**1 | INTRODUCTION**

Despite often being neglected in ecological studies (Morley, 2012; Scholz & Choudhury, 2014), parasites are key components of natural communities and ecosystem functioning (Dobson & Hudson, 1986; Frainer et al., 2018; Lafferty et al., 2008; Marcogliese, 2004; Minchella & Scott, 1991; Pascal et al., 2020; Poulin, 1999). They often involve physiological and behavioral changes of their hosts (Barber et al., 2000; Iwanowicz, 2011), are major elements of food webs (Lafferty et al., 2006, 2008; Marcogliese & Cone, 1997a) and respond to global changes (Brooks & Hoberg, 2007; Cable et al., 2017; Carlson et al., 2020; Mostowy & Engelstädter, 2010). Thus, host-parasite association dynamics are crucial to understand as parasite are ubiquitous in ecological systems (Windsor, 1998). Despite that recognition, infection patterns within a population or community can vary across taxa, time and/or space making it difficult to understand and model the drivers of infection within ecological systems (Happel, 2019; Poulin, 2006; Poulin & Dick, 2007; Thieltges & Reise, 2007; Villalba-Vasquez et al., 2018; Young & Maccoll, 2017). Consequently, our understanding of the processes explaining variation in parasite infection across spatial scales is still poor (Bolnick et al., 2020; Poulin, 1998). Studies are constraint by context-dependencies such as spatial scaling, biological scaling, and sampling design. In this context, multi-scale approach to host-parasite ecology is imperative. As humans modify ecosystems (physically and biologically) it is essential to understand the full extent of complexity of disease dynamics to improve future predictions and select appropriate scale for management and conservation strategies (Cohen et al., 2016).

The distribution of organisms in space is constrained by environmental filtering (i.e. local abiotic conditions must be ecophysiologically suitable for species to occur), species interactions and dispersal limitations (Leibold et al., 2004). Spatial scale-dependance of these processes have long been established in ecology (Rietkerk et al., 2002; Viana & Chase, 2019). In this regard, single-scale studies tend to overlook the full extent of ecological processes shaping species distribution and interactions, hence drawing biased conclusions (Levin, 1992; Peterson & Parker, 1998). This has also been addressed in disease ecology. For example, Cohen et al., (2016) found that the relative importance of processes driving the distribution of disease emergence (host richness, abiotic factors, and human population density) varied with the spatial extent of the study. Scaling-level on which empirical data is scoped for estimating infection parameters can mislead conclusions if cross-scale dependencies are unknown. For instance, in a study on nematodes infecting alfalfa (*Medicago sativa*) at three scale levels (river basin, field and microhabitat), the abundance of parasites at one scale did not explain the abundance at another scale revealing the importance of cross-scale processes (e.g., dispersion by irrigation water) (Simmons et al., 2008). One of the first steps to clarify these context-dependencies in infection dynamics is to address the importance of spatial scaling for the estimation of infection parameters such as the prevalence of infection in biotic communities. Patterns of regional-scale infection parameter can be caused by different underlying local patterns of infection. For instance, a regional prevalence of 20% could be caused by all sites having the same prevalence with no variance (i.e., all sites at 20%) or by the average prevalence of all sites being at 20% with large inter-site variance (e.g., half at 0% and half at 40%). Thus, context-dependencies might be the reason why infection patterns are still misunderstood across scales.

Scaling is especially relevant in parasite ecology given the hierarchical organization of both the parasite and host component. As an example, the simplest clustering organization of parasites is called an infrapopulation (a parasite population within a host individual) but parasite species can also co-exist with other parasite species within an individual host (infracommunity) or within a host population (component community) (see Bush et al., 1997 for more extended terminology). Considering the biological organizational complexity of host-parasite associations, there are still many biological scale combinations (consisting of a parasite and a host element) that need to be investigated. For instance, component communities of metazoan parasites in fish host-populations have been the focus of many studies in the past decades regarding spatiotemporal patterns (e.g. Carney & Dick, 2000; González & Poulin, 2005; Pérez-del-Olmo et al., 2009; Villalba-Vasquez et al., 2018). For exemple, Villalba-Vasquez et al. (2018) looked at infracommunities and component communities of parasites in Panama spadefish (*Parapsettus panamensis*) collected over 6 years from 4 locations and found similar patterns of low species richness, low diversity and dominance from a single parasite species across locations, but high variations in species composition and community structure between years and locations. Conversely, species-level infection patterns in host-communities (i.e., one parasite species infecting many host species in a community) remains largely unexplored across spatial scales (but see Bielby et al., 2021; Moore et al., 2014; Olsson-Pons et al., 2015). In an ecological perspective, studying infections at the host-community level is coherent because hosts can co-exist within the same habitat exposing them to similar encounter chances with infectious stages of parasites. Besides, a study on macaques found that omitting individuals of a social network can change the strength of the relationship between parasites intensity and social network centrality (Xu et al., 2022), suggesting that the interactions between hosts of a population or community are a structuring factor of parasite infection.

Despite recent efforts, it remains unclear whether infection patterns result from stochasticity (i.e., infection patterns do not differ from randomness) or determinist filtering (i.e., infection patterns are explained by a set of known drivers and mechanisms) (e.g., Carney & Dick, 2000; González & Poulin, 2005; Kennedy, 2009; Poulin & Valtonen, 2002). Studies have shown that both local biotic (e.g., parasite-parasite interactions, host behavior, feeding preference) and abiotic (e.g., habitat structure, water chemistry, pollution) components can be correlated to variation in infection metrics at various spatial scales (Altman & Byers, 2014; Falke & Preston, 2021; Lagrue et al., 2011; Lagrue & Poulin, 2015; Poulin & Morand, 1999; Thieltges et al., 2008). Individual host characteristics such as sex (Zuk & McKean, 1996), age/size (Marcogliese et al., 2001; Poulin, 2000) and genetics (Williams-Blangero et al., 2012) drive host susceptibility leading to sources of variation in infection parameters of host-populations. For example, Poulin (1996) found that infection prevalence of trematodes was higher in male individuals across bird and mammal hosts. Infection prevalence can thus be sex-biased within host-populations (Kowalski et al., 2015). On a larger scale, host community properties such as species richness and host population density can create a “dilution effect” by reducing a parasite’s encounter rates with hosts (Ahn & Goater, 2021; Buck & Lutterschmidt, 2017; Civitello et al., 2015; Dargent et al., 2013; Lagrue & Poulin, 2015). For instance, alternative host species can act as a decoy deceiving infection on a focal host species (Ahn & Goater, 2021). Local habitat characteristics have also been correlated to variation in parasitological parameters in host communities. In American eels (*Anguilla rostrata*), parasite diversity decreases when water pH is below 5.4, with some parasite families such as digenean trematodes being absent below pH 4.7 (Marcogliese & Cone, 1997b). Similarly, lentic water bodies with dense vegetation display higher prevalence and abundance of *Posthodiplostomum cuticola* parasites in host fish than rivers and reservoirs with steep banks (Ondrackova et al., 2004), suggesting that local habitat and morphometry of the water body are drivers of encounter filtering (sptatiotemporal window that allows encounter between the parasite and its host). Furthermore, spatial features of an ecosystem (e.g., watershed, connectivity) act as large scale filtering by limiting dispersal of both parasites and hosts (Bolnick et al., 2020) thus creating infection patchiness at the landscape level. Happel (2019) provided evidence for consistent geographical pattern in the prevalence of trematodes between watersheds. Bolnick et al. (2020) also found that increased waterways distance between waterbodies lead to more different parasite community’s composition in threespine stickleback (*Gasterosteus aculeatus*). Waterbodies such as lakes are therefore good natural study systems to investigate scaling effect as they are delimited entities, connected or not in space through streams. Investigating a wide range of predictors has the potential to enlighten processes driving infection patchiness (i.e., infection hotspots) within a system that appears homogenous (Bolnick et al., 2020). Consequently, a complete ecological perspective on host-parasite systems must incorporate abiotic, biotic and spatial ecosystem elements to highlight mechanisms shaping patterns of infection as some filters are scale-dependent (Bolnick et al., 2020; Cohen et al., 2016).

Relevance of sampling design has been long established for empirical studies on wild populations. Researchers working on wildlife must deal with a tradeoff between minimizing stress of focal species and impact of natural habitats while generating accurate estimates of populations and communities when designing their sampling protocols. Precision of population parameters (e.g., abundance, recruitment, age classes, sex-ratio) can also be influenced by the sampling method and/or the sampling effort (i.e., the number of sampling). For example, Khaemba et al., (2001) simulated three sampling designs based on empirical data and showed that the intensity of sampling (here the closeness of transects) improved precision of the estimated population in all three designs. Sampling methods can introduce bias into estimates based on animal personality and behavior (Biro & Dingemanse, 2009). Animal personality is often described on a shy-bold continuum that influences risk-driven decision (Wilson et al., 1993), on what relies on a lot of detection methods used in the field. For example, a study on the black rat (*Ruttus rattus*) showed that sampling devices that required a higher level of intimacy detected fewer individuals, as the perceived risk gets higher the closer they got to the traps thus creating a “personality filtering” favoring sampling of bold individuals (Johnstone et al., 2021). Trappability in aquatic habitats follow the same pattern. In Biro & Post, (2008), bold rainbow trout were caught three times as often as shy individuals in gillnets. Thus, estimations based on empirical surveys are context-dependent on how the methodology used is personality-biased. Although it has not thoroughly been investigated yet, there is no reason indicating different outcomes for estimates of infection parameters in the wild. A study on the chronic wasting disease in deer species showed that the survey method used to estimate the disease prevalence can lead to overestimation or underestimation of the true infection parameter (Nusser et al., 2008). Wilson et al. (1993) also observed different infection levels in Pumpkinseed sunfish (*Lepomis gibbosus*) depending on the fishing method. Poulin (2013) found a weak correlation between the aggregation level of helminth parasites in fish hosts and the number of individual-host sampled (sample size). Consequently, sampling design elements must be considered when studying scale-dependencies of infection parameters.

Here, we explore the effect of spatial scale on infection prevalence estimates across different sampling methods using data on the black spot disease in littoral fish communities across 15 lakes varying in morphometric attributes and local biotic and abiotic conditions. We analyze infection prevalence data at the host-community level (all fish hosts) for scaling-dependencies through three spatial scale levels (landscape, lake and site-scale) in order to investigate (i)the effect of increasing sampling effort on landscape prevalence estimation (random resampling accumulation curves) through different sampling methods (ii)the distribution of observed lake prevalence estimates across the landscape and (iii) the importance of ecological predictors on infection prevalence on a fine-scale sampling. For landscape-scale analysis, we generated random prevalence accumulation curves by resampling across all lakes. This approach allows us to compare regional-scale prevalence estimates among different sampling methods along a gradient of increasing sampling effort (or area sampled) in order to evaluate the number of samples needed to correctly estimate the landscape prevalence. For lake-scale analysis, we used a frequency distribution of observed infection prevalence in lakes to better understand the infection dynamics in the landscape (Hess et al., 2002; McGeoch & Gaston, 2002). The final step was to test a suit of deterministic environmental predictors underlying different scale-dependent processes to understand the observed site-scale infection prevalence. The shapes and strength of the relationships between infection parameters and drivers are a key element to better understand the mechanisms behind infection patterns (Poulin et al., 2011).

Ahn, S., & Goater, C. P. (2021). Nonhost species reduce parasite infection in a focal host species within experimental fish communities. *Ecology and Evolution*, *11*(15), 10155‑10163. https://doi.org/10.1002/ece3.7823

Altman, I., & Byers, J. E. (2014). Large-scale spatial variation in parasite communities influenced by anthropogenic factors. *Ecology*, *95*(7), 1876‑1887. https://doi.org/10.1890/13-0509.1

Barber, I., Hoare, D., & Krause, J. (2000). Effects of parasites on fish behaviour : A review and evolutionary perspective. *Reviews in Fish Biology and Fisheries*, *10*(2), 131‑165. https://doi.org/10.1023/A:1016658224470

Bielby, J., Price, S. J., Monsalve-CarcaÑo, C., & Bosch, J. (2021). Host contribution to parasite persistence is consistent between parasites and over time, but varies spatially. *Ecological Applications*, *31*(3), e02256. https://doi.org/10.1002/eap.2256

Biro, P. A., & Dingemanse, N. J. (2009). Sampling bias resulting from animal personality. *Trends in Ecology & Evolution*, *24*(2), 66‑67. https://doi.org/10.1016/j.tree.2008.11.001

Biro, P. A., & Post, J. R. (2008). Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(8), 2919‑2922. https://doi.org/10.1073/pnas.0708159105

Blasco-Costa, I., Rouco, C., & Poulin, R. (2015). Biogeography of parasitism in freshwater fish : Spatial patterns in hot spots of infection. *Ecography*, *38*(3), 301‑310. https://doi.org/10.1111/ecog.01020

Bolnick, D. I., Resetarits, E. J., Ballare, K., Stuart, Y. E., & Stutz, W. E. (2020). Scale-dependent effects of host patch traits on species composition in a stickleback parasite metacommunity. *Ecology*, *101*(12), e03181. https://doi.org/10.1002/ecy.3181

Brooks, D. R., & Hoberg, E. P. (2007). How will global climate change affect parasite–host assemblages? *Trends in Parasitology*, *23*(12), 571‑574. https://doi.org/10.1016/j.pt.2007.08.016

Buck, J. C., & Lutterschmidt, W. I. (2017). Parasite abundance decreases with host density : Evidence of the encounter-dilution effect for a parasite with a complex life cycle. *Hydrobiologia*, *784*(1), 201‑210. https://doi.org/10.1007/s10750-016-2874-8

Bush, A. O., Lafferty, K. D., Lotz, J. M., & Shostak, A. W. (1997). Parasitology meets ecology on its own terms : Margolis et al. revisited. *The Journal of Parasitology*, *83*(4), 575‑583.

Cable, J., Barber, I., Boag, B., Ellison, A. R., Morgan, E. R., Murray, K., Pascoe, E. L., Sait, S. M., Wilson, A. J., & Booth, M. (2017). Global change, parasite transmission and disease control : Lessons from ecology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1719), 20160088. https://doi.org/10.1098/rstb.2016.0088

Carlson, C. J., Hopkins, S., Bell, K. C., Doña, J., Godfrey, S. S., Kwak, M. L., Lafferty, K. D., Moir, M. L., Speer, K. A., Strona, G., Torchin, M., & Wood, C. L. (2020). A global parasite conservation plan. *Biological Conservation*, *250*, 108596. https://doi.org/10.1016/j.biocon.2020.108596

Carney, J. P., & Dick, T. A. (2000). Helminth communities of yellow perch (Perca flavescens (Mitchill)) : Determinants of pattern. *Canadian Journal of Zoology*, *78*(4), 538‑555. https://doi.org/10.1139/z99-222

Civitello, D. J., Cohen, J., Fatima, H., Halstead, N. T., Liriano, J., McMahon, T. A., Ortega, C. N., Sauer, E. L., Sehgal, T., Young, S., & Rohr, J. R. (2015). Biodiversity inhibits parasites : Broad evidence for the dilution effect. *Proceedings of the National Academy of Sciences*, *112*(28), 8667‑8671. https://doi.org/10.1073/pnas.1506279112

Cohen, J. M., Civitello, D. J., Brace, A. J., Feichtinger, E. M., Ortega, C. N., Richardson, J. C., Sauer, E. L., Liu, X., & Rohr, J. R. (2016). Spatial scale modulates the strength of ecological processes driving disease distributions. *Proceedings of the National Academy of Sciences*, *113*(24), E3359‑E3364. https://doi.org/10.1073/pnas.1521657113

Dargent, F., Torres-Dowdall, J., Scott, M. E., Ramnarine, I., & Fussmann, G. F. (2013). Can Mixed-Species Groups Reduce Individual Parasite Load? A Field Test with Two Closely Related Poeciliid Fishes (Poecilia reticulata and Poecilia picta). *PLoS ONE*, *8*(2), e56789. https://doi.org/10.1371/journal.pone.0056789

Dobson, A. P., & Hudson, P. J. (1986). Parasites, disease and the structure of ecological communities. *Trends in Ecology & Evolution*, *1*(1), 11‑15. https://doi.org/10.1016/0169-5347(86)90060-1

Falke, L. P., & Preston, D. L. (2021). Freshwater disease hotspots : Drivers of fine-scale spatial heterogeneity in trematode parasitism in streams. *Freshwater Biology*, *n/a*(n/a). https://doi.org/10.1111/fwb.13856

Frainer, A., McKie, B. G., Amundsen, P.-A., Knudsen, R., & Lafferty, K. D. (2018). Parasitism and the Biodiversity-Functioning Relationship. *Trends in Ecology & Evolution*, *33*(4), 260‑268. https://doi.org/10.1016/j.tree.2018.01.011

González, M. T., & Poulin, R. (2005). Spatial and temporal predictability of the parasite community structure of a benthic marine fish along its distributional range. *International Journal for Parasitology*, *35*(13), 1369‑1377. https://doi.org/10.1016/j.ijpara.2005.07.016

Happel, A. (2019). A volunteer-populated online database provides evidence for a geographic pattern in symptoms of black spot infections. *International Journal for Parasitology: Parasites and Wildlife*, *10*, 156‑163. https://doi.org/10.1016/j.ijppaw.2019.08.003

Hess, G., Randolph, S., Arneberg, P., Chemini, C., Furnanello, C., Harwood, J., Roberts, M. G., & Swinton, J. (2002). Spatial Aspects of Disease Dynamics. In *The ecology of wildlife diseases* (p. 102‑118).

Iwanowicz, D. (2011). *Overview On The Effects Of Parasites On Fish Health*.

Johnstone, K. C., McArthur, C., & Banks, P. B. (2021). Behavioural drivers of survey bias : Interactive effects of personality, the perceived risk and device properties. *Oecologia*, *197*(1), 117‑127. https://doi.org/10.1007/s00442-021-05021-7

Kennedy, C. R. (2009). The ecology of parasites of freshwater fishes : The search for patterns. *Parasitology*, *136*(12), 1653‑1662. https://doi.org/10.1017/S0031182009005794

Khaemba, W. M., Stein, A., Rasch, D., De Leeuw, J., & Georgiadis, N. (2001). Empirically simulated study to compare and validate sampling methods used in aerial surveys of wildlife populations. *African Journal of Ecology*, *39*(4), 374‑382. https://doi.org/10.1046/j.0141-6707.2001.00329.x

Kowalski, K., Bogdziewicz, M., Eichert, U., & Rychlik, L. (2015). Sex differences in flea infections among rodent hosts : Is there a male bias? *Parasitology Research*, *114*(1), 337‑341. https://doi.org/10.1007/s00436-014-4231-z

Lafferty, K. D., Allesina, S., Arim, M., Briggs, C. J., De Leo, G., Dobson, A. P., Dunne, J. A., Johnson, P. T. J., Kuris, A. M., Marcogliese, D. J., Martinez, N. D., Memmott, J., Marquet, P. A., McLaughlin, J. P., Mordecai, E. A., Pascual, M., Poulin, R., & Thieltges, D. W. (2008). Parasites in food webs : The ultimate missing links. *Ecology Letters*, *11*(6), 533‑546. https://doi.org/10.1111/j.1461-0248.2008.01174.x

Lafferty, K. D., Dobson, A. P., & Kuris, A. M. (2006). Parasites dominate food web links. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(30), 11211‑11216. https://doi.org/10.1073/pnas.0604755103

Lagrue, C., Kelly, D. W., Hicks, A., & Poulin, R. (2011). Factors influencing infection patterns of trophically transmitted parasites among a fish community : Host diet, host–parasite compatibility or both? *Journal of Fish Biology*, *79*(2), 466‑485. https://doi.org/10.1111/j.1095-8649.2011.03041.x

Lagrue, C., & Poulin, R. (2015). Local diversity reduces infection risk across multiple freshwater host-parasite associations. *Freshwater Biology*, *60*(11), 2445‑2454. https://doi.org/10.1111/fwb.12677

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M., & Gonzalez, A. (2004). The metacommunity concept : A framework for multi-scale community ecology. *Ecology Letters*, *7*(7), 601‑613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Levin, S. A. (1992). The Problem of Pattern and Scale in Ecology : The Robert H. MacArthur Award Lecture. *Ecology*, *73*(6), 1943‑1967. https://doi.org/10.2307/1941447

Marcogliese, D. J. (2004). Parasites : Small Players with Crucial Roles in the Ecological Theater. *EcoHealth*, *1*(2), 151‑164. https://doi.org/10.1007/s10393-004-0028-3

Marcogliese, D. J., & Cone, D. K. (1997a). Food webs : A plea for parasites. *Trends in Ecology & Evolution*, *12*(8), 320‑325. https://doi.org/10.1016/S0169-5347(97)01080-X

Marcogliese, D. J., & Cone, D. K. (1997b). Parasite communities as indicators of ecosystem stress. *Parassitologia*, *39*(3), 227‑232.

Marcogliese, D. J., Dumont, P., Gendron, A. D., Mailhot, Y., Bergeron, E., & McLaughlin, J. D. (2001). Spatial and temporal variation in abundance of Diplostomum spp. In walleye (Stizostedion vitreum) and white suckers (Catostomus commersoni) from the St. Lawrence River. *Canadian Journal of Zoology*, *79*(3), 355‑369. https://doi.org/10.1139/z00-209

McGeoch, M. A., & Gaston, K. J. (2002). Occupancy frequency distributions : Patterns, artefacts and mechanisms. *Biological Reviews*, *77*(3), 311‑331. https://doi.org/10.1017/S1464793101005887

Minchella, D. J., & Scott, M. E. (1991). Parasitism : A cryptic determinant of animal community structure. *Trends in Ecology & Evolution*, *6*(8), 250‑254. https://doi.org/10.1016/0169-5347(91)90071-5

Moore, J. W., Lambert, T. D., Heady, W. N., Honig, S. E., Osterback, A.-M. K., Phillis, C. C., Quiros, A. L., Retford, N. A., & Herbst, D. B. (2014). Anthropogenic land-use signals propagate through stream food webs in a California, USA, watershed. *Limnologica*, *46*, 124‑130. https://doi.org/10.1016/j.limno.2014.01.005

Morley, N. J. (2012). Cercariae (Platyhelminthes : Trematoda) as neglected components of zooplankton communities in freshwater habitats. *Hydrobiologia*, *691*(1), 7‑19. https://doi.org/10.1007/s10750-012-1029-9

Mostowy, R., & Engelstädter, J. (2010). The impact of environmental change on host–parasite coevolutionary dynamics. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1716), 2283‑2292. https://doi.org/10.1098/rspb.2010.2359

Nusser, S. M., Clark, W. R., Otis, D. L., & Huang, L. (2008). Sampling Considerations for Disease Surveillance in Wildlife Populations. *The Journal of Wildlife Management*, *72*(1), 52‑60. https://doi.org/10.2193/2007-317

Olsson-Pons, S., Clark, N. J., Ishtiaq, F., & Clegg, S. M. (2015). Differences in host species relationships and biogeographic influences produce contrasting patterns of prevalence, community composition and genetic structure in two genera of avian malaria parasites in southern Melanesia. *Journal of Animal Ecology*, *84*(4), 985‑998. https://doi.org/10.1111/1365-2656.12354

Ondrackova, M., Bartosova, S., Valova, Z., Jurajda, P., & Gelnar, M. (2004). Occurrence of black-spot disease caused by metacercariae of Posthodiplostomum cuticola among juvenile fishes in water bodies in the Morava River Basin. *Acta Parasitologica*, *3*(49). https://www.infona.pl//resource/bwmeta1.element.agro-article-5d8e90ef-9221-415e-b62f-e6e574152bf0

Pascal, L., Grémare, A., de Montaudouin, X., Deflandre, B., Romero-Ramirez, A., & Maire, O. (2020). Parasitism in ecosystem engineer species : A key factor controlling marine ecosystem functioning. *Journal of Animal Ecology*, *89*(9), 2192‑2205. https://doi.org/10.1111/1365-2656.13236

Pérez-del-Olmo, A., Fernández, M., Raga, J. A., Kostadinova, A., Morand, S., & Bellwood, D. (2009). Not Everything Is Everywhere : The Distance Decay of Similarity in a Marine Host-Parasite System. *Journal of Biogeography*, *36*(2), 200‑209.

Peterson, D., & Parker, V. (1998). Ecological Scale : Theory and Applications. In *Journal of Environmental Quality—J ENVIRON QUAL* (Vol. 28). https://doi.org/10.2307/1522131

Poulin. (1998). Large-scale patterns of host use by parasites of freshwater fishes. *Ecology Letters*, *1*(2), 118‑128. https://doi.org/10.1046/j.1461-0248.1998.00022.x

Poulin, R. (1996). Sexual Inequalities in Helminth Infections : A Cost of Being a Male? *The American Naturalist*, *147*(2), 287‑295. https://doi.org/10.1086/285851

Poulin, R. (1999). The functional importance of parasites in animal communities : Many roles at many levels? *International Journal for Parasitology*, *29*(6), 903‑914. https://doi.org/10.1016/S0020-7519(99)00045-4

Poulin, R. (2000). Variation in the intraspecific relationship between fish length and intensity of parasitic infection : Biological and statistical causes. *Journal of Fish Biology*, *56*(1), 123‑137. https://doi.org/10.1111/j.1095-8649.2000.tb02090.x

Poulin, R. (2006). Variation in infection parameters among populations within parasite species : Intrinsic properties versus local factors. *International Journal for Parasitology*, *36*(8), 877‑885. https://doi.org/10.1016/j.ijpara.2006.02.021

Poulin, R. (2007). Are there general laws in parasite ecology? *Parasitology*, *134*(Pt 6), 763‑776. https://doi.org/10.1017/S0031182006002150

Poulin, R. (2013). Explaining variability in parasite aggregation levels among host samples. *Parasitology*, *140*(4), 541‑546. https://doi.org/10.1017/S0031182012002053

Poulin, R., & Dick, T. A. (2007). Spatial Variation in Population Density across the Geographical Range in Helminth Parasites of Yellow Perch Perca flavescens. *Ecography*, *30*(5), 629‑636.

Poulin, R., Guilhaumon, F., Randhawa, H. S., Luque, J. L., & Mouillot, D. (2011). Identifying hotspots of parasite diversity from species–area relationships : Host phylogeny versus host ecology. *Oikos*, *120*(5), 740‑747. https://doi.org/10.1111/j.1600-0706.2010.19036.x

Poulin, R., & Morand, S. (1999). Geographical distances and the similarity among parasite communities of conspecific host populations. *Parasitology*, *119 ( Pt 4)*, 369‑374. https://doi.org/10.1017/s0031182099004795

Poulin, R., & Valtonen, E. T. (2002). The predictability of helminth community structure in space : A comparison of fish populations from adjacent lakes. *International Journal for Parasitology*, *32*(10), 1235‑1243. https://doi.org/10.1016/s0020-7519(02)00109-1

Rietkerk, M., van de Koppel, J., Kumar, L., Langevelde, H. H. T., & Prins. (2002). The ecology of scale. *Ecological Modelling*, *149*(1), 1‑4. https://doi.org/10.1016/S0304-3800(01)00510-5

Scholz, T., & Choudhury, A. (2014). Parasites of Freshwater Fishes In North America : Why So Neglected? *Journal of Parasitology*, *100*(1), 26‑45. https://doi.org/10.1645/13-394.1

Simmons, B. L., Niles, R. K., & Wall, D. H. (2008). Distribution and abundance of alfalfa-field nematodes at various spatial scales. *Applied Soil Ecology*, *38*(3), 211‑222. https://doi.org/10.1016/j.apsoil.2007.10.011

Thieltges, D. W., Jensen, K. T., & Poulin, R. (2008). The role of biotic factors in the transmission of free-living endohelminth stages. *Parasitology*, *135*(4), 407‑426. https://doi.org/10.1017/S0031182007000248

Thieltges, D. W., & Reise, K. (2007). Spatial heterogeneity in parasite infections at different spatial scales in an intertidal bivalve. *Oecologia*, *150*(4), 569‑581. https://doi.org/10.1007/s00442-006-0557-2

Viana, D. S., & Chase, J. M. (2019). Spatial scale modulates the inference of metacommunity assembly processes. *Ecology*, *100*(2), e02576. https://doi.org/10.1002/ecy.2576

Villalba-Vasquez, P. J., Violante-González, J., Monks, S., Marino-Romero, J. U., Ibáñez, S. G., Rojas-Herrera, A. A., Flores-Garza, R., & Rosas-Guerrero, V. (2018). Temporal and spatial variations in the metazoan parasite communities of the Panama spadefish, Parapsettus panamensis (Pisces : Ephippidae), from the Pacific coast of Mexico. *Invertebrate Biology*, *137*(4), 339‑354. https://doi.org/10.1111/ivb.12232

Williams-Blangero, S., Criscione, C. D., VandeBerg, J. L., Correa-Oliveira, R., Williams, K. D., Subedi, J., Kent, J. W., Williams, J., Kumar, S., & Blangero, J. (2012). Host genetics and population structure effects on parasitic disease. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1590), 887‑894. https://doi.org/10.1098/rstb.2011.0296

Wilson, D. S., Coleman, K., Clark, A. B., & Biederman, L. (1993). Shy-bold continuum in pumpkinseed sunfish (Lepomis gibbosus) : An ecological study of a psychological trait. *Journal of Comparative Psychology*, *107*, 250‑260. https://doi.org/10.1037/0735-7036.107.3.250

Windsor, D. A. (1998). Most of the species on Earth are parasites. *International Journal for Parasitology*, *28*(12), 1939‑1941. https://doi.org/10.1016/s0020-7519(98)00153-2

Xu, Z., MacIntosh, A. J. J., Castellano-Navarro, A., Macanás-Martínez, E., Suzumura, T., & Duboscq, J. (2022). Linking parasitism to network centrality and the impact of sampling bias in its interpretation. *PeerJ*, *10*, e14305. https://doi.org/10.7717/peerj.14305

Young, R. E., & Maccoll, A. D. C. (2017). Spatial and temporal variation in macroparasite communities of three-spined stickleback. *Parasitology*, *144*(4), 436‑449. https://doi.org/10.1017/S0031182016001815

Zuk, M., & McKean, K. A. (1996). Sex differences in parasite infections : Patterns and processes. *International Journal for Parasitology*, *26*(10), 1009‑1024. https://doi.org/10.1016/S0020-7519(96)80001-4