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

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Author Contribution Statement: Conceptualisation: AL, AH, QW (equal); Writing - Original draft: AL, AH (lead); QW (supporting); Writing - Review and editing: AL, AH, QW (equal); Supervision: QW (lead)

Data Availability Statement: This paper is a review and has no associated data.

Abstract:

Behavioural avoidance of parasites in the environment generates what is known as the "landscape of disgust" (analogous to the predator-induced "landscape of fear"). Despite the potential for improving our inference of host-parasite dynamics, three limitations of the landscape of disgust restrict the insight that is gained from current research: 1) many host-parasite systems will not be appropriate for invoking the landscape of disgust framework, 2) 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, and 3) relevant ecological and evolutionary theory has yet to be integrated into the framework, challenging our ability to interpret the landscape of disgust within the context of most host-parasite systems. In this review, we explore the specific requirements for implementing a landscape of disgust framework in empirical systems. We also propose greater integration of habitat selection and evolutionary theories, aiming to generate novel insight, by exploring how the landscape of disgust varies within and across generations, presenting opportunities for future research. Despite interest in the impacts of parasitism on animal movement and behaviour, many unanswered questions remain.

Keywords: Co-evolution; disease ecology; habitat selection; host-parasite dynamics; natural selection; parasite avoidance

1. **Introduction**

Individual organisms interpret cues from their environment to evaluate risks and inform decisions to increase fitness. Animal behaviour can change based on perceived associations between a given cue and potential fitness costs or benefits, in time leading to possible behavioural adaptation and predictable responses [1,2]. When cues are associated with the risk of infection with micro- or macro-parasites (hereafter ‘parasites; [3]), the perception of cues can result in feelings akin to the human feeling of disgust [4–6] and can elicit behavioural avoidance of infectious agents [5–12]. The distribution of cues in an environment and the resulting spatial distribution of organisms has been termed the ‘landscape of disgust’ [4], analogous to the predator-induced “landscape of fear” in which organisms respond to predator-associated cues (*sensu* [13]). By describing the cues that hosts 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 [4,14,15], in particular the non-consumptive effects (i.e., impacts to hosts beyond direct consumption, including changes to behavioural and developmental traits, among other traits; [16–18]).

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 because potential hosts will not always behaviourally avoid infection risks [5,6]. Although parasite infection risks are ubiquitous in nature, the costs of parasitism vary widely - ranging from infections with limited fitness impacts to infections that cause mass mortality as they spread throughout populations [19]. 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 [1,8], which would not be present for many asymptomatic infections. For infections that have strong fitness impacts, and therefore selection for preventing infection, detectable cues may allow for selection of behavioural avoidance. Infections with no detectable cues may result in selection for alternative strategies to prevent fitness costs such as increased resistance (the ability to limit or prevent infection) or tolerance (the ability to reduce fitness consequences of infection) [20]. Second, in systems where the landscape of disgust does exist, empirical research has focussed on small spatiotemporal scales. Although small-scale studies remain critical for improving mechanistic understanding of disgust, limited research at larger scales results in a knowledge gap about how parasite avoidance scales up to landscapes. Increasing the spatiotemporal scales of the landscape of disgust is indeed critical for increasing the value of the framework; we expect 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 integration of relevant ecological theory (e.g., habitat selection theory: [21]) and evolutionary theory (e.g., foundational evolutionary forces driving adaptation: [22]). 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 primarily aims to illustrate how critical insight could be gained by expanding the landscape of disgust interpretation to include habitat selection theory (Section 2: Landscape of disgust within a generation) and evolutionary theory (Section 3: Landscape of disgust across generations). To provide context for this review, we provide background knowledge of the landscape of disgust (Box 1), and a visual aid to show how aspects of the landscape of disgust could change within and across generations (Box 2). We finally provide examples of outstanding questions and suggestions on how to empirically approach researching these topics to expand our understanding of the landscape of disgust (Section 4: Conclusions and future directions; Box 3).

2. 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) [38], with habitat selection being the process through which animals differentially use habitats relative to their availability at a given population density to maximise fitness [39]. 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. In this section, we first discuss how the landscape of disgust will be shaped by the dynamic effects of parasite transmission, density, and sociality (Section 2.1). Next we consider ways to increase the spatial and temporal scales at which the landscape of disgust is assessed within a generation (Section 3.2).

2.1 Density dependence and sociality

Habitat selection, by definition, is density dependent [40,41]. 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 [39,42]. 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. However, the conceptual link between density-dependent habitat selection and parasitism is lacking; an absence which is striking given that density is often associated with parasite transmission risks [43,44].

An increase in population density is predicted to result in more social contacts and therefore higher parasite transmission, and this effect has been observed in several meta-analyses (e.g., [45,46]). However, transmission does not always increase with increasing density owing to the encounter-dilution effect [47], or because of increased (natural) selection for individual-level avoidance behaviours (e.g., [48]). Associations between density and parasite infection risk can change over time (e.g., [49]). For example, increased density surrounding waterholes in dry seasons substantially increases the prevalence of oral-faecal parasites, causing a tight association between seasonality and parasite prevalence [50] (see Figure B1). Notably, it is not solely conspecific density that can impact risk, but heterospecific density can also impact risk [51]. To provide important context to the landscape of disgust, both social behaviour and density-dependent habitat selection must be incorporated into estimates of the landscape of disgust (Figure 1).

The landscape of disgust does not only exist for uninfected individuals avoiding infectious agents. Infected individuals with clinical symptoms are also a part of the landscape of disgust (Figure B1a) and their behaviours affect how uninfected and infected conspecifics interact and the extent to which they can avoid infection risks in the environment. For instance, parasites can impact social behaviour to facilitate further infection (e.g., increased shoaling in infected fish; [52]) or alternatively, parasite infection can maintain social behaviour even as host movement and habitat selection change [53]. Conversely, infected individuals may not be accepted into social groups (e.g., guppy, *Poecilia reticulata,* shoals avoid infected conspecifics) [54], 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 social can impact the behavioural defences employed against parasites, including avoidance [10]. 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 [36].

Social behaviour contributes to the spatial structuring of populations [55], which in turn affects the placement of one type of infection risk (i.e., direct transmission from conspecifics) on the landscape of disgust. Although infection risk of directly transmitted parasites (i.e., parasites that require direct contact between hosts for transmission; [56]) is generally higher in large social groups [45,57], social behaviours such as allogrooming and social learning of parasite cues can offset these costs [25,58]. Further, animals can modify their movement to reduce infection risks for themselves or group-mates. For instance, primates are thought to cycle through sleeping groves and defecate in specific areas to reduce parasite transmission [59,60] and bats avoid recolonization of recently used roosts with potential for infection [61]. 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). Taken together, the interactive effects of sociality, habitat selection, density, and parasitism are multifaceted and can contribute to a dynamic landscape of disgust within the lifetime of an individual or group of individuals. It is well known that sociality and density operate on various biological scales [55], suggesting that the interactions with the landscape of disgust will vary from small to larger scales.

2.2 Expanding spatiotemporal scales

Habitat selection theory proposes that habitat decisions are hierarchical [62,63]; animals select habitats first at larger spatial scales and then make smaller-scale decisions within that habitat. Habitat selection is 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) [64]. Most landscape of disgust research focuses on third and fourth order scales. Intake maximisation is the most heavily studied driver of habitat selection in the context of landscape of disgust (e.g., [34,65,66]). For example, high risk food sources such as carcasses and faeces can be avoided behaviourally while foraging at the fourth order of habitat selection [32,67]; a process that could be quantified with the use of cafeteria style experiments measuring 'giving up densities' (a metric used to indicate when an animal quits harvesting from a patch) [13]. Within the third and fourth orders of habitat selection we would expect individuals to typically avoid areas or resources where parasite-associated cues are perceived (e.g., [68,69], Figure 1), however in natural systems selecting risk-free habitat may not be possible, leading to trade-offs in habitat selection. For example, individuals typically favour taking parasite risks over predation risks [70], though not always (e.g., additive avoidance responses; [71]).

Connecting ecological processes across the orders of habitat selection has become a hallmark of empirical and theoretical habitat selection studies. At the broadest spatial and temporal scales, the landscape of disgust should correlate with infection risks for a given parasite. For example, climatic conditions like temperature and precipitation could predict infection prevalence at population or species levels [72]. Some behaviours, such as migration, can allow animals to seasonally avoid infested habitats and reduce prevalence as they traverse diverse climatic conditions [73]. Selection on anti-parasite behaviours also exists within the context of larger-scale processes [74]. For instance, temperature can be associated with not only parasite presence, but also host immune function [75]. We might expect species (first order) or populations (second order) living in less ‘desirable’ climatic environments (where ‘desirable’ is context-dependent and species-specific) to have evolved stronger behavioural defences against parasites, which could be reflected in broad-scale geographical patterns [74]. Drivers of broad-scale patterns could also be biotic. For instance, in diverse communities where the dilution effect is observed (i.e., increased diversity is associated with decreased prevalence; [76]), we might expect to see reduced avoidance behaviours. Diversity varies at large spatial scales, with the most diverse communities often occurring closer to the equator [77], and this variation could similarly lead to broad-scale patterns in the strength of avoidance.

In the context of avoidance behaviour, this relationship between different orders of habitat selection is likely akin to a feedback loop. The presence or efficacy of avoidance at one order may impact the need for avoidance at higher or lower orders. Although we expect animals to place their home ranges to minimise infection risk [78], home ranges may still include areas with higher risk (third order; [79]), in which case finer scale avoidance is an important adaptive behaviour (fourth order; [80]). Another aspect that may affect the relevance of avoidance behaviours is the predictability of risk [81]. In areas with high spatial and temporal predictability in infection risk, third and fourth order avoidance behaviours should be most effective as individuals can reliably change their foraging behaviour and habitat selection to prevent risk exposure. In contrast, when predictability of risk in space or time is low the efficacy of fine scale avoidance is lower and therefore it may be more adaptive for individuals to select areas with lower risk - if available - or invest in other anti-parasite defences such as resistance or tolerance. Indeed, the predictability of risk could impact the trade-offs for selecting habitat that has associated infection risk. If there is a high fitness cost to infection and no potential for fine scale avoidance at the fourth order of habitat selection then we expect avoidance at third or second order habitat selection decreasing exposure to risky areas [82].

We suggest the importance of avoidance in habitat selection behaviour at different scales should be a priority for future empirical work. For example, tests of where animals place their home range might develop inference about whether they avoid potential environmental reservoirs of infection at the landscape scale. At the first and second orders of selection, biogeographic patterns of parasite avoidance behaviour can provide insight into historical avoidance or the factors driving selection for these traits at smaller scales. The process of ‘scaling up’ the landscape of disgust from fourth-order to the first-order of habitat selection will rely on the integration of macroecological principles with existing knowledge and theory [74]. Broader-scale research is necessary given that small-scale processes, although providing important mechanistic insight, rarely scale linearly, and emergent properties at the higher organisational levels require broad-scale investigation to be identified [74].

3. Landscape of Disgust Across Generations

Within an animal's lifetime the landscape of disgust can be static or dynamic depending on how various mechanisms develop or continue to develop via evolutionary processes (Figure 1). 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"; [83]), or through non-behavioural avoidance (e.g., morphological adaptations [84]) [11] . Variation will affect all three components of the landscape of disgust framework: actual infection risks, perceived infection risks, and the threshold for avoidance behaviour. Not all variation in the landscape of disgust is a product of evolution; plasticity could underlie some phenotypic variation, although plasticity can also be a product of evolutionary forces [85]. Below, we discuss how the landscape of disgust will be shaped by evolutionary change in the hosts (Section 3.1), 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 3.2).

3.1 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 [7,11]. In the landscape of disgust, natural selection could improve cue detection (adding resolution to the landscape of disgust; see Figure B2a-b) and increase avoidance of risks (how an individual reacts to the landscape of disgust it perceives). Importantly, cue detection and avoidance are likely under correlated selection, as these traits go hand in hand [86], while detection and avoidance also presumably correlate with resistance and tolerance [6,11]. Populations with high resistance or tolerance may not have as strong selection for avoidance behaviours, as they handle infection with a different strategy [7,87,88]; in which case, high resistance or tolerance strategies could translate to a higher threshold for parasite avoidance (Figure B2c) or a lower perceived risk (e.g., decreased detection of parasite cues). For instance, house finches (*Carpodacus mexicanus*) that have stronger behavioural avoidance responses invest less in immune defences [89]. Raccoon (*Procyon lotor*) latrines tend to have high prevalence of raccoon roundworm (*Baylisascaris procyonis*), and tolerant species (e.g., raccoons and rats) use latrines frequently, whereas intolerant species (e.g., birds and small mammals) avoid them [90]. Although these ‘strategies’ (cue detection vs. altered avoidance threshold vs resistance and tolerance) may be difficult to tease apart empirically, modelling provides an avenue that could attempt to investigate the independent effects of these strategies (Box 3). For instance, theory suggests that the evolutionary dynamics leading to behavioural defences can differ from resistance or tolerance depending on avoidance behaviour type and cost of infection [91]. Researchers could also conduct comparative analyses among populations or species that occupy different environments that might select for different cue detection methods, as detection mechanisms are likely highly associated with the organism’s ecology and the environment they inhabit [6].

Sexual selection could also generate variation in host parasite defences. For instance, more vibrant or ornamented individuals are typically hypothesised 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 [92]. When the choosier sex selects mates that are more resistant, tolerant, or best at avoiding infection, variation in parasite avoidance could arise, leading to variation in the landscape of disgust if subsequent generations inherit these anti-parasite defences. Increased anti-parasite defences owing to sexual selection could present in the landscape of disgust similar 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 individuals from populations that are the most resistant, tolerant, or least effective at avoiding infection 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., [93]). The balance (“trade-off”) between these two selective pressures will likely impact the landscape of disgust, owing to selection acting differently on host behaviour. In empirical studies this expectation that healthier and more conspicuous individuals will be preferred by the choosier sex is often not met ([94]). Many hypotheses exist to explain the lack of expected trade-offs, including that the association will be shaped by characteristics of the host or parasite (e.g., host sex or past pathogen exposure; [95]), that the association is not being investigated at the appropriate scale of inference (i.e., at the genomic level; [94]), or that other sources of selection in the environment could be ‘confounding’ the expected association (e.g., [96]). In other words, the association can be context dependent and is likely to be variable within and among populations, but could nevertheless help to shape the landscape of disgust over time.

Natural and sexual selection are not the only mechanisms that can generate evolutionary change. Some host populations are more susceptible to genetic drift (e.g., if they are small and isolated; [97]), and the associated randomness could create challenges for predicting parasite avoidance as it relates to the landscape of disgust. In systems where behavioural defences are particularly effective at reducing infection, it has even been suggested that immune based responses could be lost through drift [7]. Additionally, in connected populations where individuals disperse, gene flow could affect host-parasite dynamics [98] 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 [99]. 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 in Figure B2) 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.

3.2 Parasite (co)evolution

Evolutionary processes affect the landscape of disgust over longer time scales as frequency-dependence or ‘arms race’ dynamics play out in host-parasite systems (e.g., ‘Red Queen’ dynamics; [100]) [11]. 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., [101]). 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 [102]. In contrast, if host populations evolve increased resistance, parasite fitness will decrease, and there will be strong natural selection acting on parasites. Likewise, if host avoidance strategies are successful at reducing infection, then parasite populations could decrease, reducing the strength of selection acting on hosts but increasing the strength of selection on the parasites to rapidly adapt in response [11]. When selection on parasites is strong, the 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 ([103]; impacting the upper layer in Figure B2). 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 [104]. 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 [105]. Such scenarios are hypothesised to explain the success of some invasive species (i.e., the novel weapons hypothesis; [106]). 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 (*S. vulgaris*), a host that had no previous exposure to the virus [107]. Scenarios of novel host-parasite interactions highlight the importance that evolutionary histories or genetic backgrounds can have in host-parasite dynamics. 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.

4. Conclusions and future directions

In this review, we emphasise the value gained by incorporating habitat selection and evolutionary theories into the landscape of disgust framework. There are many practical ways to integrate concepts from ecological and evolutionary theory into the landscape of disgust that could be leveraged in future work (Box 3). We recognize that determining the level of information required to map actual and perceived infection risks in natural systems may be difficult. The work required to quantify and map or predict the infection risks a host may encounter, or the evolutionary processes acting on hosts and parasites, 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 simulation tools such as Agent-Based Modelling [108] to investigate how the landscape of disgust changes and how it can impact other aspects of natural systems to inform future empirical work (Box 3).

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. Many future avenues of work remain that would complement the ideas presented in this manuscript. For instance, individual variation owing to acquired immunity or plastic behavioural responses may impact how a potential host interacts with the landscape of disgust [109] and should be investigated alongside repeatable host behavioural defences (e.g., ‘hygienic personalities’: [110]). 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; [111]). Little work has explored how parasites may interact with, or compensate for, the landscape of disgust. Finally, because ecology and evolution can have reciprocal effects [22], we also suggest investigations that explore how these two processes could interact to influence the landscape of disgust, particularly in natural systems. Clearly, many outstanding questions regarding the landscape of disgust framework remain. 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 and theories to create a more holistic - and therefore even more powerful - framework.

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Figures and Boxes

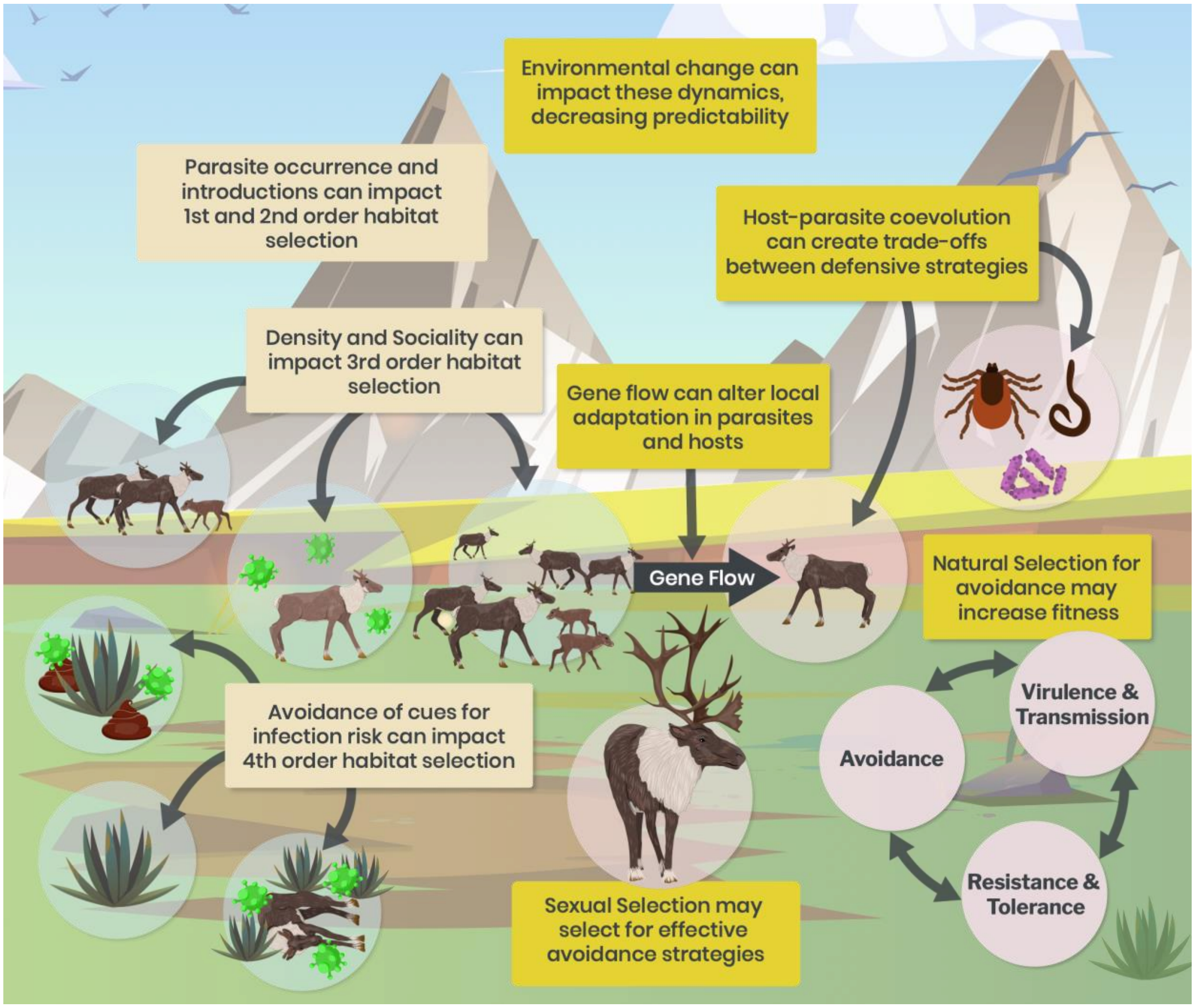

Figure 1: Factors affecting the formation and demonstration of the landscape of disgust. Here we illustrate a hypothetical system to demonstrate different factors that affect the landscape of disgust both within (tan boxes on left) and across (yellow boxes on right) generations. These factors include principles from habitat selection theory operating at varying spatial scales that could be impacted by detection of risk and ecological context, along with evolutionary principles such as selection for traits associated with the detection and avoidance of parasites, or geneflow or genetic drift impacting genetic variation for selection. This is not an exhaustive representation

of factors impacting the landscape of disgust but demonstrates several factors that should be considered when interpreting avoidance behaviour and making predictions in natural systems.

Box 1: Describing the landscape of disgust

The landscape of disgust represents behavioural responses to parasite infection risks [4]. Researchers have emphasised the role of host anti-parasite behaviours for decades [1,23], and the landscape of disgust provides a framework to renew previous lines of research, inspire new approaches to classic questions, and concentrate research efforts on the investigation of non-consumptive effects of parasitism.

Host-parasite dynamics influencing the landscape of disgust can vary between species, populations, and individuals within populations. 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 - which can be visual, auditory, olfactory, or mechanosensory - must be produced either directly by a parasite, the infected host, or something associated with risk of infection [6]. For example, the avoidance of faeces which may or may not be infested with parasites. 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; [24]). Finally, parasitism must be costly enough to impact potential host behaviour, and this change must prevent or reduce infection resulting in a fitness benefit to the host [5,6]. Both cue detection and response behaviour could be learned [25–27] or adaptive if sufficient time and genetic variation are present to evolve a connection between the cue and response [28]. Selection can act on phenotypes involved in different stages of infection, including recognizing parasite cues, and responding to infection [29]. 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.

Box 2: Visualising landscape of disgust within and across generations

We visualise the landscape of disgust as the summation of any ‘perceivable’ parasite infection risks within an individual’s spatial perception, relative to the ‘active’ infection risks (Figures B1, B2). We primarily discuss and interpret the landscape of disgust as a two-dimensional plane, as this reflects the movement of most terrestrial individuals, although in some systems a third axis of movement is available to avoid parasite infection, such as in aquatic systems [12], or for aerial or arboreal animals that can use vertical movement to avoid transmission (e.g., [30]). Because not all parasites can be detected, and not all perceived risks warrant a response [5,6], we visualise a biologically relevant threshold for infection risk that determines whether an avoidance response occurs at all (represented by the horizontal line overlapping perceived risks in Figures B1, B2), which parallels the “cost-benefit” structure used in other parasite avoidance and disgust reviews [5,6,11]. An avoidance threshold can be affected by individual state or past experiences, such as an individual’s body condition or hunger levels [31] and prior or current infection status [32,33]. Although we illustrate avoidance as binary in the context of this threshold, the strength of an avoidance response can vary. We predict the avoidance response to be correlated with the size of the perceived risk (represented as height of peak in Figures B1, B2). The risk of parasite infection also often exists as a gradient, and variation in parasite risk can occasionally be detected (e.g., [35,36]); this variation in risk is represented with simple peaks here but in natural systems there will be variation in the gradient around the cue as well [37]. In visualising the landscape of disgust across two timescales - within a generation (Figure B1) and across generations (Figure B2) - we provide a visual aid to help the reader understand how ecological and evolutionary theory fit into, and would expand, the existing framework.

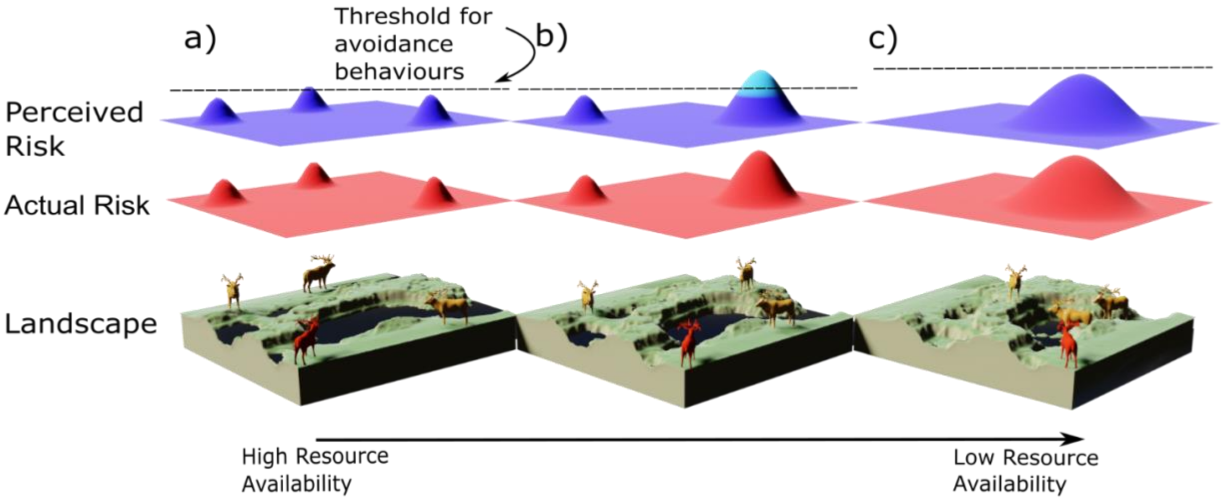

Figure B1. Visual depiction of a hypothetical change to the landscape of disgust that can occur across seasons, within a generation of a host. A critical resource (water) becomes increasingly scarce from wet to dry seasons, increasing density of conspecifics (animals per unit area) around water sources that could harbour infection through time. The 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).

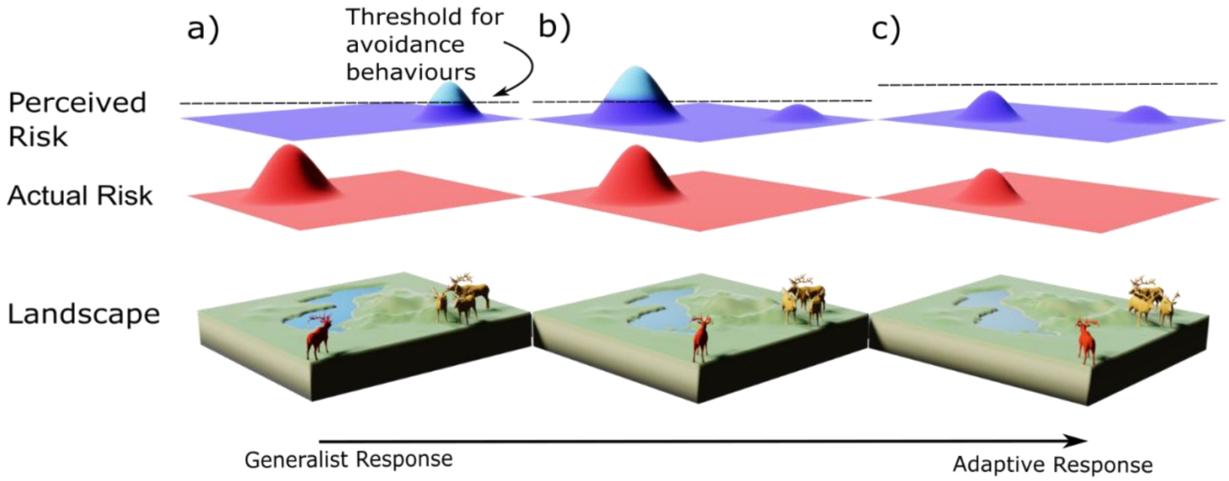

Figure B2. Visual depiction of a hypothetical change to the landscape of disgust over generations. A novel environmentally transmitted parasite is introduced to a landscape via a contaminated waterbody that represents the environmental reservoir; the introduction of this parasite drives adaptive changes over multiple generations in the host population over generations. 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 3: Tools for measuring and interpreting the landscape of disgust in nature.

1) *Mapping parasites on the landscape:* To predict both the benefits of avoidance and where avoidance should occur, quantifying the parasites that actually exist in a given environment provides important context. It is possible to map parasite distributions when they are inside hosts or outside hosts. Species distribution models (SDM) [112] and resource selection functions (RSF) [41] are useful tools for estimating organismal distribution through space and time. One way to estimate parasites without intermediate or external stages (e.g., viruses) is to develop SDMs or RSFs for infected hosts through space and time (e.g., [113]). For hosts with intermediate or external stages (e.g., nematodes or ectoparasites), we propose a multi-step approach, similar to the joint-SDM approach [114], 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; [115]) up to ecosystem level processes (e.g., landscape heterogeneity; [116]). 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., stabilising, disruptive) of selection in the context of the landscape of disgust, a researcher could measure any given trait (e.g., avoidance behaviour, resistance or tolerance) and a fitness proxy (e.g., number of offspring that survive to reproductive age, number of offspring produced) [22]. 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; [117]), researchers can gain insight into whether selection on a trait (or correlated traits) will lead to evolutionary change in the landscape of disgust [118,119]