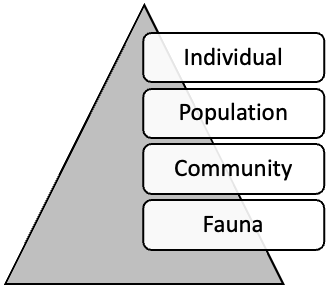
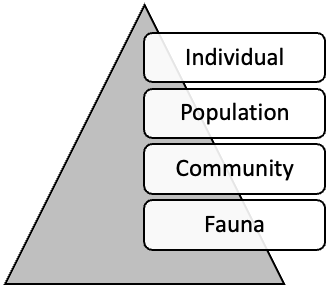
**1 | INTRODUCTION**

**[PAR1]** 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 implicate 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). It is then important to understand host-parasite association dynamics as parasites are ubiquitous in ecological systems (Windsor, 1998) and co-evolute with host populations (Dunn et al., 2009; Papkou et al., 2016). 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). Still, the literature currently fails to disentangle the processes explaining variation in parasite infection across spatial scales as parasite species filtering (the series of processes influencing species distribution) is widely scale-dependent (Bolnick et al., 2020; Poulin, 1998). Studies are then 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).

**[PAR2]** Distribution of organisms is constrained by environmental filtering (local abiotic conditions must be ecophysiologically suitable for species to occur), species interactions (e.g., competition, predation, parasitism) and dispersal limitations (Guisan et al., 2017). 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 scale magnitude. 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 (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.

**[PAR3]** Scaling is especially relevant in parasite ecology given the hierarchical organization of both the parasite and host component (Fig1?). 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 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 example, 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.



Parasite

Host

Fig1.

**[PAR4]** Since current literature lacks consistency (Poulin, 2007), 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) (Carney & Dick, 2000; González & Poulin, 2005; Kennedy, 2009; Poulin & Valtonen, 2002). Studies have shown that both local biotic (e.g., parasite-parasite interactions, host behaviour, 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 metrics 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).

**[PAR5]** 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.

**[PAR6]** 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 14 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 (regional, local and fine-scale) in order to investigate **(i)** the effect of random sampling effort on regional prevalence estimation through different sampling methods **(ii)** the distribution of observed local prevalence estimations and **(iii)** the importance of ecological predictors on infection prevalence on a fine-scale sampling. For regional scale analysis, we generated random prevalence accumulation curves by resampling across all lakes. This approach allows us to compare regional-scale prevalence estimates (and associated variance) among different sampling methods along a gradient of increasing sampling effort (or area sampled). Akin to interpretations of species-area relationships, the accumulation curves can show evidence for scale-invariance (“flat curve” – infection prevalence does not change with increasing sampled area because it is well mixed across samples) or for spatial patchiness (“non-linear curve” – the number of infected individuals sampled and the number of individual sampled increase at different rates). For local-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 fine-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). Our goal here was not to make predictions on spatial distribution of the parasitic infection but rather to disentangle how patterns are shaped through a scaling perspective.

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