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Editorial

Disease ecology and pathogeography: Changing the focus to better interpret and anticipate complex environment-host-pathogen interactions

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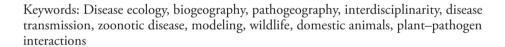
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Introduction

Over the past 15 years, disease ecology has become a discipline in its own right. It is fundamentally based on training in ecology and evolution, with solid theoretical foundations and skills in computational biology and statistics, and it differs from a medical approach to the interpretation of disease. It is concerned with how species interactions, including host–pathogen relationships and environmental conditions (e.g. temperature and rainfall), affect patterns and processes of disease presence and spread, how pathogens impact host individuals, populations, communities, and ultimately ecosystem function (Ostfeld et al. 2008). Initially rooted in parasite ecology, particularly among researchers working on transmission cycles and host–disease population dynamics, disease ecology mainly focuses on parasitic and infectious diseases but is not exclusive to them (Ostfeld 2018). A booming subfield currently concerns research linking different areas such as infectious transmission, agriculture development, and development aid policies, notably in the world's poorest countries (Ngonghala et al. 2014). Unlike ecologists, disease ecologists focus on understanding the causes and consequences of the maintenance and transmission of pathogens in animal species, including humans,



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plants, and communities of species. It has become much more widespread in studies among wild animal species, also in their contacts with domestic species, e.g. livestock, and their interactions with human populations, and much less so in plant diseases and their transmission, which in some respects are the focus of more plant-pathology molecular-orientated research (Guégan et al. 2023a). We cannot say that the development of disease ecology has involved the gradual integration of several distinct lines of inquiry because it is the heir of ecology. It has an ecosystem-based approach and takes into account natural complexity (Johnson et al. 2015, Hassell et al. 2021, Petrone et al. 2023); it develops experimental methods in the laboratory or mesocosms and has an essential background in statistical and mathematical analysis. The spatial scales of disease ecology study are experimental or local and, depending on the questions posed, can extend to the most global scales (Guernier et al. 2004, Jones et al. 2008, Allen et al. 2017, Carlson et al. 2022). In the temporal domain, these can be daily or weekly studies or multi-decadal investigations, such as in disease population dynamics (Keeling and Rohani 2007). By definition, disease ecology is concerned with understanding patterns and processes on large spatial and temporal scales. It integrates different levels of life organization, i.e. from genes to the global ecosystem, which is not the case, or only to a limited extent, of medical and veterinary approaches (Ezenwa et al. 2015). Over the years, however, disease ecology has gained the confidence of other disciplines, particularly the medical and veterinary ones, and is now published in top-leading generalist journals (Mahon et al. 2024, Pfenning-Butterworth et al. 2024, Chevillon et al. 2024). Today, disease ecology is also challenging established dogmas in human and veterinary medicine, reconsidering several aspects of infectious transmission in-depth, raising the question of possible larger host species spectra, and questioning the origin and nature of pathogen virulence (Chevillon et al. 2024).

We are happy to present this special issue on disease ecology in the journal *Ecography*. At least two other contributions recently published in Ecography could have contributed to this special issue in disease ecology. Both constitute remarkable illustrations of macro-scale studies on host-parasite interactions. They are: Latitudinal distributions of the species richness, phylogenetic diversity and functional diversity of fleas and their small mammalian hosts in four geographic quadrants by Krasnov and colleagues (Krasnov et al. 2023); and Continental-scale climatic gradients of pathogenic microbial taxa in birds and bats by Xu and coauthors (Xu et al. 2023). As illustrated in the different sections of this special issue, disease ecology is a highly interdisciplinary field, drawing on molecular biology and population genetics, immunology, epidemiology, time-series and spatial biostatistics, and ecological and epidemiological modeling. It takes an interdisciplinary approach, often questioning disease distribution, transmission, and intensity from another angle, and this with the wish to propose methods of surveillance, control, and research that are innovative sometimes breakthrough, and more in line with the complexity of the observations made.

In summary, the papers we present in this issue illustrate diverse scientific work and confirm the significant growth of disease ecology in the international research landscape.

Climate change and disease spillover and expansion

Climate change is accepted as an important driver of infectious disease emergence and spread for humans, wildlife, and domestic animals (Mora et al. 2022). However, there is considerable controversy as to whether climate change operates directly on the ecology of host–pathogen interactions (Franklinos et al. 2019, Casadevall 2020) or whether it intervenes more indirectly by exacerbating prevailing environmental, socioeconomic, or political conditions (Guégan et al. 2023b).

In a disease–biogeography study based on field observations, entitled *Climate change linked to vampire bat expansion and rabies virus spillover*, Van de Vuurst and collaborators (Van de Vuurst et al. 2023) report the impacts of global warming on the distributional range and expansion of the common vampire bat, *Desmodus rotundus*, across the Americas over the last century. Through a cogent correlation-based statistical analysis, the authors document the gradual expansion of vampire-borne rabies virus outbreaks in cattle herds in the last 50 years of the multi-decadal study period. The results presented here confirm the numerous observations of vampire-borne rabies cases in livestock on the continent while situating it in a macroecological dimension and pathogeography research perspective (Murray et al. 2018).

Then, Garcia-Carrasco and coauthors in an article, Present and future situation of West Nile virus in the Afro-Palaearctic pathogeographic system (Garcia-Carrasco et al. 2024), analyze the impacts of climate change on West Nile virus transmission and spread, a disease system that is highly sensitive to weather conditions and change. This virus is transmitted by insect vectors, genus Culex, and is also hosted by a wide range of bird species, making this zoonotic disease highly sensitive to climatic conditions. Using an innovative machine learning and fuzzy logic approach to model the effects of climate change scenarios for 2040 and 2070, this study evaluates the risk of West Nile virus outbreaks in two biogeographic regions, the Afrotropical and the Western Paleartic. They report that the Afro-Paleartic land masses could experience significant upsurges of epizootic and epidemic West Nile virus, with central and northern European regions at notable risk of disease expansion beyond the current distribution range. This study also confirms a broader comparative study on spillover risk in the context of climate change and wild species range shifts (Carlson et al. 2022).

Next, Aliaga Samanez and colleagues, in their article Climate change is aggravating dengue and yellow fever transmission risk (Aliaga-Samanez et al. 2024), model dengue and yellow fever diseases, two severe human infectious diseases, considering for the first time urban and sylvatic vectors, and non-primate hosts, to identify areas where climatic favourability for the two viral agents could change with global warming. Both viruses spilled over into human transmission

and were translocated in many regions, opening a path for spillback onto sylvatic cycles mainly for yellow fever (Santos de Abreu et al. 2022, Tuells et al. 2022) and DENV-2 serotype (Hanley et al. 2024). Using the same methodological framework as for previous studies, they obtain projections of future transmission risk for dengue and yellow fever and show that global favourability could increase by 10% for dengue and 7% for yellow fever, providing details of regions and subregions at particular risk for each disease. Furthermore, pathogeographical patterns of viral transmission are discussed in light of both vector and non-human primates' geographical distribution and potential range shifts.

Projections of disease spread scenarios within the current context of climate change become particularly relevant since these changes disrupt ecological equilibria among vectors, host reservoirs, and human populations. These three examples illustrate the application of disease ecology and biogeography tools to assess the risk of infectious diseases and anticipate their future spread.

Habitat alteration, biodiversity change, and zoonotic infectious diseases

Human activities modify, either directly or indirectly, the environments in which host–pathogen interactions take place (Lindahl and Grace 2015), leading to more encounters with reservoirs (Rhyan and Spraker 2010) or changes in the natural dynamics of complex multi-species systems (Hassell et al. 2017). In this section, contributors to the Special Issue investigate how habitat alterations and loss can reshape the risk of disease transmission or emergence.

Among the drivers that disease emergence and biodiversity loss share, land use features prominently. In their contribution, García-Peña and Rubio (2024) investigate how reservoirs of pathogenic and non-pathogenic New World Hantaviruses (NWH) respond to disturbances alongside a continent-wide gradient going from primary forest to agriculture. Through multivariate analysis, their results suggest that the prevalence of hosts is increased in rangelands and agricultural landscapes, corroborating global comparative studies exploring drivers of spillover transmission from rodent hosts (Ecke et al. 2022). Increased chances of encountering NWH reservoirs in agricultural lands suggest that ongoing widespread reconversion of the forest into cropland, such as the Brazilian Amazon (Morton et al. 2006), may increase the burden of infectious disease. Remarkably, this analysis also highlights a potential hotspot for reservoirs of NWH in northern Canada, a prediction that is well-supported in, for example, the case records of infections of humans by Sin Nombre virus since 1993 (Warner et al. 2020).

The question of how much habitat degradation will reshape the global risk of zoonotic diseases is, likewise, the core of the contribution by (Heckley et al. 2023). Through a metaanalysis of neotropical bat prevalence and seroprevalence, they examine the consequences of various classes of habitat degradation (including forest loss) on infection dynamics. Although sampling biases led to an over-representation of data on *D. rotundus* and rabies virus (see also Van de Vuurst et al. 2023 in this issue), they report that the highest prevalences (above 50%) were only observed in regions with the greatest extents of forest loss in the year before sampling. Identifying these potential causal mechanisms linking habitat degradation to zoonotic disease spillover is critical for more accurate prediction (Plowright et al. 2017, Mahon et al. 2024). The strength of the study by Heckley et al. (2023) is to show how diffuse these effects can be, even within relatively well-described systems (bats in the Neotropics). One possible explanation is that seasonal dynamics (Kessler et al. 2018) can profoundly change the landscape hosts experience, and these intra-annual variations can only be captured with a significantly larger amount of data.

In their contribution, Teitelbaum et al. (2024) look at how wild waterfowl interact with domestic poultry farms and how variations in these interactions shape the risk of transmission of avian influenza. The data used in this study (GPS data at the individual scale for over 400 individuals of ten species) offer a high-resolution view of space, time, and taxonomy; this allows for developing an appreciation of the risk of avian influenza transmission at a very fine scale. Different species of wild waterfowl used the habitats provided by domestic poultry farms at different rates, both across day/night and seasonal changes. Coupled with changes in abundance and influenza prevalence, the (multiplicative) interactions between these factors led to substantial changes in transmission risk, even within the relatively homogeneous study environment of California's Central Valley.

These studies highlight the challenges of understanding how habitat alteration will reshape the risk associated with disease. Because the ecological processes linking species (and species interactions) to their habitats play out over heterogeneous space and time, the amount of data required to draw general conclusions remains the main obstacle. Advances in Earth Observation through, e.g. remote sensing or the increased availability of high-resolution data with GPS collars are likely to provide good data to generalize our understanding of these questions in the coming years.

Ecological complexity and symbiont and disease patterns and processes

In this section, the authors illustrate the inherent complexity in host–pathogen or host–symbiont interactions. Indeed, a microbe cannot cause disease on its own without a host (Casadevall and Pirofski 2014). Still, this host–pathogen interaction is also mediated by the relationships it may maintain with other host and non-host species and with abiotic and biotic environmental conditions. Disease is one of several possible outcomes of an interaction between a host and a microbe, and this section also proposes research on host–symbiont relationships.

A first contribution by Clark and contributors entitled Aggregation of symbionts on hosts depends on interaction type and host traits analyzes aggregation patterns in both barnacle-limpet and gill helminth-poecilid fish associations

(Clark et al. 2023). The aggregation of symbionts and parasites among hosts is a near-universal pattern, and it also has important consequences for the stability of hostparasite associations and disease impacts (Morrill et al. 2022). Identifying which potential drivers are contributing to levels of observed aggregation in these systems has always been a pillar of parasitological ecology, the precursor of what would become disease ecology. This research has also contributed to developing high-performance biostatistical methods, another feature of disease ecology (McVinish and Lester 2020, Lester and Blomberg 2021). Using null models to analyze aggregation patterns in the two systems, Clark et al. (2023) show that aggregation of barnacles on limpets mirrors random partitioning, with variation observed across sites depending on limpet body size. Differently, helminth worms across fish populations were less aggregated than expected by chance, with aggregation decreasing with host fish size. The authors conclude that stochastic processes can account for the aggregation of symbionts on their hosts but do not explain the levels of aggregation observed in host-parasite interactions for which host traits may help to explain aggregation observations.

In a second macroecological study, Pinheiro and colleagues describe a latitudinal specialization gradient for a set of bird-malarial parasite networks that do not conform to the rule of accepted higher specialized interactions towards the equator (Pinheiro et al. 2023). Using bird species communities within different biomes on a gradient of temperate to tropical biomes across South America, they show that while specialization of host-parasite pairs interactions, i.e. network connectedness, increases towards lower latitude, quantitative specialization, i.e. including frequencies of host-parasite interactions and host phylogenetic relatedness, on the opposite, decreases. Overall, this study indicates that, near the equator, despite the fact that each malarial lineage parasitizes a more restricted range of available bird species, infections are more evenly distributed among tropical bird species than in temperate regions. In addition to providing strong arguments against a critical ecological hypothesis about species specialization, this work also echoes recent explanations concerning zoonotic viral infections in Southern America (Thoisy et al. 2024). It also contributes to a tradition in disease ecology of conducting comparative studies of non-human systems to better understand human host-pathogen interactions.

In essence, ecology is about understanding complex systems and their dynamics, and disease ecology integrates host–pathogen interactions to understand their origin, balance, and imbalance in host–pathogen equilibria and infectious transmission processes, including to humans. Sundaram and collaborators' contribution to this issue examines the origin of Ebola virus in sub-Saharan Africa, adopting an ecosystem-based approach (Sundaram et al. 2024). Instead of exclusively targeting Ebola virus linked to frugivorous bats, suspected to be the active reservoir hosts, this study investigates the role that multiple factors from bats, primates, fruiting tree species, their spatial habitat suitability, and biometeorological

parameters play in driving Ebola virus disease outbreaks. Using sophisticated phylogenetically-based path analyses and comparing different plausible path scenarios, it concludes that the factors most associated with previous Ebola virus outbreaks are spatial habitat suitability for *Ficus* trees and the diversity of *Cercopithecus* monkeys in the area. Furthermore, frugivorous species guilds, including bats, primates, and several other mammals, plus Pteropodid bat species richness, are good indicators of local Ebola virus circulation but do not explain zoonotic risk. Recent studies (Pleydell et al. 2024) have highlighted the importance of understanding the phenology of various species and the disturbances natural ecosystems and their biodiversity face. This goes beyond simply observing what is readily visible, as the current research demonstrates.

In a third investigation, Wallén and colleagues propose a research work entitled Consequences of repeated sarcoptic mange outbreaks in an endangered mammal population (Wallén et al. 2024). Parasites and infections are major factors influencing the population dynamics of wild animals (Hudson et al. 2002, Keesing et al. 2010). The Scandinavian arctic fox, Vulpes lagopus, is and endangered species showing a fragmented spatial distribution and suffering from interspecies competition, prey scarcity, genetic inbreeding and disease pathogens. Wallén et al. (2024) show that sarcoptic mange, caused by Sarcoptes scabiei, is responsible for repeated outbreaks in the artic fox metapopulation, and introduced by a few red fox specimens. Sarcoptic mange effects are severe and affect arctic fox demography and reproductive output. This case study also demonstrates that implementation of non-invasive treatment against *V. scabiei* can be effective, but only in the short-term, for spatially complex systems with overlapping species (e.g., see Haydon et al. 2006 for another illustration).

In the last part of this section, Hjermann and colleagues propose a study entitled Individual and temporal variation in movement patterns of wild alpine reindeer and implications for disease management (Hjermann et al. 2024), in which they analyze animal movement patterns based on GPS-marked wild reindeer individuals to identify chronic wasting disease transmission and potential behaviour risk. Research on wild animal movements and their health situation is scarce (Calenge et al. 2024), and this work attempts to re-establish the situation. Using an extensive individual-based dataset of surveyed Norwegian alpine reindeer with individuals infected by a fatal prion causing chronic wasting diseases, this work shows that the rut season favors an increase in male home ranges, greater home range overlaps and shorter geographic distance between males, and between males and females. These conditions facilitate individual-to-individual transmission of the prion agent, and management measures to prevent excessively high transmission rates affecting livestock survival are suggested. One of the aims of this study is to propose adequate surveillance systems of wildlife to assess disease risk in the most affected regions and reconcile surveillance in the research agenda (Guégan 2024).

Disease-plant and tri-trophic relationships

The final section of this special issue deals with plant–pathogen interactions in space. Tree pests are a global threat to plant biodiversity (Freer-Smith and Webber 2017) and can have cascading effects on a broad range of ecosystem services (Boyd et al. 2013). As plant health is a core factor in maintaining food security (Flood 2010) and human health more broadly (Hulme 2020), these articles highlight how relevant plant–pathogen interactions are to the conversation about disease biogeography.

In their contribution Climatic variability, spatial heterogeneity and the presence of multiple hosts drive the population structure of the pathogen Phytophthora ramorum and the epidemiology of Sudden Oak Death, Kozanitas et al. (2024) investigate how Sudden Oak Death epidemiology changes under the joint effects of climate variation, habitat heterogeneity, and host species turnover. Primarily affecting species from the Quercus genus, the pathogen is transmitted through a mostly unaffected host, the California Bay laurel. This causes an interesting challenge for the distribution of the pathogen, as the range of predictors required involves abiotic factors (here, precipitation is particularly determinant) and biotic ones (the distribution of the transmissive host). This situation is not specific to plants and resembles similar systems like the Cryptococcus complex, where the risk of transmission is shaped by climatic variables and the tree composition (Mak et al. 2010, 2015).

Caballol et al. (2024) cover much of the same conceptual ground in their manuscript entitled Climate, host ontogeny and pathogen structural specificity determine forest disease distribution at a regional scale, but consider how different pathogen species (Dothistroma pini and Diplodia sapinea) jointly interact with their host (Pinus nigra) and the climate. Although both diseases cause additive effects (on tree defoliation), they report no evidence of competition in adult trees. Environmental heterogeneity manifested itself by changing which pathogen had the largest impact on tree mortality; Dothistroma resulted in more seedling mortality in cold and moist areas, and Diplodia in dry, warm areas. In addition to their different environmental responses, these two pathogens are likely to differ in the micro-habitat they use within the host at the adult and seedling stages. The combination of these factors resulted in a marked variation in the drivers of forest health within the study region: the host-pathogen interaction was regulated by local bioclimatic conditions, even though both pathogens were widely distributed. This is an intriguing observation, as it highlights the need to consider how coinfection may be mediated (and its outcome determined) by environmental conditions.

In the final manuscript of this special issue, Contrasting effects of beekeeping and land use on plant-pollinator networks and pathogen prevalence in Mediterranean semiarid ecosystems, Martínez-López et al. (2023) study the interactive effects between beekeeping and land use on the biotic interactions between plants and pollinators, in the context of the emergence of a novel insect pathogen, Vairimorpha ceranae. V.

ceranae can be transmitted during pollination (Zbrozek et al. 2023) and may lead to secondary infections by the bacterial genus Serratia (Braglia et al. 2024). In the semiarid ecosystems studied, the authors report that the prevalence of the pathogen is not predictive of its spread but varies considerably within the year. Although communities with more diverse pollination interactions and more plants tended to show a lower prevalence, this effect was only weakly significant. Yet, this is an interesting observation that should lead to future investigations of how the structure of interactions within communities can shape the potential for dilution effects. A striking takeaway from this article is that several causal relationships may only become apparent once temporal delay is considered; this emphasizes the need for temporal data collection that would re-survey several sites/communities to capture these complex temporal interactions.

Discussion and further recommendations

The interdisciplinary field of disease ecology has significantly evolved over the past 15 years, establishing itself as a distinct discipline within ecology and evolution. This special issue of *Ecography* underscores the importance of understanding the ecological and evolutionary dynamics of diseases, emphasizing the intricate interactions between hosts, pathogens, and their environments. The studies presented herein reflect the diverse and growing body of research that characterizes modern disease ecology, spanning topics such as climate change, habitat alteration, and the complex interplay of ecological and disease processes.

The insights from this special issue suggest several areas warranting further exploration. Future research in disease ecology should prioritize integrating advanced climate models with data on ecological interactions to predict disease dynamics under changing environmental conditions. Such studies are likely to benefit from longitudinal studies tracking disease patterns over time, which are essential for identifying trends and informing management practices. Embracing interdisciplinary research that combines molecular biology, genetics, epidemiology, and ecological modeling will enhance our understanding of disease processes. Such an approach will foster innovative solutions for disease surveillance and control and for maintaining environmental health, for instance, by advancing our understanding of biodiversity's role in disease resilience. Interdisciplinary thinking applied to research on the human-wildlife interface (social science, ecology, and epidemiology) will be critical for mitigating spillover transmission risks to humans as human activities increasingly impact natural habitats.

Health geography and, *a fortiori* biogeography and pathogeography of infectious disease, have suffered a significant loss of importance over the last 30 years in human and veterinary medicine. It is very common in the medical world to speak of ecological studies to describe the finding of spurious correlations, which in medicine are not convincing compared with the gold standard of cohort analysis studies. At the

heart of this discrepancy lies the subject of changes in spatial and temporal scales, and scale-dependency, which are major concerns for science in general. Several investigations have been developed to estimate biologically relevant spatial and temporal scales at which environmental conditions impact ecological patterns and processes in ecology (Pease 2024), but this is less common in disease ecology (Becker et al. 2019; but see Halliday et al. 2020, Liu et al. 2022). Temporal and/ or spatial varying scales of effect are plausible in host-disease interactions, but they remain largely untested in both theoretical and empirical studies. The debate around the dilution effect is illustrative of this. Disease-biodiversity relationships reveal contrary relationships depending on different parameters, like disease transmission categories, land types or spatial scales. Temporal and/or spatial variation in scales of effect can strongly depend on available variables at scales of interest, making that host-pathogen interactions and changes can be best explained by changes in human development at local scale because these parameters are measured and available, and explained by climatic variables and climate change at largest scale, at which these variables can be obtained, i.e. the Elton's sound hypothesis (Chavy et al. 2019 for an illustration on human leishmaniasis in southern America). This also indicates an important issue about collected data since biotic and human behaviour and attitude data exist at lower scales and quasi-absent at largest scales when abiotic parameters, e.g. meteorological data, dominate. We strongly encourage disease ecologists towards this research avenue in order to elucidate host-pathogen and also tri-trophic interactions at specific scales of effect and deciphering their ecological and evolutionary drivers. This will help disease ecology to be better understood, taught in veterinary and medicine schools, and interpreted by disciplines that are either reticent or still too hegemonic, and to play a part in the process of aiding animal and public health efforts worldwide.

Disease ecology is poised for continued growth and impact in a world where change is visible at every observable scale. The advances in our field will be driven by the need to understand and take action to address the complex challenges of infectious diseases. This special issue highlights the current state of knowledge across numerous systems and scales, and sets the stage for future research to further unravel the web of interactions that define disease ecology.

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Competing interests

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