991; Šimková et al., 2000; Dallas et al., 2019). Negative interactions can occur, especially between parasites co-infecting the same

host tissue, competing for resources and space (resource-mediated competition (Lello et al., 2004; Graham, 2008; Daniels et al., 2013; Vaumourin et al., 2015; Dallas et al., 2019)). Negative interactions can also arise from cross-immunity: one parasite elicits an immune response that is also effective against other species of parasites (immunity-mediated competition (Lello et al., 2004; Porrozzini et al., 2004)). Although uncommon, interference competition can also take place: compounds secreted by a parasite can negatively affect the fitness of a competitor (Behnke et al., 2001; Cox, 2001).

Cichlid fish of the Great East African Lakes (Lakes Malawi, Tanganyika and Victoria) form a well-studied example of adaptive radiation (Kornfield and Smith, 2000; Kocher, 2004; Seehausen, 2006), with a high diversity in macrohabitat, microhabitat and trophic specialization (Sturmbauer and Meyer, 1992; Bouton et al., 1997; Genner et al., 1999). Previous studies have shown that cichlids are typically infected by multiple species of parasites, with different parasite communities and abundances between species (Lake Victoria: Maan et al., 2008; Karvonen et al., 2018; Gobbin et al., 2020; Lake Tanganyika: Vanhove et al., 2015; Hablützel et al., 2017; Lake Malawi: Blais et al., 2007). Consequently, it has been suggested that cichlid parasites may contribute to host diversification (reviewed in Vanhove et al., 2016; Gobbin et al., 2020). However, large-scale investigations of parasite ecology and inter-specific interactions between parasite taxa are scarce. Previous studies of microhabitat distribution of gill parasites in cichlids and other fish suggest that parasites with low within-host abundances are not saturating the available niche space in the gills, and thus they lack competition (Rohde, 1991, 1994). Consequently, the observed spatial niche restriction could be driven by other processes than competition, such as facilitation of mate finding (in siganid fishes, Geets et al., 1997; in pomacentrid fishes, Lo, 1999). Although monogeneans were long assumed to lack inter-specific competition (e.g. Morand et al., 2002; Rohde, 2002), some studies found evidence for competition-driven microhabitat selection and reduced niche overlap between monogenean species (*Dactylogyrus carpathicus* and *Dactylogyrus malleus*; Kadlec et al., 2003 and *Pseudodactylogyrus anguillae* and *Pseudodactylogyrus bini*; Matějusová et al., 2003).

In the present study, we aimed to determine if there is cryptic differentiation and microhabitat specialisation of ectoparasites infecting 14 sympatric Lake Victoria cichlid species. We investigated infection of *Lamproglana monodi* Capart, 1944 (Copepoda: Cyclopoida: Lernaedidae), *Ergasilus lamellifer* Fryer, 1961 (Copepoda: Poecilostomatoida: Ergasilidae), and *Cichlidogyrus* Paperna, 1960 (Monogenea: Dactylogyridea: Dactylogyridae) (the latter at both genus and species level). Several species of *Cichlidogyrus* occur in Lake Victoria, most of which are not formally described. This flatworm gill parasite primarily infests members of the family Cichlidae (Paperna, 1960) (but also killifishes within *Aphyosemion* (Messu Mandeng et al., 2015) and the nandid *Polycentropsis abbreviata* (Pariselle and Euzet, 2009)). Some species of *Cichlidogyrus* are specific to a single cichlid species or a few closely related species (Pariselle and Euzet, 2009; Roux and Avenant-Oldewage, 2010; Mendlová and Šimková, 2014). Others have a broad host range (Jorissen et al., 2018). The presence of several cryptic species of *Cichlidogyrus* was previously revealed by molecular investigations in cichlids from the Ivory Coast (Pouyaud et al., 2006). Many species descriptions of *Cichlidogyrus* only report host species, and the gills in general as the infection site, and no other ecological data; here we also report within-host microhabitat distribution within the gills.

We explored the relationships between different parasite taxa and how they differ between host species. If parasite taxa are competing, their abundances may be negatively correlated. A positive correlation would emerge if parasite interactions are synergistic. Differences between host species in the strength and/or direction

of such parasite associations could indicate that the host–parasite relationship is species-specific.

Finally, we also investigated whether the reproductive activity of copepods differs between host species and whether this may be influenced by the presence of conspecific or heterospecific parasites.

## 2. Materials and methods

### 2.1. Fish collection

Cichlid fish were collected in June–October 2014 at Makobe Island, in southern Lake Victoria, Tanzania, by angling and with gillnets of variable mesh sizes, set at different depths (0.5–19.0 m). We collected 332 fishes from 14 sympatric cichlid species belonging to the Lake Victoria haplochromine radiation, with different ecological specializations (i.e. diet and water depth distribution (Witte and van Oijen, 1990; Seehausen, 1996; Bouton et al., 1997; Seehausen and Bouton, 1998); Supplementary Table S1) and different levels of genetic differentiation among them (Wagner et al., 2012; Karvonen et al., 2018). Since females are difficult to identify in the field, only males were considered. Fish were euthanised with an overdose of 2-phenoxyethanol (2.5 ml/l) immediately after capture. In the field, immediately after collection, 148 fish (whole body) were preserved in 4% formalin and subsequently transferred to increasing concentrations of ethanol (final concentration 70%), 184 fish were directly preserved in 100% ethanol (for future genetic analysis). Samples were shipped to Europe for analyses. Each individual fish was measured (standard length (SL), body depth (BD), to the nearest 0.1 mm) and weighed (to the nearest 0.1 g) on the same day as parasite screening (901 ± 129 days after collection (mean ± S.D.)). We calculated individual fish condition factor (CF) as  $CF = 100 * (\text{weight}/SL^3)$  (Sutton et al., 2000). Sampling was conducted with permission from the Tanzania Commission for Science and Technology (COSTECH - No. 2013-253-NA-2014-117).

### 2.2. Parasite screening

We examined the gills on the right side of each fish, under a dissecting stereoscope. All macroparasites were counted and identified (following Paperna, 1996 and monogenean literature: Vanhove et al., 2011; Muterezi Bukinga et al., 2012). We observed 1414 individuals in five ectoparasite taxa: *Cichlidogyrus* spp. (Paperna, 1960 (Monogenea: Dactylogyridea: Dactylogyridae), *Gyrodactylus sturmbaueri* Vanhove, Snoeks, Volckaert & Huysse, 2011 (Monogenea: Gyrodactylidea: Gyrodactylidae), *Lamproglana monodi* Capart, 1944 (Copepoda: Cyclopoida: Lernaecidae), *Ergasilus lamellifer* Fryer, 1961 (Copepoda: Poecilostomatoida: Ergasilidae), glochidia mussel larvae (Bivalvia: Unionoidea). *Gyrodactylus sturmbaueri* was found only once and therefore not included in analyses. The attachment site on the gills was recorded for *Cichlidogyrus* spp., *L. monodi* and *E. lamellifer* (but not for glochidia; Supplementary Table S2), according to a subdivision of each gill arch into nine microhabitats (resulting in a total of 36 gill microhabitats (Gel'nar et al., 1990)). This subdivision was based on coarser spatial units: gill arches (from anterior to posterior: I, II, III, IV), longitudinal segments (dorsal, medial, ventral) and vertical areas (proximal, central, distal; from the tip of the gill filaments to the gill bar) (Fig. 1A). The presence or absence of egg clutches in copepod females was recorded.

### 2.3. *Cichlidogyrus* morphospecies identification

For morphological identification of *Cichlidogyrus* we randomly selected a subset of specimens ( $n = 213$ ) from 11 host species that each carried more than 10 parasite individuals. We aimed to identify 15 specimens of *Cichlidogyrus* per host species, by sampling all worms infesting each fish individual ( $1 < n > 7$ ) from a randomly selected pool of each host species. If the total number of worms available per host population was less than 15, then all worms of that host population were identified (see Supplementary Table S1 for sample sizes).

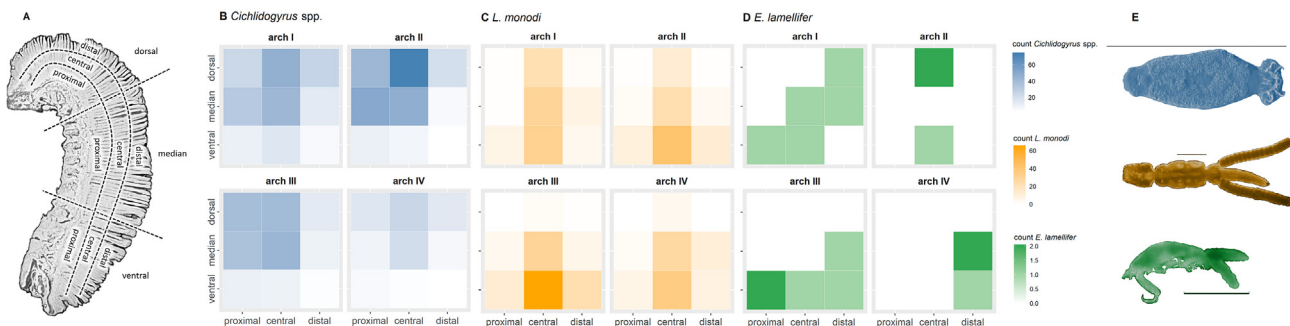
Specimens of *Cichlidogyrus* were mounted on slides in Hoyer's medium, after prior treatment with 20% sodium dodecyl sulphate to soften tissues. They were examined with a microscope (Olympus BX41TF) under 1000× magnification using differential interference phase contrast. Although most of the species of *Cichlidogyrus* that we found are not formally described, species can be discriminated based on the shape and size of sclerotized parts of the attachment organ (haptor) and, in particular, on those of the male copulatory organ (MCO) (e.g. Grégoir et al., 2015; Gobbin et al., 2020). Morphological assessment of worms belonging to *Cichlidogyrus* revealed the presence of five different morphospecies, provisionally named with roman numbers following Gobbin et al. (2020; unpublished formal taxonomical description).

### 2.4. Data analysis

#### 2.4.1. Parasite spatial distribution

To investigate the spatial distribution of each parasite taxon and of each morphospecies of *Cichlidogyrus* on the 36 gill microhabitats, we used generalized linear models in R (R Core Team, 2019). Fixed effects included gill microhabitat and the total abundance of the respective parasite per fish individual, to correct for interindividual variation in infection. Since the preservation method (formalin or ethanol) had an effect on the intensity of one of the parasite taxa (*Cichlidogyrus* spp., Supplementary Table S3), we included that as a fixed effect. Random effects included: fish individual identity, to account for repeated sampling (as each fish individual could be infected by several parasites) and host species, to control for pseudoreplication. A random effect at the level of observation was included to correct for overdispersion. We determined the significance of fixed effects by likelihood ratio tests (LRTs). Host species represented by fewer than five individuals were excluded from analyses (14 host species analysed at the parasite genus level, seven at the *Cichlidogyrus* morphospecies level).

To obtain a general overview of the parasite spatial distributions and assess host species differences in parasite spatial distribution, we also analysed coarser spatial units than the 36 microhabitats considered above. These are: gill arches (I, II, III, IV), longitudinal segments (dorsal, medial, ventral) and vertical areas (proximal, central, distal) (Fig. 1A). We used generalized linear models, followed by post-hoc Tukey tests. Fixed effects included host species (to account for species differences in parasite abundance), gill microhabitat (four arches or three longitudinal segments or three vertical areas) and their interactions, as well as the total abundance of the respective parasite per fish individual (to correct for interindividual variation in infection). Since the preservation method (formalin or ethanol) had an effect on the intensity of one of the parasite taxa (*Cichlidogyrus* spp., Supplementary Table S3), we included that as a fixed effect. In particular, the interaction species:microhabitat indicates whether the spatial distribution differs between host species. This was not assessed for the 36 sites analysis as comparisons were too numerous to achieve sufficient statistical power. Random effects included fish individual identity, to account for repeated sampling (as each fish



**Fig. 1.** Gill microhabitat distributions of three ectoparasite taxa infecting cichlids sampled at Makobe Island, Lake Victoria, Tanzania. (A) Spatial subdivision of gill arches into longitudinal segments (dorsal, medial, ventral) and vertical areas (proximal, central, distal). Microhabitat distribution, expressed as abundance, of (B) *Cichlidogyrus* spp., (C) *L. monodi* and (D) *E. lamellifer*. (E) Microscope photographs of the studied gill parasites (dorsal view for *Cichlidogyrus* spp. and *L. monodi*, lateral view for *E. lamellifer*). Scale bars = 500 μm.

individual could be infected by several parasites). A random effect at the level of observation was also included to correct for overdispersion. We determined the significance of fixed effects by LRTs.

To investigate if the overall spatial distribution pattern was present in each host species or only in some, we applied the same models separately on each host species. The significance level was corrected for pseudoreplication (Benjamini and Hochberg, 1995).

#### 2.4.2. Interactions between parasites

We used generalized linear models to investigate if the abundance of a given parasite genus or a morphospecies of *Cichlidogyrus* was correlated with the abundance of another genus or morphospecies. Fixed effects included host species and the abundance of each parasite genus. In parasite genus models (not *Cichlidogyrus* morphospecies models due to low sample size) we also included as fixed effects all interaction terms between host species and abundance of each parasite genus. We selected the Minimum Adequate Model (MAM) by stepwise removal of non-significant variables, determined by LRT. Where overdispersion was detected, we corrected the standard errors using a quasipoisson model (Zuur et al., 2009). Host species represented by fewer than 10 fish individuals were excluded from analysis at parasite genus level. This was not done for the analysis of morphospecies of *Cichlidogyrus*, to allow comparisons between a sufficient number of different host species.

To investigate if interspecific interactions among parasite genera (not morphospecies of *Cichlidogyrus* due to low sample size) were present in each host species or only in some, we applied the same models separately on each host species. Significance level was corrected for pseudoreplication (Benjamini and Hochberg, 1995).

#### 2.4.3. Reproductive activity of copepods

Female parasitic copepods attached to gills produce egg clutches appended to their body. We used the presence of egg clutches as a proxy for copepod reproductive activity. This may provide indications of species specificity of the host–parasite relationship (Paperna, 1996). We compared the proportion of copepods carrying egg clutches between host species using generalized linear models. Fixed effects included host species, host SL and host CF, capture water depth, abundance of conspecifics and of heterospecifics, fish preservation method (formalin versus ethanol) and days elapsed between fish collection and parasite screening. As above, we determined the significance of fixed effects by

LRT and we used Tukey’s post-hoc test to obtain parameter estimates.

### 3. Results

#### 3.1. Non-random spatial distribution on fish gills: parasite genera

The spatial distribution of *Cichlidogyrus* spp. and of *L. monodi* was non-random across the 36 gill attachment sites (Table 1). In contrast, the spatial distribution of *E. lamellifer* did not significantly deviate from random, probably due to the low sample size (18 parasites in 248 fish individuals).

When considering the lower resolution distributions over gill arches, segments and areas, we also observed a non-random spatial distribution of *Cichlidogyrus* spp. and *L. monodi* (Table 1). Overall, *Cichlidogyrus* spp. were less abundant on the fourth gill arch, compared with the three other arches, whereas *L. monodi* were more abundant on the third arch than on the fourth. Distribution patterns of longitudinal segments were reversed for *Cichlidogyrus* spp. and *L. monodi*: the former were more abundant on the dorsal segment and less on the ventral one, while the latter were more abundant on the ventral segment and less on the dorsal one (Table 1, Fig. 2). Both *Cichlidogyrus* spp. and *L. monodi* were more abundant in the central area, but this was more pronounced in the latter. *Ergasilus lamellifer* followed the longitudinal distribution pattern of the other copepod, *L. monodi*, with an increasing abundance towards more ventral segments.

The non-random distributions of *Cichlidogyrus* spp. and *L. monodi* were also observed when testing each host species separately (Supplementary Table S4). *Cichlidogyrus* spp. were non-randomly distributed across all gill microhabitats in eight out of 13 infected host species (Fig. 3); *L. monodi* were non-randomly distributed across all gill microhabitats in 12 out of 14 infected host species (Fig. 3). For the lower resolution distributions: *Cichlidogyrus* spp. were non-randomly distributed across vertical areas in nine out of the 13 infected host species, *L. monodi* were non-randomly distributed across vertical areas in 10 out of 13 and in longitudinal segments in 11 out of 14 infected host species (Supplementary Fig. S1 and Supplementary Table S4).

The spatial distribution of *L. monodi* and *E. lamellifer* did not differ between host species (the only exception was the vertical distribution of *L. monodi*, Supplementary Fig. S1C). In contrast, the spatial distribution of *Cichlidogyrus* spp. did differ between host species (Fig. 3 and Supplementary Fig. S1). These differences in distribution were observed at each level of spatial subdivision considered (gill arches, longitudinal segments and vertical areas; Table 1).

**Table 1**

Differences in the spatial distribution of parasites on the gills of cichlids inhabiting Makobe Island, Lake Victoria, Tanzania (all 36 microhabitats, gill arches, longitudinal segments and vertical areas). The reported contribution of each fixed effect was assessed through ANOVA. For all microhabitat analyses, starting models included parasite location on the gill and total parasite intensity per host individual (*n* parasites), and preservation method (random effects: host species, fish individual identity, number of observations). For other analyses, starting models included host species, parasite location on the gill, their interaction term and total number of parasite individuals per host individual (*n* parasites), and preservation method (random effects: fish individual identity, number of observations). Tukey pairwise comparison between spatial locations (except all 36 microhabitats) revealed significant parasite microhabitat selection.

	Parasite	Fixed effect	Chi sq	df	<i>P</i>	Comparison	Estimate	<i>Z</i>	<i>P</i>		
All microhabitats (36)	<i>Cichlidogyrus</i> spp.	Site36	215.29	35	<0.0001	<sup>d</sup>					
		<i>n</i> parasites	216.98	1	<0.0001	<sup>d</sup>					
		Preservation	0.11	1	0.745						
	<i>Lamproglena monodi</i>	site36	252.90	35	<0.0001	<sup>d</sup>					
		<i>n</i> parasites	135.90	1	<0.0001	<sup>d</sup>					
		Preservation	0.01	1	0.939						
	<i>Ergasilus lamellifer</i>	Site36	1.80	35	1.000						
		<i>N</i> parasites	NA								
		Preservation	0.00	1	1.000						
Gill arches (4)	<i>Cichlidogyrus</i> spp.	Species	16.69	12	0.162		II vs. I	0.15	1.36	0.522	
		Arch	46.61	3	<0.0001	<sup>d</sup>	III vs. I	-0.06	-0.49	0.962	
		<i>n</i> parasites	239.10	1	<0.0001	<sup>d</sup>	IV < I	-0.75	-5.52	<0.001	
		Species:arch	61.31	36	0.005	<sup>c</sup>	III vs. II	-0.21	-1.85	0.248	
		Preservation	0.00	1	0.977		IV < II	-0.90	-6.80	<0.001	
	<i>L. monodi</i>	Species	26.88	13	0.013	<sup>b</sup>	II vs. I	0.01	0.07	0.999	
		Arch	7.42	3	0.060	<sup>a</sup>	III > I	0.29	2.31	0.096	
		<i>n</i> parasites	303.24	1	<0.0001	<sup>d</sup>	IV vs. I	-0.09	-0.62	0.925	
		Species:arch	41.24	39	0.373		III vs. II	0.28	2.24	0.111	
		Preservation	0.22	1	0.640		IV vs. II	-0.10	-0.69	0.901	
	<i>E. lamellifer</i>	Species	NA				IV < III	-0.38	-2.92	0.018	
		Arch	NA				II vs. I	-0.51	-0.70	0.897	
		<i>n</i> parasites	NA				III vs. I	0.00	0.00	1.000	
		Species:arch	NA				IV vs. I	-0.51	-0.70	0.897	
		Preservation	NA				III vs. II	0.51	0.70	0.897	
	Longitudinal segments (3)	<i>Cichlidogyrus</i> spp.	Species	27.80	12	0.006	<sup>c</sup>	Median < dorsal	-0.19	-2.25	0.062
			Segment	115.51	2	<0.0001	<sup>d</sup>	Ventral < dorsal	-1.43	-11.86	<0.001
			<i>n</i> parasites	291.78	1	<0.0001	<sup>d</sup>	Ventral < median	-1.24	-10.13	<0.001
			Species:segment	47.81	24	0.003	<sup>c</sup>				
			Preservation	0.03	1	0.870					
		<i>L. monodi</i>	Species	2.49	14	0.999		Median > dorsal	1.13	6.85	<0.0001
			Segment	103.86	3	<0.0001	<sup>d</sup>	Ventral > dorsal	1.68	10.77	<0.0001
			<i>n</i> parasites	203.40	1	<0.0001	<sup>d</sup>	Ventral > median	0.55	5.39	<0.0001
			Species:segment	35.54	26	0.100					
Preservation			0.00	1	0.994						
<i>E. lamellifer</i>		Species	2.80	9	0.972		Median vs. dorsal	0.51	0.70	0.762	
		Segment	0.00	3	1.000		Ventral vs. dorsal	0.98	1.45	0.313	
		<i>n</i> parasites	NA	0	NA		Ventral vs. median	0.47	0.82	0.686	
		Species:segment	0.00	16	1.000						
		Preservation	0.00	1	1.000						
Vertical areas (3)		<i>Cichlidogyrus</i> spp.	Species	15.14	12	0.234		Central > proximal	0.31	3.22	0.004
			Area	79.69	2	<0.0001	<sup>d</sup>	Distal < proximal	-0.80	-6.60	<0.001
			<i>n</i> parasites	277.66	1	<0.0001	<sup>d</sup>	Distal < central	-1.11	-9.44	<0.001
			Species:area	95.16	24	<0.0001	<sup>d</sup>				
			Preservation	0.05	1	0.823					
		<i>L. monodi</i>	Species	57.16	34	0.008	<sup>c</sup>	Central > proximal	1.86	12.34	<0.001
			Area	204.08	23	<0.0001	<sup>d</sup>	Distal > proximal	0.49	2.74	0.016
			<i>n</i> parasites	202.53	1	<0.0001	<sup>d</sup>	Distal < central	-1.37	-11.16	<0.001
			Species:area	48.09	26	0.005	<sup>c</sup>				
	Preservation		0.00	1	0.996						
	<i>E. lamellifer</i>	Species	4.37	9	0.886		Central vs. proximal	0.60	0.98	0.587	
		Area	2.56	3	0.464		Distal vs. proximal	0.85	1.23	0.434	
		<i>n</i> parasites	NA	0	NA		Distal vs. central	0.15	0.28	0.958	
		Species:area	0.00	16	1.000						
		Preservation	0.00	1	1.000						

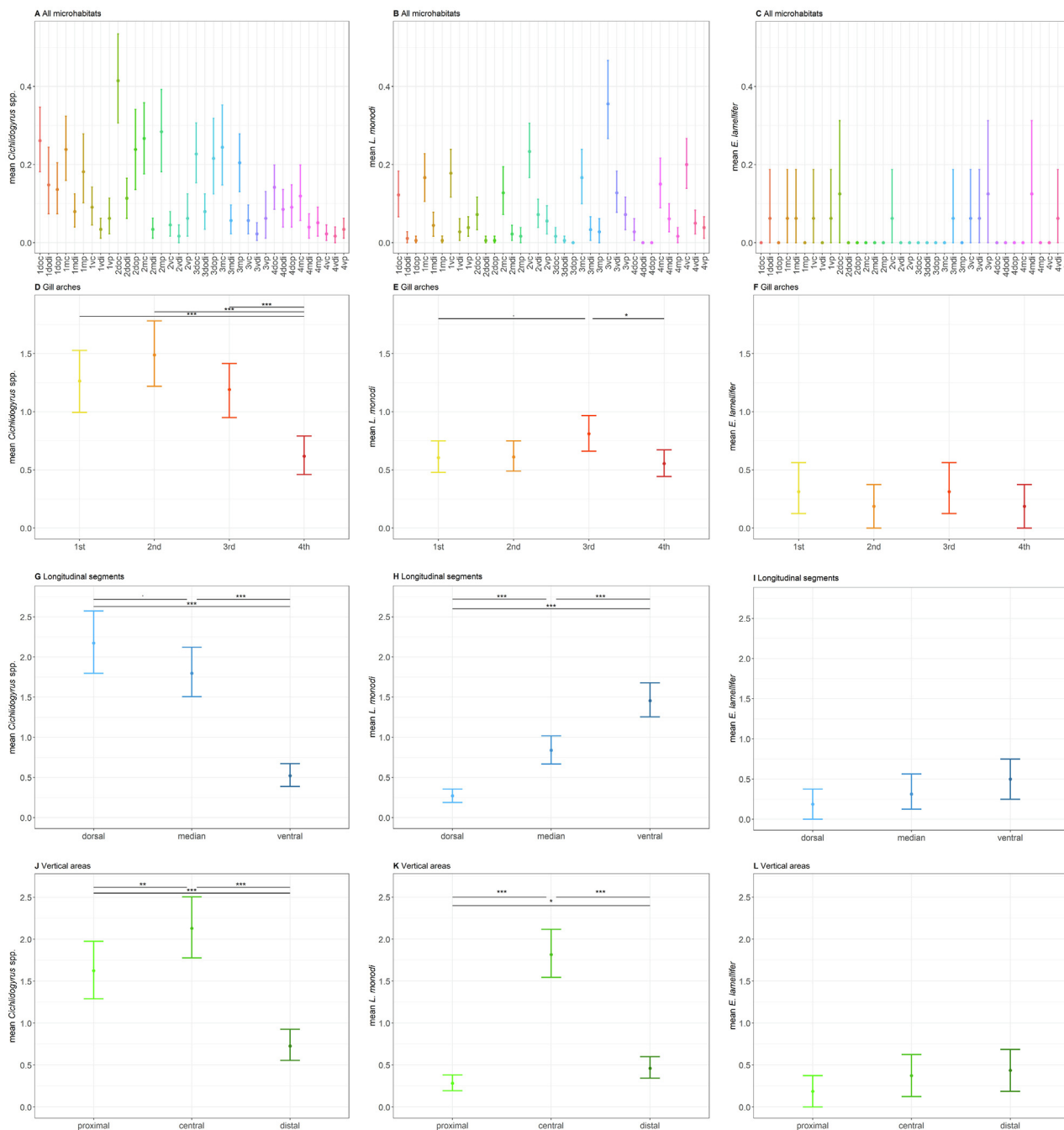
df, degrees of freedom; NA, not available.

<sup>a</sup> *P* ≤ 0.1.

<sup>b</sup> *P* ≤ 0.05.

<sup>c</sup> *P* ≤ 0.01.

<sup>d</sup> *P* ≤ 0.001.



**Fig. 2.** Spatial distribution of *Cichlidogyrus* spp., *Lamproglena monodi* and *Ergasilus lamellifer* infecting cichlid gills at Makobe Island, Lake Victoria, Tanzania. (A–C) Thirty-six microhabitats, (D–F) gill arches, (G–I) longitudinal segments and (J–L) vertical areas. Asterisks indicate a significant difference in parasite spatial distribution between microhabitats ( $P \leq 0.01$ ,  $*P \leq 0.05$ ,  $**P \leq 0.01$ ,  $***P \leq 0.001$ ) (except in (A–C), where post-hoc tests were not performed).

### 3.2. Non-random spatial distribution on fish gills: morphospecies of *Cichlidogyrus*

Sample size allowed statistical analysis only for the two most common morphospecies (*Cichlidogyrus* sp. I and sp. II). In line with the aforementioned pattern, morphospecies of *Cichlidogyrus* was non-randomly distributed on fish gills. *Cichlidogyrus* sp. I was non-randomly distributed regardless of the spatial subdivision considered (all 36 microhabitats, gill arches, longitudinal segments and vertical area); sp. II was non-randomly distributed among gill arches, longitudinal segments and vertical areas (Table 2, Supplementary Fig. S2).

The two morphospecies had approximately similar distributions. Both were least abundant on the fourth gill arch and ventral segments, and most abundant in the central areas of the gills (for significant differences see Table 2 and Supplementary Fig. S2).

The non-random distributions of *Cichlidogyrus* sp. I and sp. II were also observed when testing each host species separately (Supplementary Fig. S3, Supplementary Table S5). *Cichlidogyrus* sp. I were non-randomly distributed across all gill microhabitats in four out of seven infected host species, across longitudinal segments (four out of seven) and across vertical areas (six out of seven). *Cichlidogyrus* sp. II were non-randomly distributed across vertical areas in three out of six infected host species.



**Fig. 3.** Within-host spatial distribution over 36 gill microhabitats of (A) *Cichlidogyrus* spp., (B) *Lamproglena monodi* and (C) *Ergasilus lamellifer*, in 14 cichlid host species inhabiting Makobe Island, Lake Victoria, Tanzania. Asterisks indicate a significant within-species non-random distribution ( $P \leq 0.01$ , \* $P \leq 0.05$ , \*\* $P \leq 0.01$ , \*\*\* $P \leq 0.001$ ). The total number of parasites and of infected host individuals per species are reported.

The spatial distribution of both morphospecies of *Cichlidogyrus* differed between host species for the majority of the spatial divisions considered (except vertical areas for both morphospecies and longitudinal segment distribution for sp. II; Supplementary Fig. S3, Table 2).

### 3.3. Relationships between parasite taxa

To assess if parasite species are competing with or facilitating each other, we tested if the abundance of one parasite taxon was correlated with the abundance of another. After taking into account the differences in parasite abundance between host species, we observed that the abundance of both *Cichlidogyrus* spp. and of *L. monodi* were positively correlated with *E. lamellifer* (Fig. 4, Table 3). The positive direction of these relationships was observed also when testing each host species separately, albeit not reaching statistical significance in most of them (Supplementary Table S6). On the other hand, there was no positive association between *Cichlidogyrus* spp. and *L. monodi*. The abundance of glochidia was not associated with other parasites. Interspecific interactions between parasite genera did not differ between host species. Since some influential outliers (Cook's distance >5) were identified in regressions of *L. monodi* and *E. lamellifer*, we repeated these analyses without those. This did not change the results (Supplementary Table S7). Adding fish individual length as a fixed effect also did not change these results.

We also investigated interactions among morphospecies of *Cichlidogyrus*. Contrary to the pattern found at higher taxonomic level, all interactions between morphospecies were negative (nine out of 10 relationships; there was one (non-significant) positive association; Fig. 5; Table 3). Differences between host species in morphospecies' interactions were not investigated due to the low sample size.

### 3.4. Reproductive success of copepods

The proportion of *L. monodi* carrying egg clutches was 77% and did not significantly differ between host species ( $33\% \pm \text{S.D. } 0.35 - 100\% \pm \text{S.D. } 0.00$ ; Table 4). It also did not covary with individual fish length, capture water depth, CF, elapsed time between fish collection and parasite screening (Supplementary Fig. S4), nor with the abundance of conspecifics or other parasites. The sample size of *E. lamellifer* was too low to perform statistical analyses (18 parasite individuals, 5.5% carrying egg sacs).

## 4. Discussion

We investigated patterns of microhabitat distribution, interspecific interactions and reproductive activity in gill parasites infecting sympatric cichlid species from Lake Victoria, to assess potential species specificity of the host–parasite relationships. We found that representatives of the two most abundant ectoparasite genera (*Cichlidogyrus* spp., *L. monodi*) and morphospecies of *Cichlidogyrus* (sp. I, sp. II) had a non-random spatial distribution on gills. *Cichlidogyrus* spp. and *L. monodi* occupied different microhabitat niches within the host, while the two morphospecies of *Cichlidogyrus* occupied similar microhabitats. In several cases, parasite spatial distributions differed between host species. Interactions among the different ectoparasite genera were synergistic, whereas among morphospecies of *Cichlidogyrus* they were antagonistic. Reproductive activity of the copepod *L. monodi* did not differ between host species and was not associated with the abundance of conspecific or heterospecific parasites.

### 4.1. Non-random spatial distribution on fish gills

We observed non-random microhabitat distributions for *Cichlidogyrus* spp. and for *L. monodi* that differed between these two parasite taxa. This suggests that they have adapted to different niches

**Table 2**

Differences in spatial distribution on fish gills (all 36 microhabitats, gill arches, longitudinal segments and vertical area) of morphospecies of *Cichlidogyrus* infecting cichlids inhabiting Makobe Island, Lake Victoria, Tanzania. The reported contribution of each fixed effect was assessed through ANOVA. For all microhabitat analyses, starting models included parasite location on the gill and total parasite intensity per host individual (*n* parasites) (random effects: host species, fish individual identity, number of observations). For other analyses, starting models included host species, parasite location on the gill, their interaction term and total parasite intensity per host individual (*n* parasites) (random effects: fish individual identity). Tukey pairwise comparison between spatial locations (except all 36 microhabitats) revealed significant parasite microhabitat selection.

	Parasite	Fixed effect	Chi sq	df	P	Comparison	Estimate	Z	p	
All microhabitats (36)	sp. I	Site36	85.07	35	<0.001					
		<i>n</i> parasites	0.15	1	0.700					
	sp. II	Site36	23.24	35	0.936					
		<i>n</i> parasites	0.09	1	0.766					
Gill arches (4)	sp. I	Species	0.00	6	1.000	II vs. I	0.02	1.30	0.560	
		Arch	20.55	3	<0.001	III vs. I	0.00	0.00	1.000	
		<i>n</i> parasites	0.00	1	1.000	IV < I	-0.14	-3.00	0.014	
		Species:arch	36.46	18	0.006	III vs. II	-0.06	-1.30	0.560	
						IV < II	-0.21	-4.30	<0.001	
						IV < III	-0.14	-3.00	0.014	
	sp. II	Species	0.00	6	1.000	II vs. I	-0.11	-1.44	0.472	
		Arch	13.09	3	0.004	III < I	-0.14	-1.86	0.247	
		<i>n</i> parasites	0.00	1	1.000	IV < I	-0.27	-3.51	0.003	
		Species:arch	29.40	18	0.044	III > II	-0.03	-0.41	0.976	
						IV < II	-0.16	-2.06	0.165	
						IV < III	-0.13	-1.65	0.268	
	Longitudinal segments (3)	sp. I	Species	0.36	6	0.999	Median vs. dorsal	0.09	1.89	0.142
			Segment	63.68	2	<0.001	Ventral < dorsal	-0.28	-5.67	<0.001
<i>n</i> parasites			0.22	1	0.639	Ventral < median	-0.39	-7.91	<0.001	
Species:segment			25.83	12	0.011					
sp. II		Species	0.31	6	0.999	Median > dorsal	0.07	1.69	0.208	
		Segment	74.98	2	<0.001	Ventral > dorsal	-0.27	-6.35	<0.001	
		<i>n</i> parasites	0.06	1	0.806	Ventral > median	-0.34	-8.04	<0.001	
		Species:segment	40.15	12	<0.001					
Vertical areas (3)	sp. I	Species	0.40	6	0.999	Central > distal	0.54	11.54	<0.001	
		Area	134.05	2	<0.001	Proximal > distal	0.25	5.37	<0.001	
		<i>n</i> parasites	0.24	1	0.621	Proximal < central	-0.29	-6.17	<0.001	
		Species:area	14.37	12	0.278					
	sp. II	Species	1.02	6	0.985	Central vs. distal	0.05	0.60	0.820	
		Area	21.48	2	<0.001	Proximal < distal	-0.29	-3.60	0.001	
		<i>n</i> parasites	0.05	1	0.815	Proximal < central	-0.33	-4.20	<0.001	
		Species:area	19.18	12	0.084					

df, degrees of freedom.

- <sup>a</sup>  $P \leq 0.1$ .
- <sup>b</sup>  $P \leq 0.05$ .
- <sup>c</sup>  $P \leq 0.01$ .
- <sup>d</sup>  $P \leq 0.001$ .

within the gills. The observed tendency for a non-random microhabitat distribution is consistent with previous findings in monogeneans (Morand et al., 2002; Bagge et al., 2005; Soylyu et al., 2013) and copepods (Tsotetsi et al., 2004). Moreover, the actual distribution of monogeneans is consistent with previous studies (see below; Koskivaara and Valtonen, 1992; Bagge and Valtonen, 1996; Bagge et al., 2005; Blahoua et al., 2018, 2019).

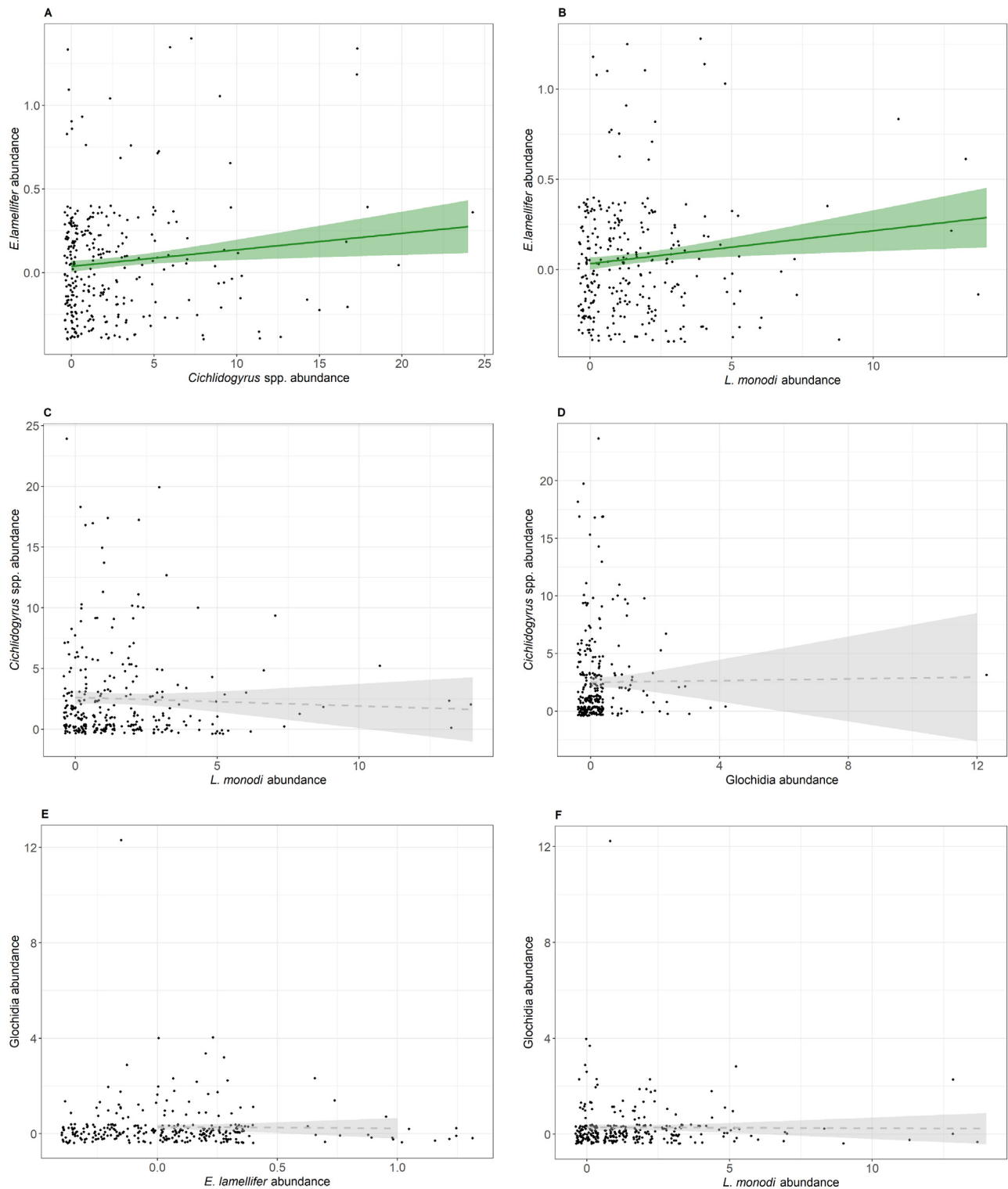
*Lamproglena monodi* was most abundant in the central area along the gill filament, as previously observed in *Lamproglena clariae* (Tsotetsi et al., 2004), presumably promoting exposure of egg clutches to water flow. The rare copepod *E. lamellifer* had a random spatial distribution, suggesting that it may be a generalist parasite in terms of niche breadth, in addition to its documented broad host range (Scholz et al., 2018). However, the lack of a clear spatial pattern could also be due to its low abundance. At a comparably low abundance, a homogeneous microhabitat distribution was previously observed in *Ergasilus lizae* (Soylyu et al., 2013). Further investigations in hosts with higher infection loads of *E. lamellifer* are needed to exclude an effect of low sample size on the observed pattern.

*Cichlidogyrus* spp. were less frequently found on the fourth gill arch, which is the smallest one. This is in line with previous findings on *Dactylogyrus*, reporting highest abundances on the largest arch in crucian carp (Bagge et al., 2005) and in roach (Koskivaara et al., 1992; Bagge and Valtonen, 1996) and low numbers on the

fourth arch in two cichlid species, *Tylochromis jentinki* and *Tilapia zillii* (Blahoua et al., 2018, 2019). This may simply result from the available gill surface, providing space and resources to sustain fewer parasite individuals on the fourth arch and more on the first arch (Geets et al., 1997; El-Naggar and Reda, 2003; Madanire-Moyo et al., 2011). However, *L. monodi* (which is a much larger parasite) showed no differences between the first and fourth gill arches, suggesting that other mechanisms may explain the distribution of *Cichlidogyrus*. It cannot be explained by differences in water flow, as simulations demonstrated that water flow is similar along the first and fourth arch (Gutiérrez and Martorelli, 1999). However, water flow may influence the vertical distribution of *Cichlidogyrus* along the gill filament: it was less frequently found on the distal tip of gill filaments, where the water flow is maximal (Paling, 1968). This seems in contrast with previous studies, that found a higher abundance of other species of *Cichlidogyrus* in the distal area (Adou et al., 2017; Blahoua et al., 2019).

The extent of niche overlap between parasites may be linked to the direction of the correlations in parasite abundance. At the genus level, parasites differed in spatial distributions and their abundances were positively correlated. This suggests a facilitating effect, in which reduced host defences by one parasite lead to an increased infection with the other parasite taxon. Indeed both the copepods and monogeneans are known to induce host defences (copepods reviewed in Fast, 2014; monogeneans in Zhi





**Fig. 4.** Significant relationships between the abundances of parasites of different genera infecting cichlids inhabiting Makobe Island, Lake Victoria, Tanzania. The abundance of *Ergasilus lamellifer* was positively associated (solid curves) with the abundance of (A) *Cichlidogyrus* spp. and of (B) *Lamproglena monodi*. The other parasites were not significantly correlated (dashed curves).

et al., 2018; Chen et al., 2019; Igeh and Avenant-Oldewage, 2020), implying that defence against one parasite could be at the expense of defence against another. On the other hand, within *Cichlidogyrus*, the analysed morphospecies had similar spatial dis-

tributions and their abundances were negatively correlated. Future studies may investigate if competition for space or other gill resources is indeed occurring among morphospecies of *Cichlidogyrus*.

**Table 3**

Interspecific abundance relationships between parasite genera and between morphospecies of *Cichlidogyrus* infecting haplochromine cichlids at Makobe Island, Lake Victoria, Tanzania. Abundance of the focal parasite taxon was related to the abundance of another parasite taxon. The Minimum Adequate Models (MAMs) were established by stepwise removal of non-significant variables from the starting model, which included host species, every parasite taxon, the interaction term between host species and each parasite taxon (this interaction was excluded in models concerning morphospecies of *Cichlidogyrus* due to small sample size).

Focal parasite	Fixed effects	LR	df	P		Direction
<i>Cichlidogyrus</i> spp.	Host species	175.33	11	<0.0001	d	
	<i>Ergasilus lamellifer</i>	8.09	1	0.004	c	+
<i>Lamproglena monodi</i>	Host species	53.07	11	<0.0001	d	
	<i>Ergasilus lamellifer</i>	8.69	1	0.003	c	+
<i>Ergasilus lamellifer</i>	<i>Cichlidogyrus</i> spp.	5.36	1	0.021	b	+
	<i>Lamproglena monodi</i>	5.26	1	0.022	a	+
Glochidia	1					
<i>Cichlidogyrus</i> sp. I	Host species	56.25	11	<0.0001	d	
	<i>Cichlidogyrus</i> sp. II	11.66	1	0.001	d	–
<i>Cichlidogyrus</i> sp. II	<i>Cichlidogyrus</i> sp. I	23.36	1	<0.0001	d	–
	<i>Cichlidogyrus</i> sp. III	11.35	1	0.001	d	–
<i>Cichlidogyrus</i> sp. III	<i>Cichlidogyrus</i> sp. I	20.97	1	<0.0001	d	–
	<i>Cichlidogyrus</i> sp. II	25.04	1	<0.0001	d	–
<i>Cichlidogyrus</i> sp. V	<i>Cichlidogyrus</i> sp. V	7.30	1	0.007	c	–
	1					
<i>Cichlidogyrus</i> sp. VI	1					

LR, likelihood ratios; df, degrees of freedom.

<sup>a</sup>  $P \leq 0.1$ .

<sup>b</sup>  $P \leq 0.05$ .

<sup>c</sup>  $P \leq 0.01$ .

<sup>d</sup>  $P \leq 0.001$ .

#### 4.2. Parasite spatial distributions in different host species

The non-random microhabitat distributions of *L. monodi* and *Cichlidogyrus* spp. (in particular the most common morphospecies, sp. I) were observed in most hosts. Such niche restriction may be a functional response to spatial variation in resource availability, or to competition between parasite taxa, even in the absence of a numerical response (i.e. reduction in the abundance, Thomson, 1980). However, since ectoparasites of cichlids from Lake Victoria are present in relatively low abundances (two to five-fold lower than in cichlids from Lake Tanganyika belonging to *Tropheus* (Raeymaekers et al., 2013); a hundred-fold lower than in Atlantic salmon in Norway (Jensen and Johnsen, 1992; Mo, 1992)), we may speculate that competition among parasites is too weak to drive niche restriction (Rohde, 1979, 1991). Niche selection may be driven by other processes such as mating strategies. In parasites that mate on the host, such as monogeneans (Geets et al., 1997; Lo, 1999), a narrow niche increases the probability of contact with conspecifics and thereby facilitates mating (e.g. in crucian carp (Bagge et al., 2005); but see review by Morand et al., 2002). Alternatively, niche restriction may be the result of competition between parasite taxa in the evolutionary past (Poulin, 2007).

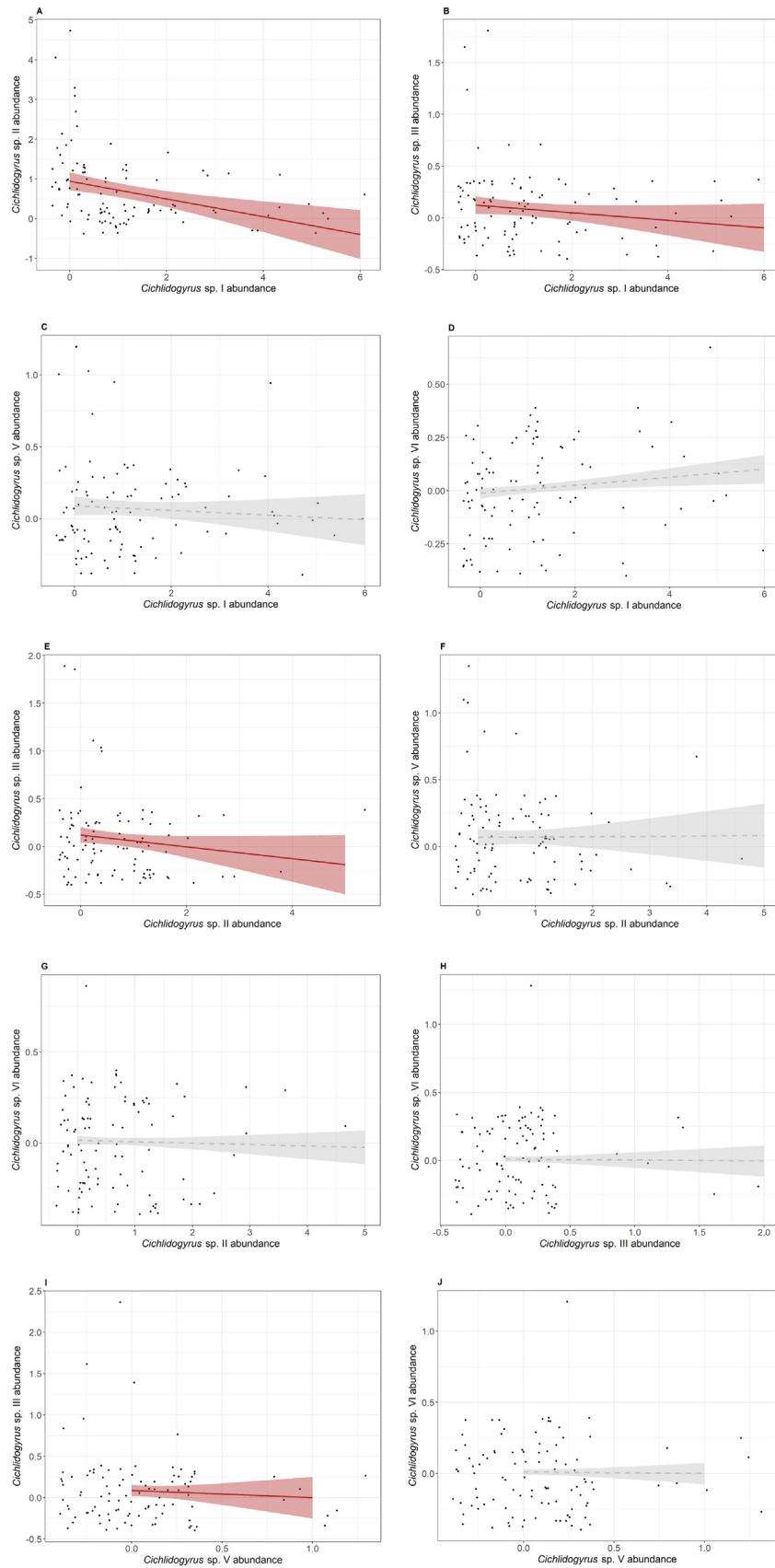
The spatial distribution of morphospecies of *Cichlidogyrus* differed between host species. This may indicate cryptic infection differences among host species, supporting specificity of the *Cichlidogyrus*–host interaction. This is in line with earlier observations that monogeneans with high host specificity have anchor sizes that match the gill arch size of their host species (Khang et al., 2016). Also, for *L. monodi* there are indications of host specificity; its spatial distribution along vertical areas differed between host species. If infection differences only accumulate after speciation, host species differences in the microhabitat distributions of their parasites might be more pronounced between more distantly related host species than between closely related species. We may then observe that spatial distribution patterns are more distinct between host species of different genera than within the same genus. Although not tested explicitly, we observed such a pattern for *Cichlidogyrus* spp., which were more abundant on the first gill arch in each of the three sampled species of *Pundamilia* than in other host genera, and for *L. monodi*, which were more abundant

on the median segment (Fig. 3). Interestingly, this pattern is shared with *Mbipia mbipi* (a likely hybrid species between *Pundamilia* and *Mbipia* (Keller et al., 2013)) and *Neochromis* sp. ‘uniscuspid scraper’ (a likely hybrid species between *Pundamilia* and *Neochromis*, (O. Seehausen, unpublished data)). To properly address this, we would need a larger sample size of parasites, especially of representatives of *Cichlidogyrus* identified to species level.

#### 4.3. Relationships between parasite taxa

Abundances of *Cichlidogyrus* spp. and *L. monodi* were positively associated with the abundance of *E. lamellifer* and vice-versa, whereas abundances of *Cichlidogyrus* spp. and *L. monodi* were not correlated. Positive associations may be explained in several ways. First, they may be true synergistic interactions, in which one parasite taxon increases the infection risk, disease severity and/or transmission rate of another parasite taxon (Hellard et al., 2015). Second, they may result from host populations sharing infection risk factors, leading to an increased co-occurrence even if parasites do not truly interact (Hellard et al., 2012). This seems unlikely, because positive associations were also observed in host species that differ in ecological specialisation (e.g. diet and water depth). Finally, we may speculate that the two copepod species (*L. monodi* and *E. lamellifer*) may facilitate each other because they may be antigenically similar enough to benefit from host susceptibility to the other copepod (Telfer et al., 2010) or from the immunomodulation induced by the other copepod (as seen in e.g. *Anaplasma* bacteria and cowpox virus in field voles (Telfer et al., 2010); HIV virus and hepatitis B virus in humans (Kellerman et al., 2003)). However, host condition was not related to parasite load, as may be expected under natural conditions with relatively low parasite loads. It is unclear if such immunomodulation can happen even without affecting host condition, as the latter was not investigated in the aforementioned studies. The observation of positive associations does not exclude antagonistic interactions, as they may be present but outweighed by synergistic interactions.

In contrast to the positive correlations between parasite genera, abundances of morphospecies of *Cichlidogyrus* were negatively related. This may indicate that congeneric parasites are more prone to compete with each other, likely because they are more similar



**Fig. 5.** Significant relationships (solid curves) between the abundances of morphospecies of *Cichlidogyrus* infecting cichlids inhabiting Makobe Island, Lake Victoria, Tanzania. The abundance of *Cichlidogyrus* sp. I was negatively associated with abundance of (A) *Cichlidogyrus* sp. II and of (B) *Cichlidogyrus* sp. III. The abundance of *Cichlidogyrus* sp. III was also negatively associated with the abundance of (E) *Cichlidogyrus* sp. II and (I) *Cichlidogyrus* sp. IV. The other morphospecies were not significantly correlated (dashed curves).

**Table 4**

Variation in the proportion of individuals of *Lamproglena monodi* carrying egg sacs in relation to host species identity, host individual length (SL), condition factor (CF), capture water depth, the abundance of conspecific and heterospecific parasites, fish preservation method (formalin versus ethanol) and days elapsed between fish collection and parasite screening (time elapsed).

Fixed factors	LR	df	P
Species	11.113	12	0.519
Species: <i>Lamproglena monodi</i>	8.299	12	0.761
Depth	0.690	1	0.406
Time elapsed	0.425	1	0.514
Glochidia	0.277	1	0.599
CF	0.235	1	0.628
Preserv	0.136	1	0.712
SL	0.072	1	0.789
<i>Lamproglena monodi</i>	0.062	1	0.804
<i>Ergasilus lamellifer</i>	0.055	1	0.815
<i>Cichlidogyrus</i> spp.	0.015	1	0.901

LR, likelihood ratios; df, degrees of freedom.

than non-congeners (and thus may have similar nutritional needs and attachment mode), as suggested by the similarity in spatial distribution between sp. I and sp. II.

Since parasite community structure is thought to be mainly shaped by interspecific interactions (Poulin, 2001) we focused on those. Intraspecific interactions may be particularly relevant in monogenean communities, as they mate on the host and gills are far from being saturated (Rohde, 1979; Morand et al., 2002). On the other hand, copepods mate before attachment on the host and many of them cannot move after attachment, thus their spatial distribution is more likely shaped by interspecific interactions and/or by other factors (e.g. egg spreading).

#### 4.4. Reproductive success of copepods

The reproductive success of *L. monodi* (measured as the proportion of copepod individuals carrying egg sacs) did not differ between host species, and was not correlated with the abundance of conspecifics nor the abundance of other ectoparasite taxa. This may support the low host specificity of *L. monodi*, which may be deduced from the observation that it is found in all Lake cichlids sampled from Victoria studied here and 48 African cichlid species in total (Karvonen et al., 2018; Scholz et al., 2018; Gobbin et al., 2020).

In conclusion, parasites had non-random gill microhabitat distributions, which differed between host species. This may indicate cryptic differences in the host–parasite interactions, potentially supporting parasite-mediated host differentiation – assuming that gill parasites exert pathogenic effects on their hosts. Microhabitat distribution may represent an important axis of differentiation between host species that is worth including in future studies.

Between and within parasite genera, we observed opposite patterns of niche overlap and abundance, suggesting that closely related parasites are more prone to compete with each other (probably due to similar resource requirements) whereas distantly related parasites tend to facilitate each other (possibly as opportunistic infections or through immunomodulation). Such parasite interactions did not differ between host species and thus do not constitute evidence for variation in host–parasite interactions.

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ijpara.2020.09.001>.

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