

# Untapped potential: The utility of drylands for testing eco-evolutionary relationships between hosts and parasites

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## ABSTRACT

Drylands comprise over 41% of all terrestrial surface area and are home to approximately 35.5% of the world's population; however, both free-living and parasitic fauna of these regions remain relatively understudied. Yet, the very conditions that make these regions challenging to study – extreme environmental conditions and low population density for various organisms – also make them potentially untapped natural laboratories for examining eco-evolutionary relationships between hosts and parasites. Adaptations and ecological patterns illustrated by desert parasite communities can serve as exemplars within the extremes regarding the evolution of virulence, breadth of host spectra, and lifecycle strategies. This review provides relevant examples for each of these three topics using parasites from dryland regions in order to encourage future empirical tests of hypotheses regarding parasite ecology and evolution within dryland ecosystems and stimulate wider investigation into the parasitofauna of arid regions in general. As global climate changes and anthropogenic disturbance increases, desertification is a growing problem which has been labeled as a threat to global health. Thus, deserts not only provide useful natural laboratories in which to study parasite transmission but understanding parasite transmission within these habitats becomes increasingly important as larger, likely highly resource insecure, populations are projected to live on the margins of desert regions in the future.

## 1. Introduction

### 1.1. Drylands: an underutilized resource for understanding host-parasite relationships

Despite the relative significance of arid environments in terms of both global landmass area and relevance to future human habitation (i.e. desertification, Patz et al., 2012), biodiversity within these areas have been relatively understudied. For example, only approximately two investigations per million km<sup>2</sup> of desert have been published as compared to 25 publications per million km<sup>2</sup> of temperate forest between 1984 and 2010 (Trimble and van Aarde, 2012). Given that free-living desert communities are understudied relative to those in other ecosystems, it follows that their corresponding parasitofauna (*sensu stricto* = eukaryotic parasites) has been understudied as well. This is unfortunate because the unique challenges that these organisms face in arid habitats can provide greater understanding of eco-evolutionary relationships between hosts and parasites in general. Most notably, parasite transmission within deserts faces the two vital challenges of low host density and harsh abiotic conditions. Thus, corresponding adaptations and ecological patterns illustrated by desert parasite communities can serve as exemplars within the extremes regarding the

evolution of virulence, breadth of host spectra, and lifecycle strategies. Additionally, as global climate changes and anthropogenic disturbances increase, desertification is a growing problem that has been labeled as a threat to global health (Kuehn, 2006; Patz et al., 2012). Thus, deserts not only provide useful natural laboratories in which to study parasite transmission, understanding parasite transmission within these habitats becomes increasingly important as larger, likely highly resource insecure, populations are projected to live on the margins of desert regions in the future (Kuehn, 2006; Safriel, 2007; Patz et al., 2012).

### 1.2. Earth: a plethora of drylands

Drylands, or areas with an annual precipitation to evapotranspiration ratio (i.e. aridity index) of 0.65 or less (Safriel, 2007), comprise approximately 41.3% of all terrestrial surface area (Patz et al., 2012). Additionally, as a whole, drylands are home to approximately 35.5% of the world's population and hold a share of 65% of the planet's rangelands as well as 25% of its cultivated lands (Safriel, 2007). Thus, from both a habitat and a land use perspective, drylands are critical areas for assessing the interface between humans and nature. Drylands themselves consist of three major types of habitat (Fig. 1): forests within dry subhumid areas (aridity index = 0.50–0.65), grasslands within

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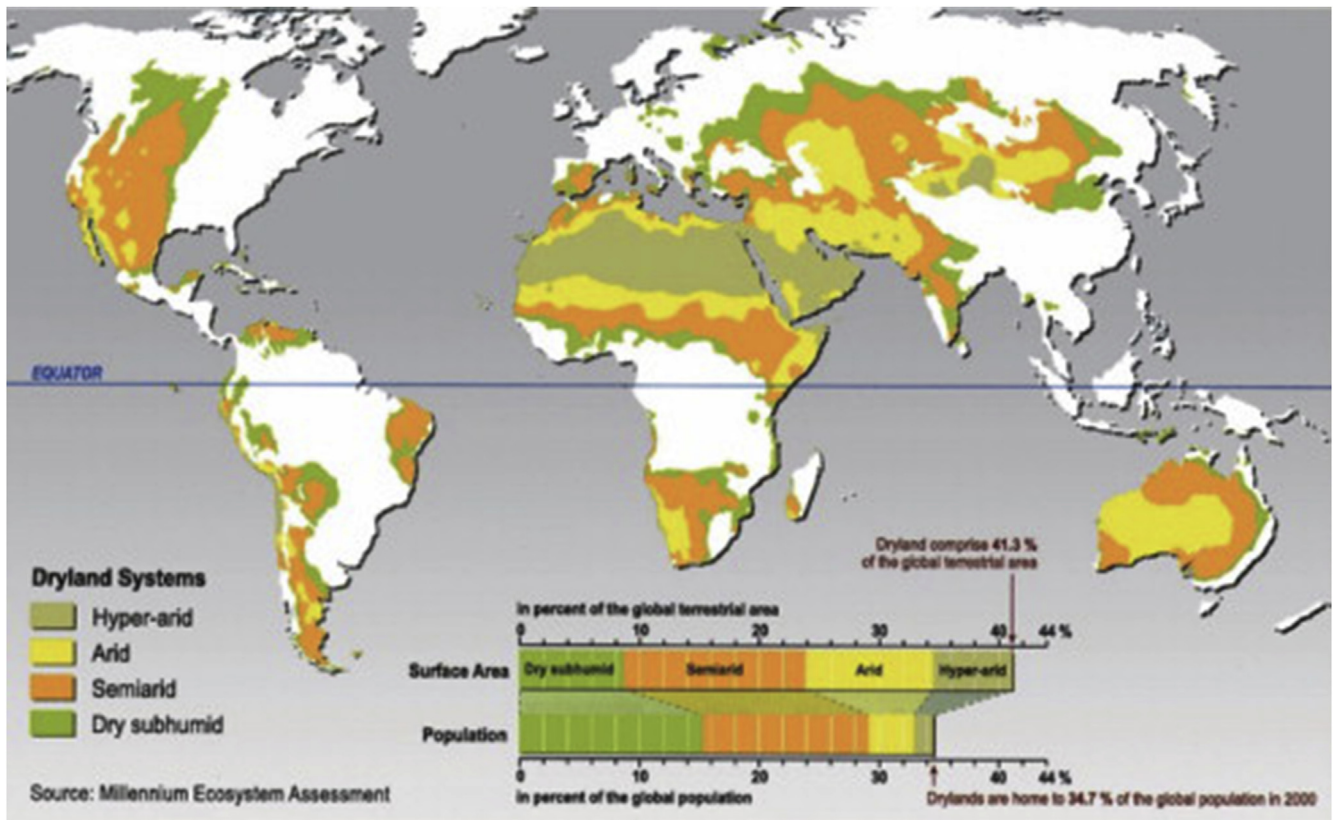


Fig. 1. Drylands consist of four major subtypes that compose approximately 41% of the Earth's terrestrial surface area and are home to over 34% of the global population. Note that white areas are non-dryland regions. Source: Millennium Ecosystem Assessment, Adeel et al. (2005)

semiarid areas (aridity index = 0.20–0.50), and deserts within arid (aridity index = 0.05–0.20) as well as hyper-arid (aridity index < 0.05) areas, with deserts accounting for slightly over 17% of the Earth's surface (Safriel, 2007).

Despite the significant extent of drylands on earth, these areas are understudied (Trimble and van Aarde, 2012). This could be due to preconceived perceptions of arid environments and that working in them can be logistically challenging, as precarious environmental conditions, limited resources, and remote locations can make research in deserts difficult. Additionally, deserts occupy well over 5 times the land area of developing nations as compared to industrialized ones, possibly making them an afterthought to researchers in typical Western industrialized countries (Safriel, 2007). Unfortunately, deserts might also have been ecological afterthoughts in the past, with less motivation for studying desert communities than, for example, temperate forest communities. Desert ecosystems have historically been considered to be of little complexity given that their aboveground net primary productivity (ANPP) is low, typically three times lower than temperate forest ecosystem ANPP (Webb et al., 1978; Hadley and Szarek, 1981; Garcia-Pichel and Belnap, 1996); therefore, these communities might not be given the full consideration by ecologists that they deserve. This is unfortunate because not only is the relationship between ANPP and biodiversity not a universal rule (Mittelbach et al., 2001) but the microscale and belowground environments, particularly soil microbes in desert crusts, are key sources of productivity in arid regions (e.g. Garcia-Pichel and Belnap, 1996; Pavón and Briones, 2000; Fierer et al., 2009). Finally, low productivity does not preclude low biological complexity and desert communities are replete with a high degree of interspecies interactions stemming from high connectivity in food webs, a large number of omnivores, and complex arthropod and soil faunas (e.g. Polis, 1991).

## 2. Challenges of transmission

Two barriers to parasite transmission in deserts are immediately apparent: 1) low host density (e.g. Munger et al., 1983; Polis, 1991; Krecek et al., 1995), and 2) harsh abiotic conditions (e.g. Dobson, 1989). Thus, the contact rate between infective stages and potential hosts becomes increasingly small as: 1) low host density means that the likelihood of host to host or host to vector decreases, and 2) survival of infective stages in the environment likewise decreases as abiotic conditions become increasingly inhospitable. However, given these two sets of conditions, deserts can act as a type of natural laboratory in which to gather test predictions related to key aspects of parasite transmission. As reviewed by Dobson (1989), transmission can be considered a “birth” in the ecological sense as it represents parasite recruitment while virulence can similarly be considered a source of mortality. The basic reproductive rate ( $R_0$ ) of a parasite, or any pathogen, represents its reproductive success and is directly influenced by the rate of new infections, the mortality rate of infected hosts, and the mortality rate of infective stages (Box 1). Thus, the means by which a parasite can increase its reproductive success are to: 1) increase transmission rate, 2) decrease host mortality rate, or 3) decrease the mortality rate of infective stages. Given that host density is low in deserts and their harsh abiotic conditions make survival of infective stages challenging, arid regions provide a unique opportunity to observe eco-evolutionary processes behind levels of virulence, breadth of host spectra, and timing of lifecycles enlisted by parasites to increase their chances of transmission.

### 2.1. Virulence evolution and drylands

The evolution of virulence is a key question when considering infectious diseases and predicting conditions that favor various levels of

parasite virulence regularly promotes ongoing discussion in this area (e.g. Ewald, 1983; Gandon et al., 2001; Choo et al., 2003; Wild et al., 2009; Hite and Cressler, 2018). Much of this discussion involves trade-offs between virulence and transmission rate. Indeed, pathogens with high virulence tend to have higher transmission rates in hosts than those with lower virulence (Kennedy et al., 2016). However, these highly virulent pathogens tend to truncate the potential infectious period by killing their hosts more rapidly. Thus, intermediate virulence has been postulated as an evolutionary optimum (e.g. Mackinnon and Read, 1999; de Roode et al., 2005; Atkins et al., 2011). However, the availability of susceptible hosts can greatly modify optimal virulence levels in eco-evolutionary models. This is because as the number of susceptible hosts in the population increases, parasite fitness increases due to increased infectiousness; however, the fitness cost of truncating any individual infection does not increase due to wide availability of new hosts (Day and Proulx, 2004; Bolker et al., 2010; Baidouri et al., 2013). Thus, high host density provides for the maintenance of a more virulent pathogen because even if hosts die quickly, the pathogen can still persist in the population (Anderson, 1986; Kennedy et al., 2016). Although a fair amount of investigation has focused on increased parasite virulence, the opposite scenario has received less attention. When host density is low, pathogen virulence has typically been predicted to be relatively low as well as maintaining a lower level of pathogenicity in return for an extended level of infectivity increases the chance of transmission (Ewald, 1983; Knolle, 1989; Lenski and May 1994; Haraguchi and Sasaki, 2000; Lively, 2006; Lion and Boots, 2010; Leggett et al., 2017; Cressler et al., 2016); however, relatively few empirical studies document concrete links between parasite virulence and host density (e.g. Herre, 1993; Bieger and Ebert, 2009).

One approach to improve empirical support for virulence predictions is to take advantage of naturally low host population densities in drylands and compare the relative virulence of parasite species from both arid and humid regions. One such candidate for such a comparative approach is the *Leishmania* species complex. Over 50 different *Leishmania* species spanning the globe occur in various habitats ranging from humid areas of the South American tropics to hyper-arid regions of the Arabian Peninsula (World Health Organization, 2019). Likewise, a variety of mammals, such as rodents, dogs, bats, hyraxes, and mongoose, act as vital reservoir hosts for many *Leishmania* species (e.g. Roque and Jansen, 2014; Ahmad, 2020; Sadlova et al., 2020; Salah et al., 2020) and few species are strictly anthroponotic (Akhoundi et al., 2017). This great variety of species also presents a wide range of virulence and pathogenicity within leishmaniasis (Matlashewski, 2001) with cutaneous leishmaniasis (CL) the most commonly encountered (Fig. 2A) and less clinically severe form while visceral leishmaniasis (VL) is less common (Fig. 2B) but more severe form (Alvar et al., 2012).

When considering Old World *Leishmania* species, approximately 90% of human CL cases are distributed within two arid regions: 1) the Middle East (i.e. Afghanistan, Iran, Saudi Arabia, and Syria) and 2) North Africa (i.e. Algeria and Tunisia); however, approximately 90% of human VL cases occur within two more humid regions: 1) South Asia (i.e. Bangladesh, India, and Nepal) and 2) East Africa (i.e. Ethiopia, Kenya, and Sudan) (Alvar et al., 2012). Molecular evidence also suggests that species causing CL and VL evolved in those regions that are home to a majority of cases (Mauricio et al., 2007; Baidouri et al., 2013). Given that reservoir hosts are vital to the maintenance of this parasite, the relative densities of possible reservoirs, such as small mammals, in these areas could provide intriguing links to how virulence evolved to its current levels in the *Leishmania* species complex. Background densities of rodents from anthropogenically undisturbed (i.e. protected) areas in East Africa (Caro, 2003; Makundi et al., 2007) and overall rodent population densities in South Asia (Prakash and Mathur, 1988) are relatively high when compared to those in the Middle East (Melville and Chaber, 2016; Shenbrot et al., 2010) and North Africa (Traba et al., 2016). Thus, the availability of various wild reservoir hosts are higher in areas where *Leishmania* species causing VL

are distributed and likely evolved. Additionally, growing levels of urbanization in some habitats have increased the availability and/or proximity of reservoir hosts, especially synanthropic ones like dogs (Wasserberg et al., 2003; Diniz, 2008; Ahmad, 2020; Salah et al., 2020). Unfortunately, broad surveys of the effects of *Leishmania* spp. on its sylvatic reservoirs are limited. Dobson (1989) suggested that CL had little obvious impact on sylvatic reservoirs but only provided a qualitative assessment. A survey of VL effects on wildlife hosts indicates that they could serve as important reservoirs of human VL infection (Souza et al., 2014) while proximity to domestic and wild animals has been indicated as an risk factor for both CL and VL (Valero and Uriarte, 2020). Several surveys suggest that dogs are important reservoirs of leishmaniasis (Singh et al., 2010; Dantas-Torres et al., 2012; Maia et al., 2015). However, domestic dogs are: 1) not necessarily the host with which these parasites coevolved, 2) have population densities that are positively correlated with human population densities, and 3) can be highly competent reservoir hosts when they are asymptomatic (Laurenti et al., 2013); thus, virulence in domestic dogs might not be a good proxy for virulence in sylvatic reservoirs. Yet, it is worth noting that understanding how growing numbers of competent reservoirs, such as domestic dogs, might change the virulence of endemic *Leishmania* spp. could be a key step toward protecting public health in the future. Therefore, taking a comparative approach toward uncovering how virulence evolved in arid versus non-arid environments could provide empirical tests of models developed at different population densities for various parasites.

## 2.2. Widening the host spectrum

For parasites, one option for overcoming low target host density is to widen the host spectrum. If suitable hosts are relatively rare, then evolving to a more generalist lifestyle would improve the likelihood of encountering a host. Broad structural host specificity, or the ability to achieve high relative abundance on or in multiple host species, acts as a key hedge against local parasite extinction (Poulin et al., 2011). Indeed, exploiting several different host species at a similar level of abundance allows parasites to resist perturbations to local host populations that result in low numbers of hosts in a given area; however, the ability to switch hosts could also be constrained by the level of phylogenetic relatedness within the potential host community (Krasnov et al., 2004a,b). Learning how parasites evolve as generalists versus specialists and the phenomenon of host switching can help elucidate the processes that underlie novel host-parasite associations. These processes are then key to understanding emerging infectious diseases within naïve host populations (Jones et al., 2008; Brooks et al., 2014; Nylin et al., 2018).

Although such investigations are relatively rare, desert organisms have provided useful tests of hypotheses related to habitat specialization when they have been examined. One such pattern is an inter-specific positive relationship between local abundance and occupancy where widely distributed species have larger local populations but species with narrower distributions tend to have smaller local population sizes (Gaston et al. 1997; Gaston 2003). The resource breadth hypothesis postulates that this pattern is due, at least in part, to inter-specific variation in niche breadth; thus, a species that can exploit a variety of habitats and resources can attain a broad distribution and high local density (Brown, 1984, 1995).

Desert communities may provide useful tests of the resource breadth hypothesis and habitat specialization in general. Indeed, a meta-analysis that analyzed the relationship between flea abundance and host specificity on small mammals across arid and semi-arid habitats found that the host spectrum became broader as flea abundance increased (Krasnov et al., 2004a). This was due to either to fleas increasing either the number of host species they exploited or the average taxonomic distance among those host species. The authors then posited that these generalist parasites achieve higher abundance because of greater

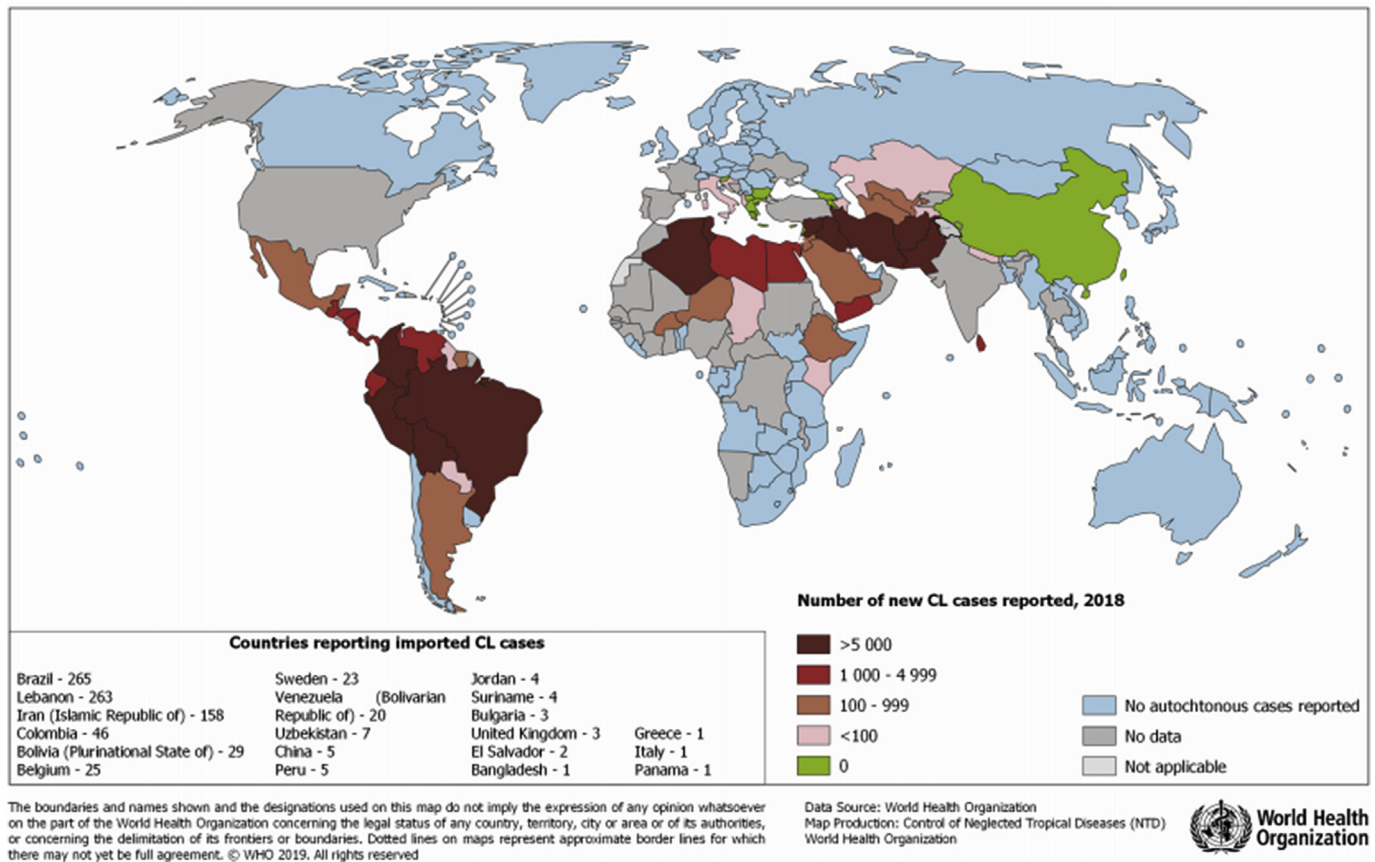


Fig. 2. Worldwide endemic and imported cases of (A) cutaneous leishmaniasis (CL) and (B) visceral leishmaniasis (VL) as of 2018. Warmer colors indicate a higher number of cases reported that year. Source: World Health Organization (2019).

resource availability (i.e. more hosts to infest), greater resource stability (i.e. number of hosts is relatively constant regardless of local perturbations), or a combination of both (Krasnov et al., 2004a). Additionally, in an experimental test of two fleas infesting desert rodents, generalist fleas *Xenopsylla ramesis* reared on taxonomically distant hosts exhibited less morphological asymmetry of leg length, meaning that their left and right legs closely matched in length. However, specialist fleas *Parapulex chaephrenis*, exhibited significantly higher leg asymmetry when reared on taxonomically distant hosts (Warburton et al., 2017). Morphological asymmetry is a key marker of low developmental stability or a decrease in the ability to produce a given phenotype in a given environment (Palmer, 1994). These results indicate that generalist fleas have greater developmental stability than specialist ones when reared on less-than-suitable hosts (Warburton et al., 2017). Thus, the types of ecological patterns exhibited by parasites in arid environments could provide unique and valuable insights when considered separately from not only free-living taxa but also taxa in different biomes.

### 2.3. Insight into parasite lifecycles

In addition to the challenge of low host density, the abiotic environment within the desert itself presents a problem for parasite transmission. Some parasites, such as nematodes and trematodes, have evolved complex lifecycles that include immature stages outside the host. These stages can take a sit-and-wait mode of transmission or a more active one. For example, the egg of *Ascaris suum*, a common geohelminth in temperate and tropical areas worldwide, can remain infective in soil for many months awaiting ingestion by a host; however, this is only the case when temperature and humidity are suitable (Roepsteroff et al., 2001). Many trematodes in temperate and tropical areas, such as *Echinostoma caproni*, utilize free-living miracidial and

cercarial stages that actively seek out and penetrate a host (Fried and Graczyk, 1997). However, these stages require some type of environmental water (e.g. dew, water body) which is highly ephemeral in arid regions. Thus, parasite transmission via extra-host stages is challenging in deserts. However, two solutions have evolved that not only meet challenging abiotic conditions but also provide a work around for low host density, namely: 1) tight synchronization between parasite life-cycles and host phenology (e.g. seasonal host aggregation), and 2) utilizing intermediate hosts as both a buffer to external environmental conditions and as a vector that can increase host contact rate.

One of the most well-known examples of tight synchronization between the lifecycle of a parasite species and the phenology of a host species, the monogenean trematode *Pseudodiplorchis americanus* and the Spadefoot Toad (*Scaphiopus couchii*), occurs in the desert of south-eastern Arizona (USA). These toads spend the vast majority of their life in estivation and are only active for approximately 8 weeks of the year, during the “monsoons” of June and July; thus, although the transmission window of their only major parasite (*P. americanus*) is very short, this monogenean uses seasonal host mating aggregations to increase its likelihood of success (Tinsley, 1990). The life cycle of *P. americanus* is unique among helminths in that the larvae, which infect the host via its nares, migrate to the bladder where adults mature and start producing offspring that are retained *in utero* until the next rainy season (Tinsley and Earle, 1983). Indeed, *P. americanus* can release its entire annual reproductive output within a 7-h period that corresponds to host spawning (Tinsley, 1990). Male toads, which typically enter multiple spawning assemblies, exhibit nearly 100% prevalence and a mean intensity of over 100 larvae per host, more than double that of females, which only spawn once (Tinsley and Jackson, 1988). Thus, even though the window of potential transmission totals less than 24 h per year, *P. americanus* has been able to exploit the toad's mating behavior to

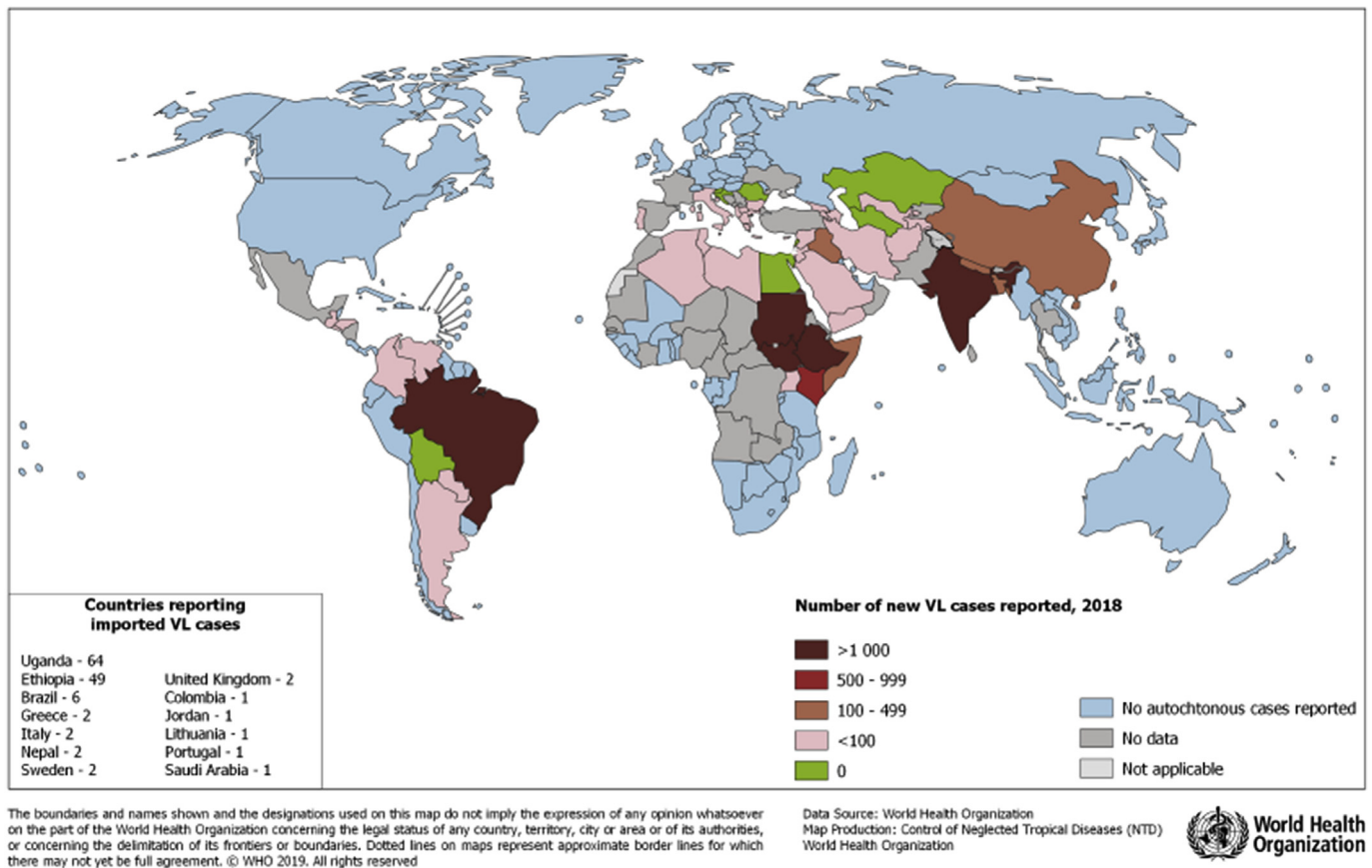


Fig. 2. (continued)

concentrate in one place, allowing for maximum likelihood of transmission. (Tinsely and Jackson, 1988). Like most desert fauna, the relationship between *S. couchii* and *P.americanus* represents an extreme; however, little investigation into the triggers between parasite life cycle and host phenology exist beyond it. Examining additional host-parasite relationships within drylands and other extreme environments could help elucidate both proximate and ultimate drivers of this aspect of parasite lifecycle evolution.

Another strategy to guard against harsh environmental conditions and low host density is to include a motile vector into the lifecycle. Thus, the use of invertebrates as intermediate hosts and vectors provides not only a stable environment in which immature parasite stages can develop but also increase the likelihood of encountering a suitable definitive host. For instance, high food web connectivity and complex arthropod faunas within deserts (Polis, 1991) make incorporating trophic transmission via invertebrate intermediates evolutionarily advantageous to parasites in arid regions. Parker et al. (2003) detail two alternatives for the insertion of a new host into a parasite lifecycle. Upward incorporation involves adding a new definitive host that is usually a predator of the original definitive host while the original host typically becomes an intermediate host allowing for the parasite to avoid mortality due this predation (Parker et al., 2003). Alternatively, a new intermediate host is added at a lower trophic level during downward incorporation. Adding this intermediate host decreases the mortality of infective propagules in the environment and increases the likelihood of transmission to the original definitive host (Parker et al., 2003).

Although the conditions in which these alternatives might evolve are dissimilar, the final products of the two – a parasite lifecycle utilizing both an intermediate and definitive host – are typically indistinguishable. However, given the high potential mortality of infective propagules in an extreme environment and the effects of low host

density on parasite transmission, deserts could provide empirical evidence to test the conditions of downward incorporation into parasite lifecycle evolution. Likewise, given high food web connectivity within deserts (Polis, 1991), they can also be an ideal environment in which to investigate upward incorporation. Consider, for example, the life cycle of nematodes belonging to superfamily Physalopteroidea that parasitize various lizard species in Australia's Great Victoria Desert. Jones (1995) found that many small lizard species that feed exclusively on termites, like geckos *Diplodactylus conspicillatus*, were also host to encysted juvenile physalopteroideans; however, the corresponding adults parasitize larger lizards, such as those belonging to genus *Varanus*. This led Jones (1995) to posit that the smaller lizards became paratenic hosts for these nematodes as they became prey for larger lizards, evidence for upward incorporation. Whether small lizards were added to the lifecycle via upward incorporation or the termites were added via downward incorporation remains less clear. However, since small lizards that do not exclusively feed on termites can also host these encysted juveniles (Jones, 1995), upward incorporation seems a logical scenario in this case.

### 3. Infection, deserts, and climate change

#### 3.1. A history of anthropogenic effects

Traditionally, tropical areas, rather than desert ones, have been seen as critical sources of infectious diseases (e.g. Sattenspiel, 2000; Artsob et al., 2009; Hennessey et al., 2016) and somewhat ironically, the challenges of arid regions may have caused them to play a role as historical barriers to disease spread. Pathogens (*sensu lato* = prokaryotic and eukaryotic parasites) that did not evolve in drylands are less likely to have transmission strategies that overcome low host density and less likely to withstand its extreme environmental conditions. The

**Box 1.**

For a parasite with transmission stages:

$$R_0 = T_1 / (M_1 M_2)$$

Where:

- $R_0$  = Parasite basic reproductive rate
- $T_1$  = Net rate of new infections produced
- $M_1$  = Mortality rate of infected hosts
- $M_2$  = Mortality rate of transmission stages

and

$$H_t = \delta M_1 / ((\lambda - 1) \beta)$$

Where:

- $H_t$  = Threshold host density
- $\delta$  = Parasite life expectancy
- $\lambda$  = Rate at which parasite produces transmission stages
- $\beta$  = Transmission rate

After Anderson (1986) and Dobson (1989)

**Box 1.** Relationships between parasite basic reproductive rate ( $R_0$ ), threshold host density ( $H_t$ ), and host mortality rate of infected hosts ( $M_1$ ). In order to maintain  $R_0$  a parasite with transmission stages must either increase the net rate of new infections produced ( $T_1$ ) and/or decrease the mortality rate of infected hosts ( $M_1$ ) and/or transmission stages ( $M_2$ ). Host threshold density ( $H_t$ ) will be high the mortality rate of infected hosts is high ( $M_1$ ) relative to the rate at which the parasite produces transmission stages ( $\lambda$ ) and the transmission rate itself ( $\beta$ ). After Anderson (1986) and Dobson (1989).

drylands of central Asia, including the Gobi desert, could have represented a natural barrier that restricted overland spread of plague to Europe for centuries (Schmid et al., 2015). Increased trading in the 1300s, particularly along maritime routes, and climatic conditions that favored large-scale wildlife plague outbreaks in Asia likely facilitated the spread of plague to Europe (Schmid et al., 2015). Similarly Rinderpest was unknown in sub-Saharan Africa until the late 1800s. Although outbreaks of the disease occurred in Egypt during the Napoleonic Wars, it did not cross the Sahara, presumably because camels, the main method of overland desert travel, were not susceptible to Rinderpest and the spread of the disease below the Sahara is linked with the import of European cattle to horn of Africa in 1887 (Rowe and Hødnebo, 1994).

Anthropogenic effects can also introduce diseases to wildlife in dryland ecosystems with potentially serious conservation consequences, notably via the transmission of livestock disease to wildlife (Beauvais et al., 2019). For example, Saiga antelope are a species of high conservation concern native the semi-arid deserts of Central Asia with populations in Kazakhstan comprising the majority of total Saiga numbers (Milner-Gulland et al., 2001). Census numbers started indicating a dramatic decline in Saiga populations beginning around 1998, although the exact reasons for this decline were not immediately obvious (Milner-Gulland et al., 2001). Subsequent years saw further loss of Saiga culminating in a mass die-off of populations in Kazakhstan in 2015 (Fereidouni et al., 2019). Further investigation suggested that a combination of anthropogenic factors and changing environmental conditions were at the root of both the longstanding decline in Saiga numbers and the mass mortality event. Key among the anthropogenic influences were transmission of pathogens from domestic livestock to

Saiga such as Aphthoviruses responsible for hoof and mouth disease and gastrointestinal nematodes *Haemonchus* sp., *Nematodirus* sp., and *Marshallagia* sp. (Milner-Gulland et al., 2001; Morgan et al., 2006). Additionally, the mass mortality event in 2015 was caused by the bacterium *Pasteurella multocida*. Although normally latent, this bacterium can become pathogenic in response to environmental triggers, such as hotter than normal temperatures, that are consistent with anthropogenic climate change in these locations (Fereidouni et al., 2019).

Similarly, reintroduction of threatened species to their historic range can be a source of anthropogenically-spread wildlife disease (Mathews et al., 2006). Houbara Bustards released by a captive breeding program in Saudi Arabia were the source of a chlamydia outbreak in wild flocks (Bailey et al., 1996) and releases of desert tortoises, *Gopherus agassizii*, were implicated in an outbreak of mycoplasmosis among wild tortoises in Nevada, USA (Lederle et al., 1997). Thus, health-screening protocols, such as screening of marsupial dippers (*Parantechinus apicalis*) for gastrointestinal helminths and pathogenic bacteria before release in Western Australia, should be a vital component of any wildlife reintroduction or translocation plan (Mathews et al., 2006). These historical examples show that anthropogenic effects stemming from human movement and climate change can serve as critical drivers of disease spread both in and around drylands.

### 3.2. Current and future risks

Climate change has been identified as a critical driver in modulating and redistributing infectious disease burden around the world (e.g. Cable et al., 2017; Carlson et al., 2017; Metcalf et al., 2017). Additionally, global climate change and other anthropogenic activities are predicted to promote desertification in multiple regions (Patz et al., 2012; Xu et al., 2019). Both of these effects could potentially shift the spatial distributions of various parasite zoonoses (Polley and Thompson, 2009) and human populations within drylands could become increasingly at risk for emerging infectious diseases. This includes the emergence of Middle Eastern Respiratory Syndrome (MERS-CoV) in 2012, with bats and camels as intermediate sources of the disease (Zumla et al., 2015) as well as papputaci fever in the Sahara Desert and Oroya fever in the Atacama Desert of Peru, both of which are zoonotic diseases vectored by sandflies (Dobson, 1989).

Desertification is widespread land degradation in dryland regions and occurs on every continent except Antarctica (Adeel et al., 2005). It is a global problem accelerating partly due to disturbance, such as increased drought brought on by climate change, and partly due to stress, such as overuse of resources brought on by rapid increases in human populations (Whitefield and Duval, 2020). For example, a 0.3% decrease in rainfall per decade of the twentieth century driven by climate change between 10° N and 20° N is consistent with increased desertification in those areas (Safriel, 2007). Additionally, populations in dryland areas have been growing. For example, on average, populations in drylands increased by 18.5% during the 1990s (Adeel et al., 2005). Indeed, approximately 10–20% of drylands are already degraded with total area affected by desertification as 6–12 million km<sup>2</sup> and 1–6% of dryland inhabitants live in these areas (Adeel et al., 2005). Food insecurity, less access to clean drinking water, and lower availability to proper sanitation often leads to poor health in these dryland populations (Patz and Kovats, 2002; Adeel et al., 2005). Perhaps even more critically, desertification also decreases biodiversity in dryland systems (Safriel, 2007; Whitfield and Duval, 2020) and biodiversity loss is widely linked to an increase in zoonotic pathogens (e.g. Mills, 2006; Ostfeld, 2009; Keesing et al., 2010). Therefore, a potent cocktail of increasing populations living in degraded landscapes at high risk of resource insecurity, poor health, and potential infection to novel pathogens follows with the spread of desertification.

As there is a relative paucity of information concerning parasite virulence, specificity, and life cycle evolution in arid environments, we also have comparatively little information with which to identify

potential emerging infectious diseases in these areas. These emerging infections are not only of concern to dryland human population but to other regions as well. Human mobility constitutes a critical driver of the spatial extent of disease spread and transmission models that include human movement components more accurately predict incidence of infection (Kraemer et al., 2019). Human mobility because critical in the spread of global MERS-CoV cases between 2013 and 2015 with cases presenting in countries such as South Korea, Malaysia, the Netherlands, and the United States (Zumla et al., 2015). However, human movement is not the only means by which infectious diseases originating in drylands can affect other regions. Dust storms from desertified areas can regularly transmit pathogens to non-desert areas (Griffin and Kellogg, 2004). For example, incidence of Kawasaki disease, a syndrome consisting of fever, vasculitis, and swollen lymph nodes (Burns et al., 1996), increases in areas affected by dust storms. Japan, Hawaii (USA) and San Diego, California (USA) have all exhibited a greater number of cases when tropospheric wind patterns carry dust from drylands in central Asia and areas of central Chile also show increased incidence when tropospheric, northerly wind patterns transport dust from the Atacama Desert (Jorquera et al., 2015). Although the symptoms of Kawasaki disease and the recruitment of immunoglobulin A into tissues of those diagnosed with it indicate an infection (Rowley et al., 2008), the etiological agent at work is unknown (Uehara and Belay, 2012; Jorquera et al., 2015), further underscoring the need for increased knowledge regarding pathogens found in dryland areas. Likewise, *Coccidioides immitis*, a pathogenic soil fungus causing respiratory distress, regularly re-emerges in the southwestern United States with highest incidence when the substrate is dry in late summer and early fall (Kirkland and Fierer, 1996). In California (USA) outbreaks of coccidioidomycosis frequently follow dust storms and these storms can spread the fungus to areas where it is not endemic, such as the San Francisco Bay area (Kirkland and Fierer, 1996). There is no practical way of eliminating *C. immitis* from soil and as the frequency and severity of dust storms increase with climate change (Griffin and Kellogg, 2004; Xu et al., 2019), the number of individuals at risk of coccidioidomycosis (Kirkland and Fierer, 1996; Tong et al., 2017), along with a host of other dust-borne infections (Griffin, 2007), also increases.

#### 4. Concluding perspectives

Although drylands comprise over 40% of all terrestrial surface area (Patz et al., 2012) and are home to approximately 35.5% of the world's population (Safriel, 2007), both free-living and parasitic fauna in these regions are relatively understudied. However, the very conditions that make these regions challenging to study – extreme environmental conditions and low population density for various host organisms – also make them potentially untapped natural laboratories for examining eco-evolutionary relationships between hosts and parasites. Thus, desert parasite communities can serve as useful exemplars with which to examine subjects such as the evolution of virulence, mechanisms for widening host spectra, and drivers of the development of different lifecycle strategies. Additionally, desertification and climate change make understanding parasite transmission within these habitats increasingly critical as larger, likely highly resource insecure, populations are projected to live in dryland regions (Kuehn, 2006; Safriel, 2007; Patz et al., 2012). Thus, human populations within drylands could become increasingly at risk for emerging infectious diseases even while we still know relatively little about the biology of various parasites and pathogens that inhabit arid regions across the globe. Hopefully highlighting this untapped potential will encourage future empirical tests of hypotheses related to parasite ecology and evolution within dryland ecosystems and stimulate wider investigation into the parasitofauna of arid regions in general.

#### Declaration of competing interest

The author declares no conflict of interest.

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