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Cross-species pathogen spillover across ecosystem boundaries: mechanisms and theory

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Pathogen spillover between different host species is the trigger for many infectious disease outbreaks and emergence events, and ecosystem boundary areas have been suggested as spatial hotspots of spillover. This hypothesis is largely based on suspected higher rates of zoonotic disease spillover and emergence in fragmented landscapes and other areas where humans live in close vicinity to wildlife. For example, Ebola virus outbreaks have been linked to contacts between humans and infected wildlife at the rural-forest border, and spillover of yellow fever via mosquito vectors happens at the interface between forest and human settlements. Because spillover involves complex interactions between multiple species and is difficult to observe directly, empirical studies are scarce, particularly those that quantify underlying mechanisms. In this review, we identify and explore potential ecological mechanisms affecting spillover of pathogens (and parasites in general) at ecosystem boundaries. We borrow the concept of 'permeability' from animal movement ecology as a measure of the likelihood that hosts and parasites are present in an ecosystem boundary region. We then discuss how different mechanisms operating at the levels of organisms and ecosystems might affect permeability and spillover. This review is a step towards developing a general theory of cross-species parasite spillover across ecosystem boundaries with the eventual aim of improving predictions of spillover risk in heterogeneous landscapes.

This article is part of the theme issue 'Dynamic and integrative approaches to understanding pathogen spillover'.

1. Introduction

Zoonotic infectious disease outbreaks in humans are triggered by the spillover of pathogens from animals, and locations where humans and animals meet frequently are potential spillover hotspots [1]. Alongside factors such as human population density, living conditions and environment characteristics, proximity to ecosystem boundaries is suspected to mediate rates and risks of infectious disease spillover events [2,3]. Many past outbreaks of Ebola virus, for example, have been traced back to contacts with infected bushmeat carcasses near the edges of tropical evergreen forest or following perturbation caused by recent deforestation [4–6], while multiple vector-borne diseases such as zoonotic malaria, yellow fever, chikungunya and Zika are caused by parasite spillover from a primate-driven sylvatic cycle to humans and other animals at the boundary between rural and natural ecosystems [7–10].

Despite the speculation that ecosystem boundaries act as potential hotspots of parasite spillover between species [2], there has been relatively little effort

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Box 1. Definitions.

Bridge host: a host species that acts as a bridge or link in an interspecies transmission chain, meaning they act as recipient host for one spillover event, and consequently as source host for another onwards spillover event [15]. Bridge vectors fulfil an analogous functional role by transmitting between two different host species.

Ecosystem interior: the part of the ecosystem that is not under the influence of edge effects. We acknowledge that this is a highly simplified definition and that this will be species-specific, but it should be appropriate for the broad purposes of the description of mechanisms and theory relating to spillover.

Ecosystem boundary: the divide between adjacent ecosystems, also called 'edge' [16].

Parasite: throughout the text, we use the term parasite to describe all organisms that infect, and are transmitted between, hosts. This includes pathogenic as well as non-pathogenic microparasites and macroparasites. This encompasses a wide range of characteristics, and the mechanisms described in this article are likely to affect different parasites in different ways.

Permeability: a concept used in movement and landscape ecology, where it is defined as the degree to which an organism is able or willing to cross a given habitat [17]. Applied to spillover across ecosystem boundaries, it can be used to represent how likely a host species is to enter or cross the boundary. Permeability also applies to the parasite, in which case it is determined by permeability for the source and recipient hosts, as well as by the parasite's ability to survive outside a host and to passively or actively move into/across the boundary.

Recipient host: a species that is infected by a parasite originating from a different host species.

Source host: a species responsible for shedding the parasite and causing a spillover exposure event, either by shedding the parasite into the environment or through direct contact with the recipient host.

Spillover: the transmission of a parasite from one host species to another, regardless of whether onwards transmission in the recipient host is successful. This definition forces a focus on spillover only, although we acknowledge that onwards transmission is a crucial component of pathogen persistence and outbreaks, especially in the case of emerging infectious diseases in humans [1]. In this article, a distinction has been made between spillover rate (the total number of spillover events for a given host-parasite system) and spillover diversity (the total number of parasite species spilling over).

directed towards determining whether this is a general biological pattern, or when and where we might expect it to hold true (but see [2,11,12]). Should we expect to see higher rates of cross-species spillover near ecosystem boundaries than in ecosystem interiors? A compelling reason to expect this is that ecosystem boundaries form the occurrence limits of many species, which implies that contacts between species occupying adjacent ecosystems should occur within these transition zones. Furthermore, the ecological theory of edge effects predicts increased biodiversity at ecosystem boundaries, including the existence of boundary-specific species [13]. Both of these factors should correspond to an increase in spillover risk [1,14], owing simply to greater opportunities for cross-species contacts, yet empirical evidence about their precise effects on spillover risk remain sparse and context-dependent. Additionally, several other interacting mechanisms could influence spillover rates near ecosystem boundaries. A first step towards understanding the role of ecosystem boundaries in shaping spillover risk is to identify and describe potential underlying mechanisms.

In this article, we critically explore the biological mechanisms that could alter spillover at ecosystem boundaries. Our goal is to address three questions: (i) are ecosystem boundaries likely to be spillover hotspots? (ii) which mechanisms are expected to contribute to spillover near ecosystem boundaries? and (iii) can we borrow from existing ecological theory to develop a better understanding of spillover near ecosystem boundaries?

Section 2 of the paper describes the application of an existing ecological concept (permeability) to spillover across ecosystem boundaries, as a way to integrate distinct mechanisms driving host and parasite presence. Sections 3 and 4 describe the most important of these mechanisms, divided into mechanisms operating at the organism level (§3) and the ecosystem level (§4). Section 5 goes into existing concepts and theories from different fields that might be useful for advancing our understanding of spillover across ecosystem boundaries. The article will not be restricted to zoonotic spillover to humans, but will rather address mechanisms that might drive spillover between any host species, with the aim of advancing general ecological theory on parasite spillover. Note also that this review focuses on ecological mechanisms only, and does not address other crucial factors such as immune defence, host competence or host/parasite phylogeny that determine host–parasite compatibility.

Throughout our discussion of drivers of spillover, we distinguish between *spillover rate* (the number of spillover events for a single host–parasite system) and *spillover diversity* (the number of parasite species spilling over). Certain drivers such as host species richness will be more important for spillover diversity, while other drivers such as population abundance are expected to be more important for the number of spillover events. Definitions of these and other key concepts used in this article are provided in box 1.

2. Towards a general framework for spillover across ecosystem boundaries

The rate of spillover across ecosystem boundaries depends on the likelihood that *source* and *recipient hosts*, as well as the *parasite* (box 1), are present in or near a boundary region. This likelihood can be represented by a boundary's *permeability* (box 1), a concept used in landscape and movement ecology to describe an organism's ability or willingness to move through a certain habitat [17]. Applied to spillover, this concept can be used to characterize how likely a parasite is to spill over across ecosystem boundaries (figure 1). Spillover of a parasite across an ecosystem boundary requires boundary permeability for at least one of the three actors involved in spillover, i.e. source host(s), recipient

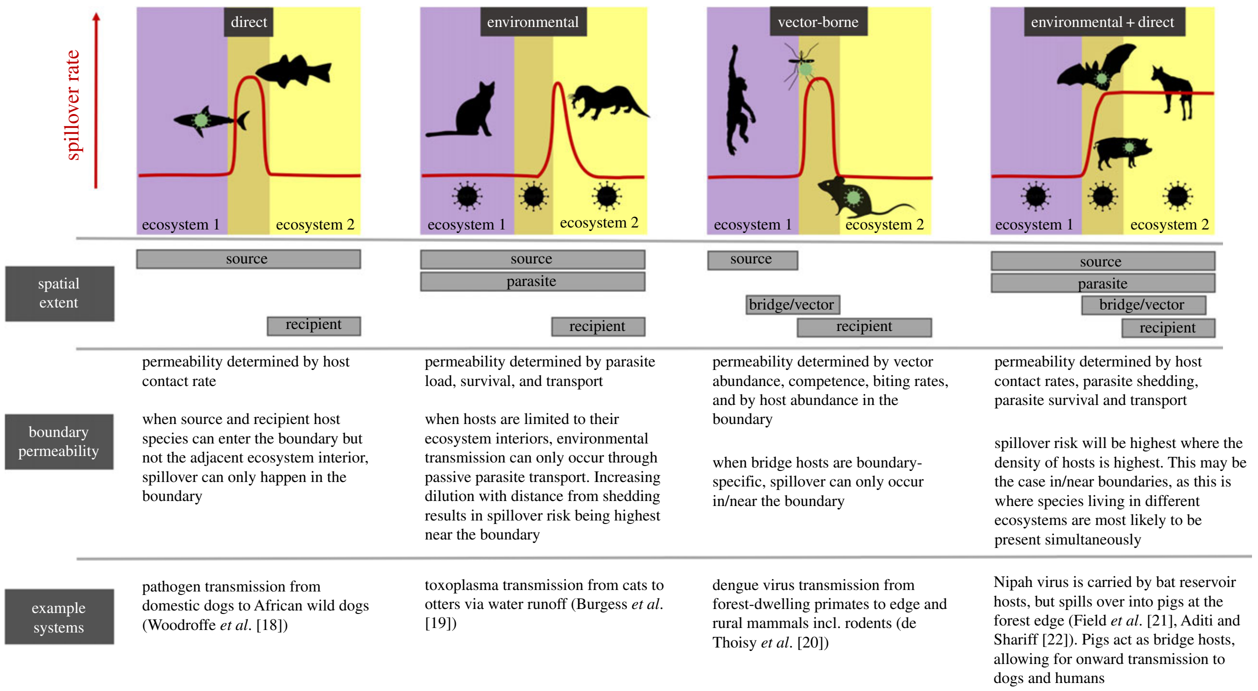

Figure 1. Conceptual model of how host and parasite characteristics affect boundary permeability to spillover. Non-exhaustive list of different ways in which general ecological mechanisms can affect parasite spillover across ecosystem boundaries. Purple and yellow background colours represent adjacent ecosystems, and the region of overlap represents their boundary. Red lines illustrate spillover rate at the different locations (ecosystem interiors and boundary). Grey boxes indicate the spatial extent of source, bridge/vector, and recipient hosts, as well as the parasite. (Online version in colour.)

host(s) or parasite. The interactions between the levels of boundary permeability for each of these components will determine spillover rate for a given system.

Permeability for hosts will depend on host traits, and all factors that influence behaviour and abundance near the boundary. For example, boundaries will have high permeability for species whose home ranges extend into both ecosystems [23] (figure 1). Some animals cross the aquatic-terrestrial boundary on a daily basis for foraging, such as the American mink (*Mustela vison*) or the Eurasian otter (*Lutra lutra*) [24]. On the other hand, highly habitat-specialized species such as the bamboo lemur (*Hapalemur* sp.) will be more likely to remain in their ecosystem interior, and experience low boundary permeability [25–27]. Permeability for parasites will depend on permeability for their hosts and vectors, as well as their abilities to persist independently outside the host on either side of the boundary, and possible physical transport in the environment (figure 1). Section 3 (below) reviews how host, vector and parasite characteristics might affect permeability.

For many host and parasite species, permeability will relate to the contrast between adjacent ecosystems [28]. Ecosystems that share many characteristics are more likely to facilitate cross-boundary movement, while boundaries dividing distinct ecosystems sharing few characteristics will more likely have low permeability for most species [29]. Ecosystem contrast can also influence the directionality of permeability, where organism movement occurs more easily from one type of ecosystem to another than vice versa. Water-borne organisms, for example, often follow the flow of water in the landscape, which means that both hosts and parasites can more easily cross from a terrestrial to an aquatic ecosystem than in the opposite direction, as is the case for *Toxoplasma gondii* transmission from terrestrial felids to sea otters [19]. Such directional permeability is also a well-known phenomenon for agricultural pest species, where cultivated areas near natural ecosystems tend to attract arthropod pests when productive [30,31]. This has direct consequences for pathogen spillover across ecosystem boundaries, as pest species can carry parasites across boundaries [32]. An important question that is relevant for the risk of spillover to humans is whether anthropogenic boundaries are less permeable to host and parasite movement than natural boundaries, owing to the stark ecosystem contrasts often created by anthropogenic boundaries. Section 4 expands on this, detailing ecosystem and boundary characteristics that can influence permeability for hosts and parasites.

3. Hosts, vectors and parasites near ecosystem boundaries

(a) Hosts and vectors near ecosystem boundaries

Host traits that increase the probability of occupying or crossing ecosystem boundaries may lead to such host species functioning as *bridge hosts* (box 1) that link different host species occupying distinct ecosystems [15]. Bridge host traits can include being a generalist consumer, having high tolerance to different habitats, or being an edge-habitat specialist. The presence of bridge hosts can be particularly important for spillover between two other host species for which the boundary has low permeability [33]. This may, for example, be the case for small mammals that transport *Ixodes ricinus* ticks between pasture and woodlands, thereby enabling them to feed on hosts that are unlikely to cross the ecosystem boundary, and hence potentially to vector infections across the boundary [34]. In turn, arthropod vectors themselves can often act as crucial bridge species (figure 1). For example, arthropod vectors are known to be responsible for spillover of important zoonoses such as Chagas disease, transmitted by *Rhodnius pallescens* kissing bugs that move readily between habitats and feed on multiple host species

[35], or the transmission of West Nile virus between wild birds and humans across the forest-settlement boundary [36].

Hosts with broad environmental tolerance and generalist resource use are more likely to be able to cross ecosystem boundaries than specialists [37]. Examples of generalists occupying a wider range of ecosystems than specialists are plentiful (e.g. dung beetles along forest-plantation boundaries [28], small mammals in a grassland-forest matrix [38]). Ecosystem boundary areas may, therefore, support a larger proportion of generalist species than ecosystem interiors. Additionally, as generalists will tend to move through a more diverse range of ecosystems than specialists, they may be more likely to encounter, and become infected with, a wider range of parasites [39], thereby elevating both spillover diversity and spillover rate near boundaries [12]. Alternatively, some host species specialize in edge habitat [13], and the presence of such edge-specific hosts might make them disproportionately more likely to be involved in spillover near ecosystem boundaries [33] (figure 1). For example, pinnipeds such as seals, whose life-history entails spending roughly half their time hauled out on land, can carry canine distemper virus from terrestrial to marine mammals [40].

(b) Parasites near ecosystem boundaries

The mode of transmission of a parasite is likely to affect which host traits and ecosystem conditions will be important for boundary permeability. Directly transmitted parasites require individuals of two different host species to come into close contact, which means that the conditions determining host movement and presence in the boundary will drive permeability for the parasite (figure 1). Parasites with a free-living stage or ectothermic host will be more sensitive to abiotic conditions, and spillover risk in the boundary will depend on conditions affecting parasite survival as well as those affecting host presence; furthermore, passive transport in the environment can lead to spillover even between host species that have no overlap in habitat use (figure 1). Permeability for vector-borne parasites depends on the presence of suitable vectors and may be less dependent on factors determining host abundance because of the movement and host-seeking behaviour of vectors.

Parasite host-specificity and tolerance to environmental conditions are probably linked to the probability of being present near ecosystem boundaries. Generalist parasites are able to infect a wider range of host species, thereby increasing the chances of infecting a host that is able to enter or cross the ecosystem boundary. Similarly, broad tolerance to environmental conditions will allow a parasite to survive in a wider range of ecosystems, which can increase the opportunities for encountering new host species in adjacent ecosystems or boundaries. This may, for example, be the case for parasites that can form stable environmental persistence stages such as spores (e.g. *Bacillus anthracis* [41]) or biofilms (e.g. *Vibrio cholerae* [42]). Generalist parasites may be particularly gregarious with respect to host breadth near ecosystem boundaries. For example, in a host–parasitoid system, generalist parasitoids infected a wider variety of host species than would have been expected at random, creating a disproportionately hyperconnected food-web specific to the boundary between natural and managed forests [26,37].

4. Properties of ecosystem boundaries

(a) Edge effects

Ecological edge effects shape host species richness and population densities [43], both of which can influence the prevalence and environmental availability of parasites to infect other host species, or ‘pathogen pressure’ as defined in Plowright *et al.* [1]. Host species richness at ecosystem boundaries tends to be higher than in the adjacent ecosystem interiors [44–47], although some systems exhibit the opposite pattern [48] (table 1). Higher species richness may result in more direct or indirect contacts between different species, thereby increasing spillover opportunities and spillover diversity [55]. Although the complex interplay between species diversity and parasite transmission *within* a given host species has been studied in some depth, and can be negative or positive depending on the context [56,57], less is known about how species diversity affects transmission *between* species [14]. All else being equal, a positive relationship between biodiversity and spillover diversity has been proposed [3,14,49,53,58], as parasite diversity is expected to increase with host diversity [59].

Host population densities are also expected to change near ecosystem boundaries, but whether they increase or decrease is species- and context-specific [16]. Certain species are known to exhibit increased densities near low-permeability edges as a result of animal movement being forced alongside the boundary, which can result in disproportionately high frequencies of interspecific contacts, both with other resident species and species from the other ecosystem for which the boundary is permeable [16,50].

(b) Ecosystem dimensions

Ecosystem patch size and shape will determine the proportions and sizes of ecosystem boundary and interior, which can have significant ecological consequences. While total ecosystem patch area (i.e. interior plus boundary) can drive host population size, density and parasite prevalence, boundary area can drive contacts between species in different ecosystems [1].

The perimeter-to-area ratio (PAR; ratio of ecosystem patch perimeter length to total patch area) is a key concept in island biogeography theory [60] (figure 2), and is used in research on the ecological effects of habitat fragmentation [3,32]. In particular, the concept has been applied extensively in the context of marine resource subsidies onto islands, which can be crucial for island ecosystem productivity [61]. In a disease ecology context, PAR is expected to correlate positively with rates of spillover across ecosystems, at least for plant pathogens [52] but likely also for animal parasites [2]. A strong indication that PAR is important for animal parasite spillover can be found in habitat fragmentation research, where spillover rate is expected to increase with the degree of fragmentation (and therefore with PAR) [2,11]. This is driven by an increase in exposure opportunities between organisms present in the two ecosystems (figure 2).

(c) Temporal variability near ecosystem boundaries

The presence of parasites near ecosystem boundaries is not static, and should be expected to vary over time owing to source host dynamics impacting pathogen release,

Table 1. Overview of mechanisms potentially important for driving spillover near ecosystem boundaries.

mechanism	state near boundaries	effect on spillover near boundaries		references
species richness	general expectation for species richness to be higher near boundaries, although there is also evidence for a negative effect	higher species diversity provides contact and spillover opportunities between a higher number of species combinations	↑ ↓	Haddad *et al.* [48]; Kark & Van Rensburg [45]; Keesing *et al.* [49]
population density	can be affected by boundary conditions, but whether positively or negatively is species- specific. Some species aggregate along boundaries when permeability is low	density effects on transmission and spillover will depend on the degree of density-dependence of the parasite. In many cases, higher density increases the transmission rate	↑ ↓	Desrochers & Fortin [50]; Fagan *et al.* [16]
perimeter-area ratio (PAR)	higher PAR will increase the influence of edge effects, and the potential area over which resources and organisms can flow between ecosystems	expected to correlate positively with spillover	↑	Despommier *et al.* [2]; Polis *et al.* [51]; Tscharntke *et al.* [52]; Wilkinson *et al.* [3]
patch size	larger patch size increases absolute boundary area, and can influence important host population characteristics incl. size and density	larger total boundary area increases the area over which spillover near boundaries can happen. Higher core population size and density can increase host movement, transmission rates	↑	Faust *et al.* [53]; Pardini *et al.* [54]
temporal variability in host/parasite presence and boundary conditions	environmental conditions near the boundary can vary more strongly, which can cause extensive variation in host and parasite presence and survival. Additionally, host movement across boundaries can vary strongly in a regular manner	variability in which, and when, hosts and parasites are present simultaneously, can result in a larger combination of different species contacting each other, thereby increasing spillover diversity. Effects on spillover rate are not clear	↑↓	Rand *et al.* [31]; Tscharntke *et al.* [52]
host traits	host traits resulting in broad environmental tolerance and generalist resource use are more conducive to movement near and across boundaries	hosts that are generalist resource consumers, and that move across multiple ecosystems, are more likely to encounter different parasites, as well different potential host species. This can make them more important drivers of spillover	↑↓	Becker *et al.* [39]; Frost *et al.* [37]
parasite traits	low host specificity and broad environmental tolerance makes it more likely for parasites to occur in different ecosystems, including the boundary area	parasites infecting multiple host species, and/or those able to survive in a wider range of environmental conditions, are expected to be more prevalent in boundary areas, and to be more likely drivers of spillover	↑↓	Frost *et al.* [37]; Peralta *et al.* [26]
boundary permeability	determined by a range of mechanisms. Boundaries can be more or less permeable for organisms, which will determine their likelihood of being present in boundary areas and of crossing into the adjacent ecosystem. Highly species-specific	hosts and parasites for which a boundary has high permeability will be more important drivers of spillover. Boundaries between highly contrasting ecosystems (e.g. marine-terrestrial) may be more likely to have low permeability, and vice versa	↑	Fagan *et al.* [16]; Peyras *et al.* [28]

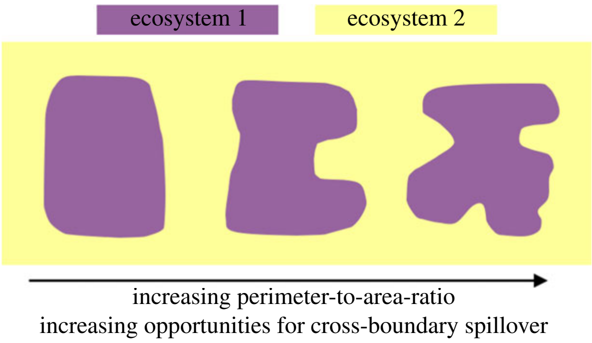

Figure 2. For a given ecosystem patch area, a higher perimeter-to-area-ratio corresponds with increased boundary length. This corresponds with increased potential for spillover across ecosystem boundaries. (Online version in colour.)

microclimate effects on parasite survival and spread, and recipient host dynamics on exposure [1]. Here, we will focus on mechanisms that can cause temporal variation in parasite pressure near ecosystem boundaries, while noting that this variability can also be affected by multiple mechanisms that are not boundary-specific, such as host population size or the presence of other host species in the ecosystem interior.

Host movement near or across boundaries can vary regularly at short (e.g. daily foraging) or long (e.g. seasonal migration) time intervals [62,63]. For example, human movement across ecosystem boundaries often varies regularly, as in daily hunting forays from villages into forests [64] or seasonal ecotourism [65], both of which are known risk factors for spillover of zoonoses [66,67]. Alternatively, movement can be triggered by changes in both ecosystem edge and interior areas. Deciduous plants in edge habitat, for example, can start to lose leaves earlier than those in the interior owing to microclimatic differences [68], with potential consequences for the transmission of parasites (e.g. earlier air-borne spread of fungal plant pathogens) [69]. Seasonal changes in the ecosystem interior can have direct effects on host and parasite movement across ecosystem boundaries [70].

Environmental conditions near boundaries can vary more strongly than conditions in the ecosystem interior, and this can have important consequences for both host and parasite species. For example, relative humidity and ultraviolet exposure are important determinants of the survival of many parasites, and can vary dramatically at ecosystem boundaries [16,71]. Environmentally mediated movement of parasites across ecosystem boundaries can also vary regularly or irregularly. Seasonal rainfall, for example, can result in seasonal transport of parasites across ecosystems [72].

In conclusion, it is clear that hosts and parasites are affected by multiple sources of variation specific to the boundary area, on top of the 'normal' boundary-independent variation. Increased variation in factors known to affect spillover is likely to result in contact opportunities between a higher diversity of hosts and parasites, thereby increasing the overall diversity of potential spillover events near ecosystem boundaries.

5. Parallels with existing ecological theory

Boundary permeability is a key determinant of spillover near ecosystem boundaries, as it is the integration of different mechanisms driving spillover dynamics. It relates closely to theory on ecological resource flow across ecosystems, particularly the concept of resource subsidies in island biogeography theory [51,61]. Parasite flow shares conceptual similarities with resource flow, while resource subsidy theory focuses specifically on the movement of resources (typically nutrients and microorganisms) across ecosystem boundaries, with a historic focus on marine-terrestrial subsidies [61]. Despite known limitations to applying island biogeography theory to terrestrial-only habitat islands (ecosystem patches) owing to the 'softer' boundaries [60], lessons might be learned that are relevant for spillover across ecosystem boundaries. For example, research on the PAR of literal as well as conceptual ecological islands provides an excellent context for developing hypotheses on the effect of the PAR on the number and diversity of spillover events near ecosystem boundaries, as discussed above.

Other opportunities to borrow theory relevant to cross-boundary spillover arise in the fields of movement ecology and landscape ecology, which both provide theory on how animals move across ecosystems [73]. Movement ecology focuses on individuals, and provides a well-developed conceptual and mathematical framework for studying why, how, when and where organisms move [74]. Landscape ecology is a broader field that focuses on a larger spatio-temporal scale than the individual level. At its core is a patch-corridor-matrix approach that is particularly relevant for understanding mechanisms behind spillover near ecosystem boundaries, connectivity of host populations, and biodiversity patterns at larger scales [75]. As landscape-level connectivity of different host populations will be a strong determinant of transmission and spillover, landscape ecology provides a solid theoretical and methodological foundation for advancing our understanding of spillover across ecosystem boundaries.

Landscape genetics offers crucial concepts and tools for understanding parasite transmission in general, and provides methods that could help quantify boundary permeability through formal testing of the existence of landscape resistance against host and parasite gene flow [76]. Similarly, phylogeography and phylodynamics have been used successfully for estimating cross-species transmission, and can easily be repurposed to cross-boundary systems [77]. Invasion biology has previously been proposed as a source of theory for understanding pathogen emergence [78], and can provide theory on directional permeability, as it by definition focuses on the spread of an organism from a source to a target ecosystem [79].

6. Discussion

This review explores and synthesizes potentially important mechanisms affecting cross-species spillover of parasites across ecosystem boundaries, as a step towards developing a general theory of spillover associated with ecosystem boundaries. Developing theory on spillover is particularly relevant for the spillover of zoonotic pathogens, and directly addresses the longstanding but untested hypothesis that areas where ecosystems meet are hotspots for the emergence of zoonotic pathogens [2].

Table 1 summarizes the most important mechanisms and how they are expected to affect spillover near boundaries. While all of these mechanisms are important in shaping spillover dynamics, many are not well suited for making robust generalizations about when cross-boundary spillover is expected to be higher or lower than in ecosystem interiors.

A few general predictions do emerge, however. For example, higher biodiversity tends to be observed in edges [74], which is expected to increase spillover risk through an increased diversity of host and parasite species available for potential spillover events [2,3]. Another factor that could consistently increase spillover opportunities near boundaries is the expectation of increased ecological variability at edges, which should result in increased contact opportunities between a wider range of different host and parasite species, thus increasing spillover diversity.

Despite the complexity and scarcity of empirical data on this topic, it is possible to make a number of further predictions that can be the focus of future empirical work. Spillover near ecosystem boundaries is expected to increase relative to ecosystem interiors when bridge hosts/vectors and edge specialists are present or abundant, when the proportion of generalist hosts and parasites is high, or when there are high levels of biodiversity, host density, and species interactions. We have argued that these factors can be integrated into an overall measure of boundary permeability, which governs spillover risk. It is less clear how temporal variability in ecological conditions and host/parasite presence should affect spillover rates; while increased variability is expected to result in a higher spillover *diversity*, it may simultaneously lower the total number of spillover events of focal host-parasite systems. At this point, we believe it is not yet possible to make more refined predictions on generalizable patterns of spillover at ecosystem boundaries. Key factors in this determination are that (i) edge effect research has revealed a high variety in responses to different conditions, as a result of general ecological complexity and stochasticity, and (ii) there is little to no empirical research that focuses specifically on comparing cross-species spillover near ecosystem boundaries with spillover in ecosystem interiors, especially in animal hosts.

While the theoretical framework for spillover is maturing, this exists in stark contrast with the relative scarcity of field studies and data on the determinants of spillover [1], especially across diverse ecosystems. There is a pressing need for fundamental research on spillover in multi-host, multi-parasite systems, and this review highlights that it might be worthwhile for some of that research to focus on spillover across ecosystem boundaries. Ideally, this is done in a model-driven synergistic context where conceptual and mathematical models of spillover inform, and are in turn informed by, field and experimental work [80], aided by the recent technological leaps in genetic sequencing and movement tracking.

Data accessibility. This article has no additional data.

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Competing interests. We declare we have no competing interests.

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