Taking cues from ecological and evolutionary theories to expand the landscape of disgust

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Abstract:

1. Individual animals can attempt to prevent or mitigate parasite risks by altering their behaviour or space use. Behavioural change in response to the presence of parasites in the environment generates what is known as the “landscape of disgust” (analogous to the predator-induced “landscape of fear”). Using a spatial description of cues that indicate parasite risk, and characterizing individual responses to those cues, can allow researchers to quantify and interpret how hosts navigate the landscape of disgust. The landscape of disgust framework could facilitate much needed research on the ecological impacts of parasitism, advancing the fields of disease, spatial, and behavioural ecology.
2. Despite the potential for improving our inference of host-parasite dynamics, three key limitations of the landscape of disgust restrict the potential insight that can be gained from current research. First, many host-parasite systems will not be appropriate for invoking the landscape of disgust framework. Second, existing research has primarily focused on immediate choices made by hosts on small scales, limiting predictive power, generalizability, and the value of the insight obtained from the landscape of disgust framework. Finally, relevant ecological and evolutionary theory has not been integrated into the framework, challenging our ability to interpret and understand the application of the landscape of disgust within the context of most host-parasite systems.
3. In this review, we explore the specific requirements for implementing a landscape of disgust framework in empirical systems. We propose an expansion to the landscape of disgust framework that integrates principles from habitat selection and evolutionary theories, aiming to generate novel insight. To discuss the integration of classic ecological

and evolutionary theory, we explore how the landscape of disgust varies both within and across generations, presenting opportunities for future research.

4. Despite recent interest in understanding the impact of parasitism on animal behavioural, spatial, and movement ecology, many unanswered questions remain. We build on the landscape of disgust framework by identifying weaknesses and possible applications in different ecological and evolutionary contexts. We encourage researchers to implement this framework empirically to further our understanding of host-parasite systems.

Keywords: Co-evolution; density dependence; disease ecology; eco-evolutionary dynamics; habitat selection; host-parasite dynamics; natural selection; parasite avoidance

1. Introduction

Individuals constantly interpret cues from their environment to evaluate risks and make decisions. Individual animals inform their behaviour based on perceived associations between a given cue and potential fitness costs or benefits, in time leading to possible behavioural adaptation and predictable responses (Hart, 1990; Lima & Dill, 1990). When cues are associated with parasite risks, the perception of these cues and resulting behavioural change can generate a "landscape of disgust" (Weinstein et al., 2018). Weinstein et al. (2018) first proposed the landscape of disgust, describing it as feelings of disgust elicited by potential contact with infectious agents that can generate host avoidance behaviour and can have cascading impacts to populations, communities, and ecosystems (but see Section 2*:* Defining the landscape of disgust). Analogous to the predator-induced "landscape of fear" (*sensu* Brown et al., 1999), in which organisms respond to predator-associated cues, the landscape of disgust contributes to the spatial organisation of individuals and populations in response to micro- or macro-parasite (hereafter 'parasites': Anderson & May, 1982) associated cues. By describing the landscape of cues that individuals encounter, and thus may interpret and respond to, the landscape of disgust is a tangible and interactive property of host-parasite systems. The landscape of disgust framework has motivated increasing research on the ecological impacts of parasitism in nature (Doherty & Ruehle, 2020; Sarabian et al., 2023; Weinstein et al., 2018), and has potential to advance the fields of disease ecology, spatial ecology, and behavioural ecology.

Despite the potential value of the landscape of disgust framework, three key limitations restrict the applicability of the landscape of disgust in natural systems. First, in many natural host-parasite systems, the landscape of disgust does not exist. Although parasite risks are ubiquitous in nature, the costs of parasitism vary widely - ranging from asymptomatic infections with limited fitness impacts to infections that cause mass mortality as they spread throughout populations (Grenfell & Dobson, 1995). Application of the landscape of disgust relies on the existence of cues and the ability for potential hosts to recognize and respond to those cues (i.e., to feel "disgust") (Hart, 1990, 2011), which would not be present for many asymptomatic infections. Second, in systems where the landscape of disgust does exist, empirical research has focussed on small spatiotemporal scales creating a gap in our knowledge of how parasite avoidance scales up to landscape level dynamics. Although increasing the spatiotemporal scales at which the landscape of disgust is investigated is critical for increasing the value of the framework, complexities introduced at higher scales may seem likely to create challenges for interpreting the findings of empirical work. We suspect the first two limitations are rooted in the basis of our third argument: the current landscape of disgust framework is limited by a lack of relevant ecological (e.g., habitat selection theory: Morris, 1987) and evolutionary (e.g., foundational evolutionary forces driving adaptation: Hendry, 2017) theory integration. Incorporating these broad bodies of literature will enhance robustness and ease interpretability for those seeking to investigate the landscape of disgust in natural settings and at larger scales.

Our review has several objectives. First, we broaden the definition of the landscape of disgust to include additional contexts and examples. Specifically, we demonstrate when the landscape of disgust would and would not exist (Section 2: Defining the landscape of disgust). Second, we illustrate how critical insight could be gained by expanding the landscape of disgust interpretation to include habitat selection theory (Section 3: Landscape of disgust within a generation) and evolutionary theory (Section 4: Landscape of disgust across generations). Because ecology and evolution can have reciprocal effects, we also briefly highlight how these two processes could interact to influence the landscape of disgust, in hopes to inspire future work (Box 1). Finally, we provide examples of outstanding questions and suggestions on how to empirically approach researching these topics to collectively expand our understanding of the landscape of disgust (Section 5: Conclusions and future directions; Box 2). While acknowledging that the landscape of disgust will not exist for every host-parasite system, we see value in expanding the existing landscape of disgust framework to increase the value from testing hypotheses related to the ecological and evolutionary impacts of parasitism in systems where it could exist (Table 1).

2. Defining the landscape of disgust

The landscape of disgust is a spatial representation of an individual's perception of infection risk (hereafter, we broadly refer to the "individual" when referring to a potential host organism) (Weinstein et al., 2018). To date, the landscape of disgust has typically been described in host-parasite systems where parasites have short-term environmental stages and are effectively fixed in space, such as contact between potential hosts and faeces or carrion (e.g., Gonzálvez, Martínez-Carrasco, Sánchez-Zapata, et al., 2021; Moleón & Sánchez-Zapata, 2021; Weinstein et al., 2018). However, faeces and carrion exist at fine temporal and spatial scales and are typically static, while infected conspecifics or mobile parasites are infection risks that are highly dynamic (Grear et al., 2013; White et al., 2017). The density and rate of risk will also change through time within a lifetime, as individuals move through environments, are exposed to different parasites, and as population dynamics change through time.

It is unlikely the landscape of disgust is a perfect representation of parasite presence or transmission risk in an environment; rather, the landscape of disgust acts as the bridge between an actual risk and the individual's response to that risk. Transmission risks can be perceived where there are none (e.g., social contact with indirect transmission), or not be detected at all where they are present (e.g., novel parasites). Here, we define the landscape of disgust as the summation of any perceivable parasite infection risks within an individual's spatial perception (Figures 1, 2). We visualise the "actual" and "perceived" infection risks as separate spatial layers on a physical landscape that can shift within and across generations. We primarily discuss and interpret the landscape of disgust as a two-dimensional plane, as this reflects the movement of most terrestrial individuals. However, we acknowledge in some systems a third axis of movement is available to avoid parasite infection, such as in aquatic systems (Behringer et al., 2018), or for aerial or arboreal animals that can use vertical movement to avoid transmission. For example, Verraux's Sifaka (*Propithecus verreauxi*) avoid the ground where there is a higher chance of infection (Loudon et al., 2006).

Host-parasite dynamics influencing the landscape of disgust can vary significantly between species, populations, and even individuals. This variation is reflected in responses to parasite-associated cues, such that a landscape of disgust may, in some cases, not exist or be observable. For a landscape of disgust to exist and impact host behaviour, there are at least three prerequisite environmental, physiological, and evolutionary factors required. First, a cue must be produced either directly by a parasite or something associated with risk of infection; for example, the avoidance of faeces which may or may not be infested with parasites. Individuals can detect different types of cues depending on the host and parasite, including chemosensory cues (Di Bacco & Scott, 2023; Kavaliers et al., 2004), visual cues such as behavioural changes (Dugatkin et al., 1994) or physical signs of the pathology (Kennedy et al., 1987; Rosenqvist & Johansson, 1995), as well as other types of cues (e.g., vibratory display of infected termites: Rosengaus et al., 1999). Second, hosts must have the capacity to detect cues; the physiological mechanisms to interpret and recognize the cue are required for the cue to be *perceived* by the host within the landscape of disgust (e.g., detection of chemical cues in mice: Kavaliers et al., 2004). Finally, parasitism must be costly enough to impact potential host movement behaviour, and movement must prevent or reduce infection resulting in a benefit to the host. Response behaviour could be learned (Kavaliers & Choleris, 2018; Keymer et al., 1983; Klemme & Karvonen, 2016) or adaptive if sufficient time and genetic variation are present to evolve a connection between the cue and response (Hart & Hart, 2018). Selection can act on genes involved in different stages of infection, including recognizing parasite cues, and responding to infection (Vinkler et al., 2023).

Not all parasites can be detected, and not all perceived risks warrant a response. We suggest a biologically relevant threshold for infection risk determines the strength of an avoidance response or whether an individual responds at all (represented by the horizontal line overlapping perceived risks in Figures 1, 2). An avoidance threshold can be affected by individual condition or past experiences, such as an individual’s body condition or hunger levels (Bustnes & Galaktionov, 2004) and prior or current infection status (Hutchings et al., 1998; Selbach et al., 2022). An individual’s behaviour is dictated by trade-offs between fundamental resource needs and risk; the urgency of any one need is relative to all other needs. For instance, red foxes (*Vulpes vulpes*) delay the consumption of conspecific carcasses to mitigate the trade-off between the nutritional value of meat and infection risks (Gonzálvez, Martínez-Carrasco, Sánchez-Zapata, et al., 2021). Further, the risk of parasite infection often exists as a gradient, and variation in parasite risk can occasionally be detected (e.g., Sarabian et al., 2021; Tacey et al., 2023). If potential hosts perceive a risk and do not respond, there is no direct way to measure the landscape of disgust or assess its impact on movement and decision-making. In natural systems these prerequisites for the landscape of disgust can take on many forms; any breakdown in the connection between the cue production, perception, and response will prevent a quantifiable landscape of disgust from forming.

3. Landscape of Disgust within a Generation

Habitat is a location in environmental space, defined by a set of conditions (e.g., temperature), resources (e.g., food), and risks (e.g., predators or parasites) (Matthiopoulos et al., 2020); habitat selection is the process through which animals differentially use habitats relative to their availability at a given population density to maximize fitness. Habitat selection theory provides a foundation for assessing how the landscape of disgust will be shaped by factors that vary within the lifetime of an individual (but see Box 1). In this section, we first discuss ways to increase the spatial and temporal scales at which the landscape of disgust is assessed within a generation (Section 3.1) Next, we consider how the landscape of disgust will be shaped by the dynamic effects of density, parasite transmission, and sociality (Section 3.2).

3.1 Expanding spatiotemporal scales

Habitat selection theory proposes that habitat decisions are hierarchical (Bailey et al., 1996; Mayor et al., 2009); animals select habitats first at larger spatial scales and then make smaller-scale decisions within that habitat. Habitat selection can more specifically be considered at four scales: first order (the geographical area used by a species), second order (the home range of an individual or group), third order (the resource selection decisions made by individuals within their home range), and fourth order (an individual's immediate decision making) (Johnson, 1980). Most landscape of disgust research focuses on first and second order scales. Intake maximisation is the most heavily studied driver of habitat selection in the context of landscape of disgust (e.g., Gonzálvez, Martínez-Carrasco, & Moleón, 2021a; Gonzálvez, Martínez-Carrasco, Sánchez-Zapata, et al., 2021b; Moisés et al., 2021), which aligns with the original framework that focuses on carcasses and faeces. Notably, carcasses and faeces can be avoided behaviourally while foraging at the fourth order of habitat selection (Hutchings et al., 1998). Within the third and fourth orders of selection, there are a multitude of examples demonstrating that individuals favour taking parasite risks over immediate risks associated with predation (Koprivnikar & Penalva, 2015), though not always (e.g., additive avoidance responses: Sharp et al., 2015).

Empirical studies at first and second orders of selection are critical to understand how fourth order decisions scale-up to shape the landscape of disgust for individuals, groups, and species. For example, individuals or populations may select home ranges with lower quality resources if there are increased parasite risks in resource-rich environments (second order) (Robertson & Hamilton, 2012). Alternatively, populations may choose to select resource-rich environments with increased parasitism risks (second order) (Mierzejewski et al., 2019), with individuals making decisions within that environment to reduce infection risks (third and fourth order) (Hutchings et al., 2002). To quantify habitat selection and the landscape of disgust on larger temporal scales, variables that are known to correlate with infection risks for a given parasite (e.g., climate) could be embedded into spatial distribution models for a given host (Box 2).

Much like the landscape of disgust, habitat selection is driven by cues that animals use to assess habitat quality. Adopting hypotheses from habitat selection theory could characterize how the landscape of disgust emerges as animals respond to parasite-associated cues. These hypotheses can similarly be tested at individual (second, third or fourth order) or population level (first or second order) scale (Table 1). For example, at the individual level, the ‘conspecific cueing hypothesis’ suggests that conspecifics release cues that an individual uses to select an optimal habitat, and the ‘conspecific performance hypothesis’ posits that conspecifics have lower or higher reproductive output in some habitats relative to others, serving as an indirect cue of the overall habitat quality (Stamps, 2009). At the population level, the ‘social attraction hypothesis’ suggests habitats should be selected at intermediate densities, because few cues are available for decision making at low densities, whereas available habitat will be limited at high densities (Fletcher, 2007; Swift et al., 2023). If such cues (either direct or indirect) are related to risks of parasitism, then conspecific cueing could shape the landscape of disgust by impacting habitat selection.

3.2 Density dependence and sociality

Habitat selection, by definition, is density dependent (Morris, 2003; Northrup et al., 2022). Following the Ideal Free Distribution and density-dependent habitat selection theory, animals should select habitat to maximise fitness relative to the availability of habitat, resulting in varying population densities among habitats in proportion to the fitness value of each habitat (Fretwell & Lucas, 1969; Morris, 2011). Density-dependent habitat selection theory therefore provides a null expectation for how animals select habitat within the context of the conditions, resources, and risks that make up their environment. Density is highly associated with parasite transmission risks for density dependent parasites (Hochachka & Dhondt, 2000; May & Anderson, 1979), and these associations can be impacted by social interactions within populations (e.g., allogrooming can sometimes reduce parasite burdens on hosts: Wilson et al., 2020). Owing to the dynamic associations among population density, parasite risks, and social behaviours, these factors must be considered together as they will cumulatively shape the landscape of disgust as density-dependent habitat selection occurs.

Ecological theory predicts that an increase in density will result in more contacts and therefore higher parasite transmission, and this effect has been observed in several meta-analyses (e.g., Cote & Poulin, 1995; Patterson & Ruckstuhl, 2013). However, density can also result in decreased transmission owing to the encounter-dilution effect (Mooring & Hart, 1992), or because of individual-level avoidance behaviours (e.g., Albery et al., 2020). These associations between density and parasite risks can change over time (e.g., Stewart Merrill et al., 2022). For example, increased density surrounding waterholes in dry seasons substantially increases the prevalence of oral-faecal parasites, and a tight association therefore exists between seasonality and parasite prevalence in this system (Titcomb et al., 2021; see Figure 1). Density is important for individuals making habitat selection decisions (Webber & Vander Wal, 2018); however, density does not necessarily equate to parasite infection risks, because social dynamics within groups can alter parasite infection dynamics (Craft, 2015).

Social behaviours must be incorporated into models of density-dependent habitat selection to develop accurate estimates of the landscape of disgust. Infected individuals with diagnosable symptoms are part of the landscape of disgust (Figure 1a) and their choices affect how conspecifics interact with each other. Parasites can impact social behaviour to facilitate further infection (e.g., increased shoaling in infected fish: Ward et al., 2005) or alternatively, parasite infection can maintain social behaviour even as host movement and habitat selection change (Turner et al., 2023). Conversely, infected individuals may not be accepted into social groups (e.g., guppy (*Poecilia reticulata*) shoals avoid infected conspecifics: Croft et al., 2011), reducing the risk for all individuals in the group and altering the structure of the landscape of disgust. Indeed, whether an animal is solitary or part of a group, and the social structure of that group, can impact the behavioural defences employed against parasites, including avoidance (Stockmaier et al., 2023). Finally, in some cases infected conspecifics with infection-associated pathologies are not avoided. For example, eastern water dragons (*Intellagama lesueurii*) do not avoid conspecifics infected with a lesion-causing fungus unless the severity of the infection is severe, presumably because the benefits of sociality outweigh the costs of most infections (Tacey et al., 2023).

Although infection risks of directly transmitted parasites are generally higher in large social groups (Cote & Poulin, 1995; Rifkin et al., 2012), social behaviours such as allogrooming and social learning of parasite cues can offset these costs (e.g., Kavaliers & Choleris, 2018; Wilson et al., 2020). Further, animals move in ways to reduce infection risks for themselves or groupmates. For instance, primates are thought to cycle through sleeping groves and defecate in specific areas to reduce parasite transmission (Gilbert, 1997; Hausfater & Meade, 1982) and bats avoid recolonization of recently used roosts with potential for infection (Reckardt & Kerth, 2007). Social behaviour contributes to the spatial structuring of populations (Webber et al., 2023), which in turn affects the placement of one type of infection risk (i.e., direct transmission of conspecifics) on the landscape of disgust. The landscape of disgust can also be shaped by social hosts mitigating risk by controlling where they generate risks (e.g., latrines or defecation behaviour).

4. Landscape of Disgust Across Generations

Within an animal's lifetime the landscape of disgust can by static or dynamic depending on how various mechanisms develop or continue to develop via evolutionary processes. Evolution generating variation in the landscape of disgust could be reflected in many ways, including the mechanisms that hosts use to recognize or avoid parasites or their ability to resist or tolerate infections by certain parasite species, ("ghosts of parasitism past": Poulin et al., 2020). This variation will affect all three components of the landscape of disgust framework: actual infection risks, perceived infection risks, and the actionable avoidance threshold. Not all variation in the landscape of disgust is a product of evolution. Plasticity could underly some phenotypic variation, although plasticity can also be a product of evolutionary forces (Ghalambor et al., 2007). Below, we start by discussing how the landscape of disgust will be shaped by evolutionary change in the hosts (Section 4.1), focusing on evolutionary processes that drive those changes (i.e., natural selection, sexual selection, gene flow and drift). Next, we discuss how the landscape of disgust will be shaped by evolutionary changes in the parasites, often in response to host evolution (Section 4.2).

4.1 Host evolution

The most apparent process by which evolution could generate change in the landscape of disgust over time is natural selection. When infection has negative fitness consequences, and where heritable variation exists in the traits that affect fitness, natural selection should drive adaptation to improve avoiding, resisting, or tolerating infection. In the landscape of disgust, natural selection could improve cue detection (adding resolution to the landscape of disgust; see Figure 2a-b) or increase avoidance of risks (how an individual reacts to the landscape of disgust it perceives). Populations with high resistance or tolerance may not have as strong selection for aversive behaviours, as they are handling infection with a different strategy (Boots & Bowers, 1999; Klemme et al., 2020); this variation could translate to a lower threshold for parasite avoidance (Figure 2c), or a lower perceived risk (e.g., decreased detection of parasite cues). At the among-species level, an example of this occurs at raccoon latrines where prevalence of the raccoon roundworm (*Baylisascaris procyonis*) is high. Tolerant species (e.g., raccoons and rats) frequent these latrines, whereas intolerant species (e.g., birds and small mammals) avoid them (Weinstein et al., 2017). Contrasting behaviours could represent reduced detection such that resistant or tolerant species have a lesser need to detect this risk or a decreased avoidance threshold such that resistant or tolerant species can detect the cues but do not need to alter their behaviour because fitness costs are low.

Sexual selection could also generate variation in host parasite defences, with similar implications for host sensitivity to parasite-associated cues and the landscape of disgust. For instance, more vibrant or ornamented individuals are typically hypothesized to be preferred by the choosier sex because they are “healthier” and more resistant to parasites and hence can afford to produce energetically costly ornamentations (Hamilton & Zuk, 1982). When the choosier sex selects individuals that are more resistant or tolerant, variation in the landscape of disgust could arise if subsequent generations inherit these anti-parasite defences. Increased anti-parasite defences owing to sexual selection could present in the landscape of disgust similarly to the outcomes of natural selection described above (e.g., high resistance or tolerance could result in decreased avoidance). However, natural selection could also remove the most resistant and tolerant individuals from populations if the individuals that cope best with parasite infections (i.e., that are more conspicuous) are also more likely to be predated upon (e.g., Møller & Nielsen, 1997). The balance (“trade-off”) between these two selective pressures will likely impact the landscape of disgust, and researchers should consider investigating more than one type of selection to understand how naturally occurring landscapes of disgust evolve over time.

Natural and sexual selection are not the only mechanisms that can generate evolutionary change. For instance, some host populations can be more susceptible to genetic drift (e.g., if they are small and isolated: Frankham, 2010), and the associated randomness could create challenges for predicting the landscape of disgust in those systems. Additionally, in connected populations where individuals disperse, gene flow could affect host-parasite dynamics (Kaltz & Shykoff, 1998) and the landscape of disgust over time. As an example, the introduction of individuals from a different population that have not co-evolved with a given parasite could reduce the extent to which the resident population is locally adapted to those parasites, which could impact selection (Chabas et al., 2016). Specifically, gene flow could swamp out evolved defence mechanisms, such as cue recognition or avoidance behaviours, essentially ‘resetting’ the landscape of disgust. In such cases, decreases in the accuracy of risk perception (upper layer) or avoidance behaviours may be observed. Alternatively, the introduction of genetic variation could shift the landscape of disgust by facilitating adaptation and the potential for more effective anti-parasite responses to evolve.

4.2 Parasite (co)evolution

Evolutionary processes affect the landscape of disgust over longer time scales as ‘arms race’ dynamics play out in host-parasite systems (i.e., ‘Red Queen’ dynamics: Ridley (1993) as cited by Dimijian, 1999). While the host is “winning” the arms race, the cost of infection may be reduced due to shifts in behaviour, resistance, and tolerance; however, similar evolutionary processes also occur for parasites, and selection can drive variation in adaptive parasite traits (e.g., Moro et al., 2021). The strength of selection acting on parasites is highly dependent on host defences. If host populations evolve increased tolerance, parasites may not suffer substantially reduced fitness, and so natural selection acting on the parasites will be weak (Gandon & Michalakis, 2000). In contrast, if host populations evolve increased resistance, parasite fitness will decrease, and there will be strong natural selection acting on parasites. Parasites may evolve less noticeable cues, or shifts may occur in the presentation of disease caused by the parasite, limiting the efficacy of avoidance behaviours for reducing infection risks. For example, for some viruses, such as SARS-CoV-2, infectiousness is highest prior to the onset of symptoms (He et al., 2020: impacting the upper layer in Figure 2). In this sense, parasites can adapt in response to host evolution to successfully infect despite their presence in the landscape of disgust (the former scenario) or can avoid entering the landscape of disgust in the first place (the latter scenario; at least for the pre-symptomatic period).

In many cases, humans alter the movement of animal hosts and parasites, increasing interactions between hosts and parasites that have no, or weak, co-evolutionary histories, which can have devastating impacts on host populations (Rogalski et al., 2017). The movement of hosts or parasites could introduce novel parasite species to host populations, or familiar parasite species (i.e., a species that the host has co-evolved with) from genetically distinct populations that the host has not co-evolved with (Dunn, 2009). Such scenarios have been hypothesized to explain the success of some invasive species (i.e., the novel weapons hypothesis: Vilcinskas, 2015). For example, when the American grey squirrel (*Sciuris carolinensis*) was introduced to Europe it also introduced a parapox virus, contributing to the grey squirrels' ability to outcompete Eurasian red squirrels (*Sciurus vulgaris*), a host that had no previous exposure to the virus (Rushton et al., 2000). Scenarios of novel host-parasite interactions highlight the importance that evolutionary histories or genetic backgrounds can have in host-parasite dynamics (see Box 1). The importance of shared evolutionary histories in shaping the landscape of disgust (affecting actual risks, perceived risks, and host responses to those risks) is a promising avenue for future work, both in natural contexts and with increasing anthropogenic impacts to host-parasite interactions.

5. Conclusions and future directions

In this review, we emphasize the value gained by incorporating habitat selection and evolutionary theories into the landscape of disgust framework. In doing so, we highlight many hypotheses that researchers could test in the context of the landscape of disgust (Table 1). There are many practical ways to integrate concepts from these theories into the landscape of disgust that could be leveraged in future work (Box 2). We recognize that determining the level of information required to map actual and perceived infection risks in a natural system may be difficult. The work required to quantify and map the risks of infection a host may engage with, or the evolutionary processes acting on hosts, poses several logistical barriers including difficulty detecting parasites, the time required to collect data, and potential cost or technological barriers. One solution is to use emerging simulation tools such as Agent-Based Modelling (DeAngelis & Diaz, 2019) to investigate how the landscape of disgust changes and how it can impact other aspects of natural systems to inform future empirical work (Box 2).

Many future avenues of work would complement our proposed ideas (see also Table 1). For instance, individual variation owing to acquired immunity or plastic behavioural responses may impact how a potential host interacts with the landscape of disgust (Barron et al., 2015) and should be investigated alongside repeatable host behavioural defences (e.g., ‘hygienic personalities’: Poirotte & Kappeler, 2019). Exploring whether some of the landscape of disgust concepts may be applied to other parasitism models that do not have classic host-parasite dynamics would also be valuable (e.g., individuals use visual cues to detect brood parasitism: Spottiswoode & Stevens, 2010). Because an objective of the landscape of disgust framework is centred around how hosts react to their perceived landscape of disgust through movement, a pertinent follow-up question would be to ask how animal movement can impact the physical landscape. Animal movement could impact nutrient distribution and landscape heterogeneity through zoogeochemical processes (Ferraro et al., 2022); determining the impact of parasite-mediated habitat selection on these processes – and how this can in turn affects risk and resources in the landscape – is a logical next step. Finally, in a similar vein, little work has explored how parasites may interact with, or compensate for, the landscape of disgust. Questions such as these will add additional resolution to the landscape of disgust, and the insight that can be gained from the framework.

Despite the fanfare and potential for widespread application, the landscape of disgust framework has been limited by a lacking integration of spatial, behavioural, and evolutionary theories. We propose a revised representation of the landscape of disgust originally visualised by Weinstein et al. (2018) that is spatially explicit (Figure 1,2). We outline how habitat selection and evolutionary theories could be integrated into this landscape of disgust framework, and the substantial value that doing so would contribute to this field of research. Our review highlights that the landscape of disgust remains in its infancy; without an understanding of how the landscape of disgust changes within and across generations, we cannot fully comprehend how parasite infection risks impact host ecology. Clearly, many interesting outstanding questions remain (Table 1.). We focus our discussion above on habitat selection and evolutionary theories given that they are the focus of the current paper, although a longer-term goal for the landscape of disgust should include integration with other frameworks to create a more holistic - and therefore even more powerful - framework.

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Figures, boxes, and tables

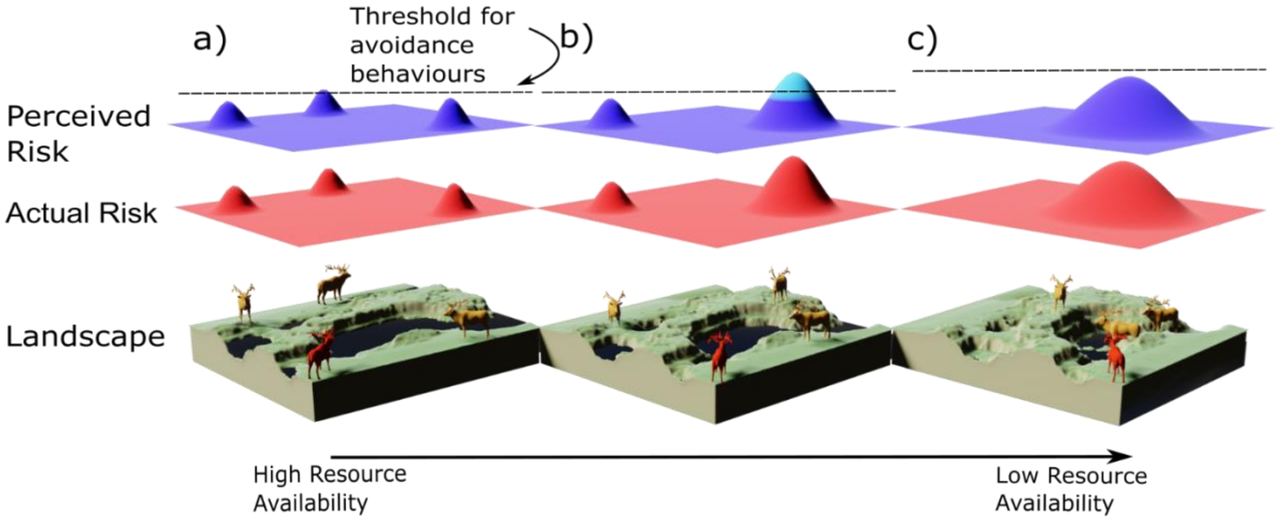

Figure 1. Visual depiction of a hypothetical change to the landscape of disgust that can occur across seasons, within a generation of a host. A critical resource (water) becomes increasingly scarce from wet to dry seasons, increasing density of conspecifics (animals per unit area) around water sources that could harbour infection through time. The different aspects of a quantified landscape of disgust, including the geographic landscape and conspecific locations (lower layer), the actual risk of infection (middle layer), and the perceived risk of infection (upper layer) are denoted as layers in each panel. From a) to b) as the resource becomes less available, individuals will choose lower density areas that present less risk but still provide access to the resource (where perceived risk is below threshold in upper layer). Between b) and c) the threshold of avoidance (upper layer) becomes higher as the resource becomes increasingly scarce. In this example, individuals will choose to increase their risks of infection (middle layer) by aggregating to gain access to remaining water resources (lower layer).

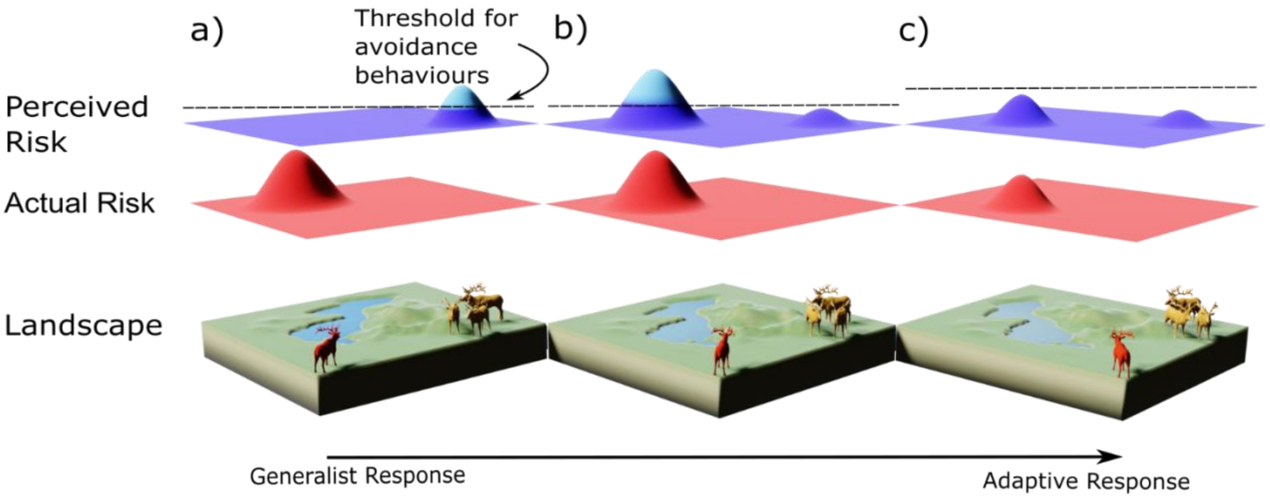

Figure 2. Visual depiction of a hypothetical change to the landscape of disgust over generations. A novel environmentally transmitted parasite is introduced to a landscape via a contaminated waterbody that represents the environmental reservoir; the introduction of this parasite drives adaptive changes over multiple generations in the host population (each panel representing subsequent generations). The different aspects of a quantified landscape of disgust, including the geographic landscape and conspecific locations (lower layer), the actual risk of infection (middle layer), and the perceived risk of infection (upper layer) are denoted as layers in each panel. Between a) and b) the host population evolves to associate the parasite cue with the environmental reservoir (there is a spatial shift in perceived infection risk) (upper layer). Between b) and c) the host population has evolved to become more tolerant to infection by that parasite (reduction in magnitude of risk in middle layer), reducing the perceived cost and aversive behavioural response; notably, there is a shift in the magnitude of perceived infection risk such that the perceived risk is now lower than the actionable avoidance threshold (avoidance threshold has increased, and magnitude of risk has decreased in upper layer).

Box 1: Exploration of the impact of eco-evolutionary feedbacks in the landscape of disgust

Recent work has emphasised feedback loops between ecological and evolutionary processes (e.g., Hendry, 2017; Pelletier et al., 2009); changes to ecology can drive evolutionary change – and evolutionary change can create feedbacks that influence ecology. Host-parasite evolutionary ecology is no exception to the importance of feedback loops (Ezenwa et al., 2016; Hawley & Ezenwa, 2022), yet interactions between evolution and ecology have been overlooked in the landscape of disgust literature. To discuss eco-evolutionary feedbacks, we can consider these from either eco-to-evo (ecological change driving evolutionary change) or evo-to-eco (evolutionary change driving ecological change) directions.

In the eco-to-evo direction, ecological change could impact how well adapted populations are, thereby changing selection strength or direction. For example, if a novel parasite is introduced (ecological change) and has high fitness costs those parasites could select for increased parasite defences (avoidance, resistance, tolerance) in subsequent generations of host populations (evolutionary change). Ecological changes could also impact other evolutionary forces such as geneflow, leading to changes in the landscape of disgust by changing the genetic structure of the population.

In the evo-to-eco direction, evolved variation in parasite defences (evolutionary change) could feed back to alter aspects of host ecology, including habitat selection (ecological change). As an example, animals that have evolved to perceive infection cues may select different habitats (as they avoid these risks) than animals that have not adapted to detect those cues. In either direction (eco-to-evo or evo-to-eco), eco-evolutionary dynamics can create a continually changing landscape of disgust that is a product of the environment, the host and parasite populations, and the adaptive landscape.

Box 2: Tools for measuring and interpreting the landscape of disgust in nature.

1) *Mapping parasites on the landscape:* It is possible to map parasite distributions when they are inside hosts or outside hosts. Species distribution models (SDM) (Elith & Leathwick, 2009) and resource selection functions (RSF) (Northrup et al., 2022) are useful tools for estimating organismal distribution through space and time. One way to estimate the landscape of disgust for parasites without intermediate or external stages (e.g., viruses) is to develop SDMs or RSFs for infected hosts through space and time (e.g., Dallas et al., 2019). For hosts with intermediate or external stages (e.g., nematodes or ectoparasites), we propose a multi-step approach, similar to the joint-SDM approach (Norberg et al., 2019), where SDMs or RSFs are developed for definitive hosts, intermediate hosts, and/or for the parasites themselves while they are outside of the host.
2) *Agent Based Modelling of the Landscape of Disgust:* Agent based models are spatially explicit individual level models. The emphasis on the individual level (the agent) provides an excellent opportunity to explore decision making and trade-offs when perceiving risks. These models are used to investigate movement and processes from individual level physiological processes (e.g., energetics: Malishev & Kramer-Schadt, 2021) up to ecosystem level processes (e.g., landscape heterogeneity: Ferraro et al., 2022). Researchers could model a landscape of disgust with agents that are a source of risk (i.e., social transmission), or that create risks (e.g., faecal deposition), tracking how

individuals who perceive these risks avoid them and how this could impact the system at varying levels (e.g., disease dynamics or nutrient cycling).

3) *Tracking the landscape of disgust across generations:* To estimate the strength and direction (e.g., stabilizing, disruptive) of selection in the context of the landscape of disgust, a researcher could measure any given trait (e.g., avoidance behaviour, infection tolerance or resistance) and a fitness proxy (e.g., number of offspring that survive to reproductive age, number of offspring produced, gonad size) (Hendry, 2017). If the traits of interest are heritable (which can be estimated in different ways, such as the traditional method of correlating offspring to parental phenotypes: Visscher et al., 2008), researchers can gain insight into whether selection on a trait (or correlated traits) will lead to evolutionary change in the landscape of disgust (Lande, 1979; Lande & Arnold, 1983).

Table 1. A non-exhaustive list of outstanding testable questions in the landscape of disgust.

Within a generation	**Across generations**	**Within and across generations**
• To what extent do hosts rely on direct versus indirect cues for parasite avoidance, and how would this affect habitat selection decisions in the landscape of disgust (i.e., conspecific cueing vs conspecific performance hypotheses)? • How does the landscape of disgust impact sociality and group dynamics? • Under what conditions would hosts select a habitat with greater parasite risks over a habitat with fewer parasite risks? (e.g., the social attraction hypothesis) • How does individual-level variation in the landscape of disgust impact the landscape of disgust at the population level? • To what extent can parasites modulate their behaviour to compensate for a well-adapted host landscape of disgust?	• To what extent do phenotypes (or genotypes) related to cue detection or avoidance shift over generations if natural and sexual selection are operating in the same or opposite directions? • By how much might arms race dynamics stabilize the landscape of disgust over time (i.e., cryptic eco-evo processes)? • How does geneflow impact local adaptation and host interpretation of the landscape of disgust? • To what extent are behavioural responses to parasitism that shape the landscape of disgust plastic or genetically based? • How do landscapes of disgust shift following the introduction of novel parasites or novel hosts?	• To what extent does a landscape of disgust exist for other forms of parasitism (e.g., brood parasitism, epiparasitism, social parasitism)? • How does host avoidance behaviour impact the zoogeochemistry and heterogeneity of the landscape? • How do epiparasites affect the habitat selection and evolutionary trajectories of their (also parasitic) hosts? • When and how does behavioural plasticity (both adaptive and nonadaptive) modulate the host's reaction to a perceived landscape of disgust? • How does intraspecific variation in parasite defences affect host ecology (e.g., habitat selection) and how does that feed back to alter the evolution of host defences? (i.e., eco-evolutionary feedbacks)