Climate change, predictive modeling and lemur health: Assessing impacts of changing climate on health and conservation in Madagascar

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ABSTRACT

Deforestation and a changing climate threaten the health and survival of lemurs in Madagascar. An important component of lemur health, parasite infection can reduce fitness and survival outcomes. Future lemur parasite richness, abundance and distribution may be highly influenced by climate change. Current knowledge of lemur parasites is narrow in geographic and temporal scope, with sampling at a limited number of sites, and thus far, there have been no attempts to assess the effects of climate change on lemur parasite distributions. We used geospatial tools to predict the distributions of six lemur parasites of high frequency and pathogenic potential. We then assessed how anticipated climate shifts in Madagascar may alter the distributions of these lemur parasites in the future. Under current climate conditions, we found that the focal parasites exhibited widespread potential distributions across Madagascar, covering 12–26% of surface land area and 40–86% of forested area. Our analyses also showed that parasites responded differently to projected climate changes, with shifts ranging from a contraction of current distributions by 7% to an expansion of 60%. A predicted net expansion in parasite distribution may expose naive lemur hosts to new parasites, which could have a profound effect on lemur health. Those parasites with the greatest potential for harmful effects are predicted to experience the largest expansion in range. Predicting these changing distributions will be critical for assessing population health, improving protected area design, preparing for reintroduction efforts and addressing potential parasite risk in lemurs, humans and domestic animals.

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1. Introduction

Madagascar is considered one of the world's top conservation priorities due to its unparalleled species diversity and endemism. Lemurs are particularly emblematic of Madagascar's biodiversity, where they comprise more than 15% of the world's extant primate species (Mittermeier et al., 2008; Wilme et al., 2006). Lemur survival is currently threatened by intense anthropogenic pressure from growing human populations, shifting land use patterns, increasing deforestation and a changing climate (Allnutt et al., 2008; Dufils, 2003; Elmqvist et al., 2007; Harper et al., 2007; Myers et al., 2000). In combination with such pressures, health is a particularly important component of lemur survival. Lemur health is af-

fected by parasitism and disease, which have been demonstrated to reduce fitness and can ultimately lead to local extinctions (Cleaveland et al., 2002; Hochachka and Dhondt, 2000; Smith et al., 2009). It is therefore essential to explore the pathogenicity of common lemur parasites, as well as the potential current and future distributions of these parasites within lemur populations in a changing environment.

Estimating the projected extinction risk for global biodiversity as a result of climate change is a daunting task, as climate change will affect biodiversity in a number of different ways (Bellard et al., 2012; Şekercioğlu et al., 2012; Thomas et al., 2004). Globally, the effect of climate change on disease has attracted much study and discussion. One view holds that a warmer and wetter world will be a sicker world due to more frequent and severe host-parasite interactions (Costello et al., 2009; Harvell et al., 2002; Patz et al., 2005), but recent perspectives offer more cautious expectations (Lafferty, 2009a,b; Randolph, 2009). Even so, empirical studies are rapidly emerging to demonstrate the significant impact of changing environmental conditions on the epidemiological dynamics of host-parasite associations (Duncan et al., 2011;

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Garamszegi, 2011; Laaksonen et al., 2010; Larsen et al., 2011; Sehgal et al., 2011). Climate change will likely alter spatial patterns of parasitism and disease, as parasite distributions are directly influenced by environmental conditions such as temperature and precipitation (Brooker et al., 2006; Guernier et al., 2004).

Current evidence suggests that temperature and rainfall patterns have already shifted in Madagascar, and are expected to continue their deviation from historic averages (Tadross et al., 2008). Climate projections estimate that temperature and precipitation will increase throughout the island, except in the dry southern region, which will become more arid (Hannah et al., 2008; Tadross et al., 2008). While the effects of projected climatic shifts in Madagascar on the health of lemurs have yet to be examined, studies have already demonstrated an impact on lemur distribution and reproductive success (Dunham et al., 2011; Raxworthy et al., 2008).

1.1. Addressing transmission risk to novel hosts

Beyond lemurs, disease transmission could occur among wildlife, humans and domestic animals in Madagascar. A number of parasites related to significant lemur parasites can infect other hosts, including humans, domestic animals, rodents and other non-human primates, yet to date no record of direct cross-species transmission has been documented (Foitová et al., 2010; Hope et al., 2004; Howells et al., 2011; Kightlinger et al., 1995; Murata et al., 2002; Sleeman et al., 2000). Madagascar's high wildlife diversity may contribute to disease transmission risk. As determined in a global assessment of emerging disease events since 1940, high wildlife host species richness was a significant predictor for the emergence of zoonotic infectious diseases (Jones et al., 2008). In another study of global pathogens, regions of high bird and mammal species host richness also exhibited high human pathogen richness (Dunn et al., 2010). The rapidly shifting land use regimes in Madagascar, which force humans, wildlife and domestic animal species into new patterns of interaction, may elevate this risk. In previous studies, land-use change in the tropics has been demonstrated to influence parasite abundance and richness in amphibian populations (McKenzie, 2007). Although inter-species interaction is an important risk factor in disease transmission, a number of other factors, such as host susceptibility, infection probability, prevalence, adaptability of the pathogen to new hosts and virulence are also important but do not fall within the scope of this study (Lloyd-Smith et al., 2009; Wolfe et al., 2007). Here we focus on how environmental changes, such as climate change, may have an effect on lemur parasite distribution and transmissibility.

1.2. Significance of parasites within lemurs and other hosts

The majority of primate pathogens exert long-term, sub-lethal effects that are often subtle and therefore difficult to detect (Goldberg et al., 2008). However, recent studies have demonstrated the deleterious effects of parasite infection on fitness in a variety of vertebrate hosts (Gooderham and Schulte-Hostedde, 2011; Ohlberger et al., 2011; Robar et al., 2010; Smith et al., 2009). These effects can be exacerbated by habitat loss and other environmental perturbations (Smith et al., 2009), and heavy parasite loads can also increase host susceptibility to other disease (Beldomenico and Begon, 2010). Disease in lemur populations has been relatively understudied compared with other primate hosts, which calls for enhanced study. Here we explore the significance of six helminths and ectoparasites documented within lemurs. These include four helminths (*Hymenolepis* spp., *Lemurostrongylus* spp., *Lemuricola* spp., *Trichuris* spp.) and two types of ectoparasites (*Haemaphysalis lemuris* and Laelapidae mites) (Table 1). We selected these parasites due to their frequent occurrence in lemur populations and

their potential for chronic pathogenic effect. Where specific knowledge of parasite pathogenicity in lemurs is understudied, we extrapolate information from related parasite species of the same taxonomic family or order.

1.3. Lemur ectoparasites

Ectoparasites are ubiquitous and extremely difficult to eradicate (Wall, 2007). While not commonly highly pathogenic, ectoparasites can decrease fitness, cause damage to the skin and stimulate immune responses (Bischoff et al., 2009; Gooderham and Schulte-Hostedde, 2011; Wall, 2007). Importantly, they may also act as vectors for protozoa, bacteria, viruses, cestodes and nematodes, including *Bartonella*, plague (*Yersinia pestis*), murine typhus (*Rickettsia typhi*) and *Ehrlichia* spp. in Madagascar (Duplantier and Duchemin, 2003; Junge and Sauther, 2007; Wall, 2007; Williams et al., 2002).

A number of different mites have been documented in lemurs, including: family Listrophoridae (*Listrophoroides* sp.), family Bdellidae, family Laelapidae (*Liponyssella madagascariensis*, also known as *Liponyssus madagascariensis*), and family Psoroptidae (*Lemuralges* spp., *Makialges* spp. and *Gaudalges* spp.) (Bochkov et al., 2011). Documented cases of infection with *Sarcoptes scabiei*, or the human itch mite, have occurred in Old World monkeys and apes (Kaur and Singh, 2009), and can cause anorexia, weakness, weight loss, severe pruritus and even death (Kalema-Zikusoka et al., 2002; Kaur and Singh, 2009). In addition to scabies, mites can also serve as vectors for other infectious diseases such as *Bartonella* and *Ehrlichia* (Junge and Sauther, 2007). They are also to persist for prolonged periods of time in soils and decaying debris, elevating the risk of transmission from environmental reservoirs (Denegri et al., 1998).

Ticks (*H. lemuris* and *Ixodes* spp.) have been documented on lemurs, tenrecs, rodents and carnivores in Madagascar, yet knowledge of associated disease is limited (Durden et al., 2010; Hoogstraal, 1953; Hoogstraal and Camicas, 1977; Uilenberg et al., 1979). Documented tick-borne diseases in humans in Madagascar include: borreliosis, Crimean-Congo hemorrhagic fever, Q fever and bartonellosis (GIDEON, 2011). In other regions, ticks are a significant vector of diseases such as babesiosis and anaplasmosis in cattle, Lyme disease, and other viruses, bacteria and filaroid nematodes (Barré and Uilenberg, 2010; Junge and Sauther, 2007; Kaur and Singh, 2009; Williams et al., 2002).

1.4. Lemur helminths

Chronic infections with helminths can be detrimental to host fitness over the long term (Gillespie, 2006; Gillespie et al., 2010; Howells et al., 2011). Although less dramatic than acute disease documented in primates, such as caused by Ebola, anthrax or SIV, various helminths can produce diarrhea in lemurs with impacts on health and survival (Rasambainarivo and Junge, 2010). These parasites can vary according to environmental conditions and among social groups, and are frequently underestimated in lemur populations (Clough, 2010; Rasambainarivo and Junge, 2010).

Pinworms are one of the most common helminthic infections in humans worldwide, and have been declared a significant neglected disease by the World Health Organization. Pinworms within lemur populations include eight different *Lemuricola* species (Irwin and Raharison, 2009). *Lemuricola* spp. have been documented from all lemur families, demonstrating their versatility, and have been the most abundant endoparasite in some lemur health studies (Wright et al., 2009). The pathogenicity of *Lemuricola* spp. in lemurs is difficult to assess due to their specificity to lemur hosts and their lack of long-term study. However, extrapolating information from related parasite species, we predict that infections may be able to cause perianal itching, dehydration, weight loss and

Table 1

The six focal lemur parasites sampled within this analysis, including each type, transmission strategy, pathogenic potential, sample size and documented occurrence in other hosts.

Type	Parasite	Transmission	Commensal or pathogenic?	Pathogenicity	Environmental influence	Domestic animals or rodents?	Human record?	Original Sample size (presence only)	Training Points used in model (presence only)	Additional references
Ectoparasites	Laelapidae mites	Though social contact	Pathogenic perhaps with coinfection or immunocompromised status	Potential vectors for *Bartonella* spp. and *Ehrlichia* spp., and cause dermatitis conditions	Free-living stage in soils, and temperature directly affects development	Yes	Yes	91	14	Loudon et al. (2006); Loudon (2009); Wright et al. (2009); Schwitzer et al. (2010)
	H. lemuris	Through social contact or indirect via environment	Can be a vector for pathogenic organisms	Potential vector for viruses, bacteria, apicomplexans and filaroid nematodes	Survival and development influenced by soil moisture and temperature	Yes	Yes	83	16	Loudon et al. (2006); Loudon (2009); Wright et al. (2009); Durden et al. (2010)
Helminths	*Hymenolepis* spp.	Ingestion of fecal matter or an insect	Pathogenic	Cramps, diarrhea, irritability, anorexia, or enteritis, nausea	Faster replication in warm temperatures, can only persist in environment for about 10 days	Yes	Yes	25	10	Raharivololona and Ganzhorn (2009, 2010)
	Lemurostrongylus spp.	Ingestion of fecal matter	Unknown	Unknown	Larvae development in the soil during free-living stage	Unknown	None found	50	11	Chabaud et al. (1961a); Faulkner et al. (2004); Loudon et al. (2006); Loudon (2009)
	Lemuricola spp.	Ingestion of fecal matter or an insect	Potentially pathogenic, needs further study	Generally nonpathogenic, but the human pinworm (*Enterobius vermicularis*) has caused death in a chimpanzee	Elevated replication in warmer temperatures	Unknown	None found	41	17	Chabaud and Petter (1958, 1959); Chabaud et al. (1961b, 1965); Petter et al. (1972); Loudon et al. (2006); Loudon (2009); Wright et al. (2009); Clough (2010); Raharivololona and Ganzhorn (2010); Schwitzer et al. (2010)
	Trichuris spp.	Larvated eggs ingested from feces	Pathogenic in captive lemurs and in humans	Can cause disease and even death in immunocompromised hosts with heavy infections	Eggs embryonate in the environment	Yes	Yes	19	7	Chabaud et al. (1964, 1965); Schad et al. (2005); Loudon (2009); Raharivololona and Ganzhorn (2009, 2010); Clough (2010)
						Total		309	75	

aggressive behavior. An infection with a human pinworm, *Enterobius vermicularis*, has led to death in a captive chimpanzee (Clough, 2010; Fowler, 1993; Kaur and Singh, 2009; Murata et al., 2002). This has not yet been documented in a wild primate.

Similarly, *Trichuris* spp. can be pathogenic in humans, potentially leading to dehydration, weight loss and itching (Clough, 2010; Kaur and Singh, 2009). *Trichuris* spp. have been recorded in many different mammalian hosts, including canids, felids, primates (human and non-human), rodents and ungulates. Despite theories that *Trichuris* spp. generally remain host-specific, novel infections have occurred, including cases in which humans have acquired canine *T. vulpis* (Dunn et al., 2002). Both dogs and cattle have been documented with *Trichuris* spp. infections in Madagascar (Loudon, 2009), and lemurs have been observed consuming cattle and dog feces, thus calling for further study of novel infections within lemurs (Loudon, 2009). Such infections are not only detrimental to lemur health, but they can also be transmitted to humans. For example, *T. trichiura* have been documented as harmful to children in Madagascar (Kightlinger et al., 1995). Additionally, a cestode documented in lemurs, *Hymenolepis* spp., can cause nausea, abdominal pain and diarrhea in human hosts (GIDEON, 2011). *Hymenolepis* spp. have also been shown to infect rats, such as *Rattus rattus*, which raises the issue of disease transmission among lemur, rodent and human hosts (Loudon, 2009; Patamia et al., 2010; Schantz, 1996).

While lemur health monitoring provides essential data on parasites in lemurs, these data can be limited in their geographic and temporal scope. With climate change and rapidly shifting land use in Madagascar, it is important to predict the potential effects of these shifts on health using geospatial tools such as Geographic Information Systems (GIS) (Bergquist and Rinaldi, 2010). Methods that deploy GIS can explore a wide range of multifactorial interactions, and may therefore be applied to assess the complex and overlapping biological processes at work in pathogen transmission (Randolph, 2009). Here we used species distribution modeling techniques to predict present-day distributions of six lemur parasites throughout Madagascar. We then assessed how these six parasites may expand or contract their distributions in the future in response to projected climate shifts. The results of this study can help to inform conservation strategies, wildlife management, and further define the risk of zoonotic disease transmission from lemurs to humans.

2. Material and methods

2.1. Parasite sampling and study area

All parasite sampling occurred within the island of Madagascar, the only place on earth where lemurs occur naturally. The following parasite species from lemur hosts were included due to available data and relevance: *Hymenolepis* spp., *Lemurostrongylus* spp., *Lemuricola* spp., *Trichuris* spp. *H. lemuris* and Laelapidae family mites (Table 1). All but two samples of mites had been identified as *L. madagascariensis*, a species within the Laelapidae family. The other two samples were identified just to the Laelapidae family level, therefore we refer to them at this family level.

Parasite samples originated from several different sources. The majority of the data came from the ongoing Prosimian Biomedical Survey Project (PBSP), a project that has assessed over 631 individuals of 32 lemur species at 20 sites since 2000 (Dutton et al., 2003, 2008; Irwin et al., 2010a; Junge et al., 2011, 2008; Junge and Garell, 1995; Junge and Louis, 2002, 2005a,b, 2007; Junge and Sauther, 2007). This project is structured to provide collaboration between field biologists and veterinarians involved in conservation projects throughout Madagascar. Veterinarians provide basic medical assistance as needed, and collect standard biomedical samples and health information from animals anesthetized or captured for other purposes. A detailed description of sample collection methodology can be found in the previously cited references.

In order to expand the sample size, we also included published accounts of lemur parasites from a number of other studies in addition to the PBSP sites (Tables A1 and A2). We acknowledge that studies may vary in parasite collection and identification methods. The Global Infectious Disease and Epidemiology Network and The Global Mammal Parasite Database were helpful tools in locating these additional studies (GIDEON, 2011; Nunn and Altizer, 2005). Sites sampled were georeferenced using location information in published reports, available maps and Google Earth. The original dataset for the six parasites, consisting of 309 presence points, was reduced to contain only non-repetitive points, yielding a total of 75 locality points for analysis. Collectively, between the PBSP data and the published literature, sites sampled for these analyses occurred in all ecoregions in Madagascar except for ericoid thickets, from a diverse range of protected and non-protected areas, and from 33 different lemur species (Fig. 1) (Olson et al., 2001).

It is important to sample widely within Madagascar due to its extensive habitat diversity. Encompassing a wide range of climates, ecoregions and topography, the island is composed of lush rainforest along the eastern escarpment, dry deciduous forest in the west, and dry spiny forest in the south. The steep eastern escarpment traps much of the easterly Indian Ocean trade winds, resulting in a western rain shadow, which contributes to the dry western forest ecoregion. Mean annual rainfall ranges from 331 to 3373 mm and mean annual temperatures range from 11.0 to 27.4 °C (Hijmans et al., 2005). The highland region, once a mosaic of forests and savannah, is now almost completely modified by people with rice cultivation in the valleys and dry farming on the hillside slopes. This region experiences a cold and dry season from May to October and a warm, rainy season from November to April (Duplantier and Rakotondravony, 1999). The west coast, typified by dry, deciduous forest is a mixture of forest, pasture and cultivation. The south is much more arid, is dominated by spiny thickets, and experiences a 10 month dry season.

2.2. Estimation of current and future distributions using species distribution models

We utilized species distribution models (SDMs) to predict both the current and future geographic distributions of six focal parasites. These models estimate the associations between known species occurrences (e.g. parasites) and suites of environmental variables, such as climate, soils, topography, vegetation and anthropogenic measures. Using these associations, a model is developed to predict distributions based upon environmental suitability, which can be expanded to new geographical areas or future climate conditions.

Maximum entropy distribution modeling (Maxent version 3.3.3e; Philips et al., 2006) was used to generate SDMs using the following parameters: random test percentage = 25%, regularization multiplier = 1, maximum iterations = 1000, convergence threshold = 0.0001, maximum number of backgrounds points = 10,000. This means that 25% of the original data was set aside for model testing and independent validation against the 10,000 random background points (pseudo-absences) in order to assess commission. The SDMs for current conditions incorporated 23 ecogeographic variables at 30 arc-second resolution (Table A1). Climate data consisted of a suite of 19 different bioclimatic variables generated by WorldClim from global weather stations at a 30 arc-second resolution (Table A1) (Hijmans et al., 2005). These data represent one of the most complete global weather datasets available.
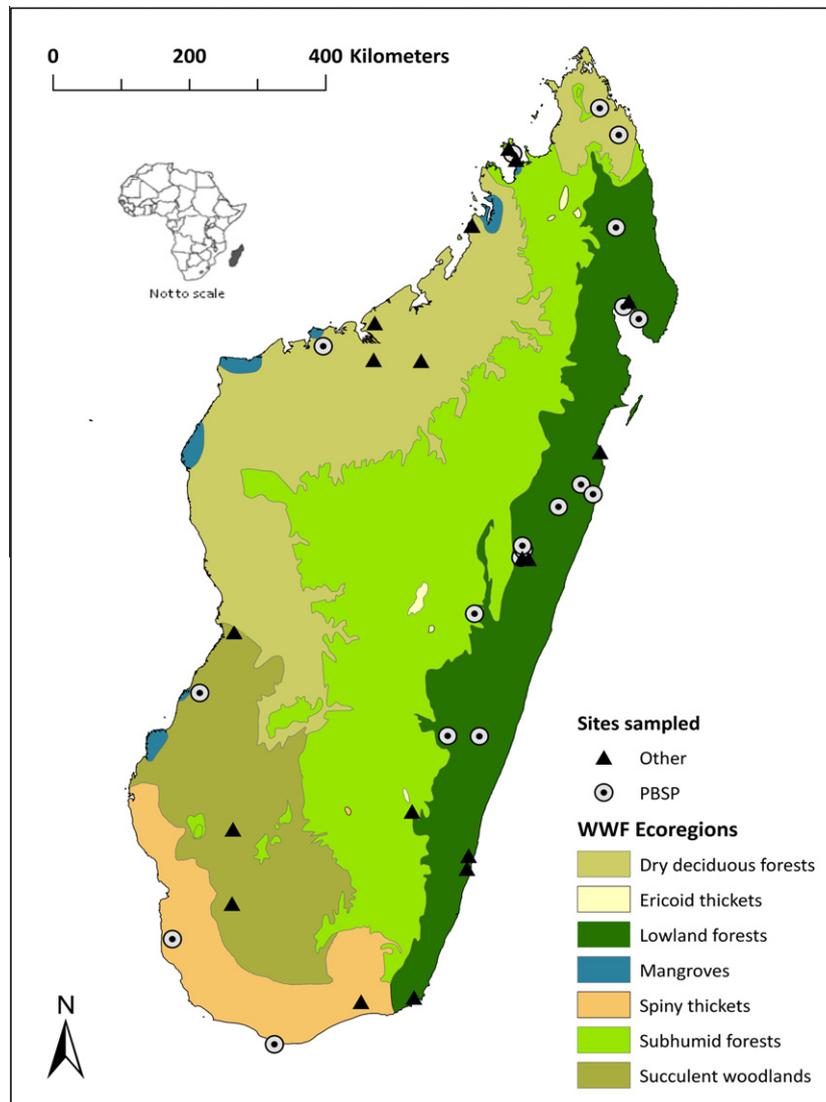
Fig. 1. Sites sampled within this study (including those from the Prosimian Biomedical Survey Project, PBSP, and published reports) originate from all ecoregions in Madagascar except for mangroves and ericoid thickets.

Weather data for Madagascar were developed from weather station recordings from 1930 to 1990 from 117 weather stations throughout the island (Pearson et al., 2007). Other environmental data included geology, solar radiation, slope, aspect, and current and proposed protected areas within Madagascar (Table A1).

SDMs predict the distribution of a species, creating a map that indicates areas of high and low habitat suitability based on an approximation of a species' ecological tolerance. To transform these models into a reflection of suitable or non-suitable habitat, we applied a decision threshold above which values are considered to be a prediction of species presence (Pearson et al., 2007). We used the "Fixed Cumulative Value 5" threshold in Maxent 3.3.3e. The 'current' SDMs were then projected into a future climate scenario using data generated by the International Center for Tropical Agriculture, a global agricultural research institution (http://www.ciat.cgiar.org). We selected the more intermediate B2 scenario, which assumes continuously increasing global population, intermediate levels of economic development, and less rapid, yet diverse, technological change (IPCC, 2007). The data were re-processed using a spline interpolation algorithm of the anomalies and the current climate distribution available from WorldClim (Hijmans et al., 2008, 2005). The data included the same 19 biocli-

matic variables predicted for year 2080 at 30 arc-second resolutions. The following variables from the current SDMs were also used in the 2080 version: geology, slope, aspect and solar radiation. These variables are based entirely on a digital elevation model or geology; therefore, we assume that they will not vary considerably over the next century. To make these distributions maximally realistic, both current and future models were then clipped by the extent of existing forested area and protected areas as of 2011 (IUCN/UNEP, 2009; MEFT and CI, 2009). We worked under the assumption that lemur populations will still exist in 2080, but will be restricted to forested and protected areas.

Models were assessed using the area under the receiver operating characteristic curve (Fielding and Bell, 1997; Phillips and Dudik, 2008), which allows for testing agreement between the observed and simulated distributions (Pearson et al., 2006). Current SDMs were also validated to assess predictive performance using a jackknifing procedure that evaluates model performance of small sample sizes based on its ability to predict an observed presence. This method employs a "leave-one-out" procedure in which each observed locality is removed once from the dataset and a model is built using $n - 1$ training localities. This method is fully described in detail in Pearson et al. (2007).
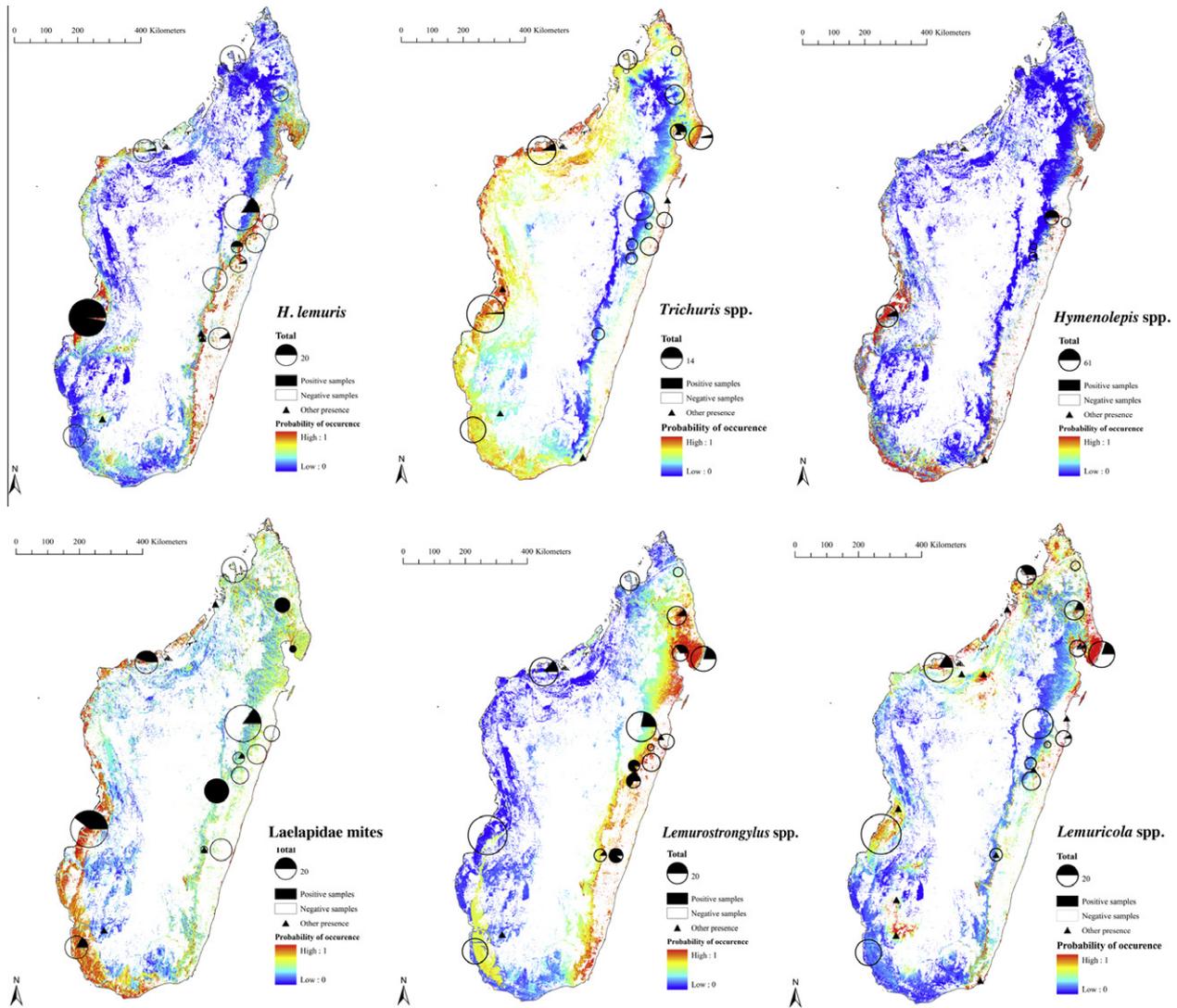
Fig. 2. Predicted parasite distribution models for parasites documented in lemur hosts, including: ectoparasites, *H. lemuris* (tick) and Laelapidae mites (L), and helminths; *Trichuris* spp., *Hymenolepis* spp., *Lemurostrongylus* spp. and *Lemuricola* spp. Warmer colors indicate a higher probability of occurrence. Bubbles indicate prevalence of parasites measured at specific sites, with black representing positive samples and clear the negative samples. The size of the circle represents the sample size at that site. Parasite distributions have been restricted to areas that maintain forest cover, where lemurs could potentially survive, therefore white areas represent non-forested regions.

We estimated the area of occupancy of current and future models for each parasite species. This was done by calculating the number of presence cells in each binary model and then transforming by the spatial resolution of the data. We additionally estimated the range expansion and contraction of each parasite species into projected future climatic conditions, by subtracting a reclassified 'current' model from the future model. We display these results as an expansion, contraction, a maintained presence or a maintained absence. We then calculated the change in distribution in kilometers and percent change of both total land area (591, 930Km²) and total forested area (176, 156Km²) in Madagascar. To make predicted parasite distribution data practical from a

Table 2
Predicted distribution of each modeled lemur parasite in square kilometers and as a percentage of Madagascar's total land surface area and total forested area.

Type	Parasite	Predicted distribution (km²)	Predicted coverage in Madagascar (%)	Predicted coverage in forested area (%)
Ectoparasites	Laelapidae mites	151,011	26	86
	H. lemuris	109,596	19	62
Helminths	*Hymenolepis* spp.	69,791	12	40
	Lemurostrongylus spp.	128,511	22	73
	Lemuricola spp.	144,022	24	82
	Trichuris spp.	132,277	22	75
Mean coverage	–	122,535	21	70
Maximum coverage	–	151,011	26	86
Minimum coverage	–	69,791	12	40
Helminth mean	–	118,650	20	67
Ectoparasite mean	–	130,304	22	74

management perspective, we intersected the parasite presence data with current and proposed protected areas throughout Madagascar, therefore providing a tool for examining baseline parasite communities and assessing fluctuations within them.

3. Results

3.1. Predicted lemur parasite species distributions

We present predicted distribution maps for the six focal parasite species (Fig. 2). These predictions ranged on a probability scale of 0–1, with a value of 1 (warmer colors) indicating an extremely likely chance of presence based upon the suite of environmental conditions. We overlaid on these maps the calculated prevalence of each parasite at sampled sites within the PBSP dataset. We also present the predicted distribution size for each parasite as both square kilometers and as a percentage of the land surface of Madagascar (Table 2).

On average, ectoparasites exhibited broader predicted ranges (22% of total area and 74% of forested area) than did helminths (20% of total area and 67% of forested area). All parasites, except for *Hymenolepis* spp., exhibited ranges that extended to more than 50% of forested area in Madagascar. Each parasite exhibited unique distribution patterns and geographic extents. Laelapidae mites were estimated to be the most widespread of the parasites, covering 26% of total area in Madagascar and 86% of forested area. They were most likely to occur in the western and southwestern coastal areas, with some likelihood along the east coast as well. *Lemuricola* spp. were estimated to occur in 24% of land area and 82% of forested area, with hotspots projected to include the southwest and northern regions, though with limited distribution along the east coast. *Trichuris* spp. also showed potential for wide distribution, with 22% of land area and 75% of forested area potentially covered. *Trichuris* spp. appeared throughout the northeast, west and south in lower elevations. While *Lemurostrongylus* spp. exhibited a similarly expansive potential distribution (22% of total land and 73% of forested area), they were far more concentrated in the eastern regions of Madagascar with only a small range in the southwest. *H. lemuris* showed smaller potential distributions, preferring the eastern and western coasts with some patchy distributions in the south. *Hymenolepis* spp. exhibited the most restricted distributions, with a potential coverage of just 12% of total area and 40% of forested area in Madagascar. Its distribution was quite distinctive, with isolated concentrations in the northeast, south and southwest. To make these data maximally relevant to wildlife health managers, we estimated which lemur parasites may occur at protected areas throughout Madagascar (Supplemental Table A3).

3.2. Predicted distribution shifts with climate change

Using projected climate data for the year 2080, we reassessed the current parasite distribution to reflect a changing climate. We observed patterns of both predicted expansion and contraction of all six parasite distributions (Fig. 3). To examine these changes numerically, we also present the expansion and contraction data in terms of square kilometers and percent land area cover in Madagascar (Table 3). The helminths were predicted to expand their ranges by 22% on average, and ectoparasites were predicted to expand their ranges by 11% on average. If these predictions hold true, then helminths and ectoparasites could exist within 79% and 81% of forested areas in Madagascar, respectively, by the year 2080.

On a species level, our predictions estimated *Hymenolepis* spp. to undergo the greatest change, with a 60% increase in potential distribution and no contraction (Fig. 3). Much of this expansion was predicted to occur in the northeast and west. *Trichuris* spp.

were predicted to expand their potential distribution by 19%, primarily along their eastern distribution with no range contraction. Similarly, *Lemuricola* spp. were predicted to expand their potential distribution by 16% by undergoing a large expansion with only limited range contraction. This expansion was predicted to occur primarily in the west and southwest. Conversely, *Lemurostrongylus* spp. contracted their potential range by 7% with climate change, experiencing no expansion and 9569 square kilometers of contraction. *Lemurostrongylus* spp. were predicted to maintain a distinctly eastern coastal range, with some slight contraction in the south. Their small western distribution was predicted to remain intact for the most part. *H. lemuris* was predicted to experience a net expansion of 23% with climate change. This expansion was expected to take place primarily in the west and southwest, with some range contraction in the east. Laelapidae mites were not predicted to exhibit dramatic areas of contraction or expansion, showing a distribution contraction of only 1%.

4. Discussion

Climate change will alter the spatial patterns of parasites worldwide (Costello et al., 2009; Patz et al., 2005). In Madagascar, clear evidence exists that temperatures have already increased and that rainfall patterns have changed (Tadross et al., 2008). Future climate change projections for Madagascar estimate that mean temperature will increase by 1.1–2.6 °C throughout the island, with the greatest warming in the south, already the driest region of Madagascar. The coastal and northern regions are expected to experience warming as well, where smaller forest fragments may be vulnerable to increased aridity. However, these effects may be mediated by rainfall and cloud cover (Hannah et al., 2008; Tadross et al., 2008). Rainfall patterns also exhibit variability, with increased levels in the summer (January–April) but reduced levels in the winter (July–September). By 2050, the whole country is expected to be wetter, with the exception of the south and southeastern coast, which will be drier. Due to Madagascar's location in the Indian Ocean, tropical cyclones frequently hit during the peak season from November to May, which wreaks severe damage on the undeveloped infrastructure and causes flooding (Tadross et al., 2008). Projections indicate a reduction in the frequency of cyclones during the early part of the peak season; however, their intensity is expected to increase toward the end of the century.

Climate shifts currently occurring in Madagascar, including precipitation and temperature changes, droughts and cyclones, have already begun to negatively impact lemur populations and their reproductive success (Dunham et al., 2011; Gould et al., 1999; Hannah et al., 2008; Raxworthy et al., 2008). As a response to such change, lemur populations will likely need to adapt and seek out suitable habitat, which may result in novel ecological interactions and challenges, a pattern that has already been observed in other regions within bird populations (Şekercioğlu et al., 2012).

Recognizing the climate shifts predicted for Madagascar, we explored how these predicted changes might affect lemur parasite distribution in the year 2080. Geospatial analysis and modeling offer essential tools in approaching these issues (Weaver et al., 2010), having been used with success for diseases such as malaria (Pascual et al., 2008), schistosomiasis (Zhou et al., 2008), fascioliasis (Fox et al., 2011), nematodiasis in ungulates (van Dijk et al., 2010), and for soil-transmitted helminths in tropical Africa (Brooker et al., 2002, 2006; Brooker and Michael, 2000).

Our analyses demonstrated that although climate change may not uniformly lead to massive range expansion of lemur parasites in Madagascar, changes in distribution – both contraction and expansion – seem to be an inevitable consequence of a changing climate. Those parasites with the most potential for deleterious ef-
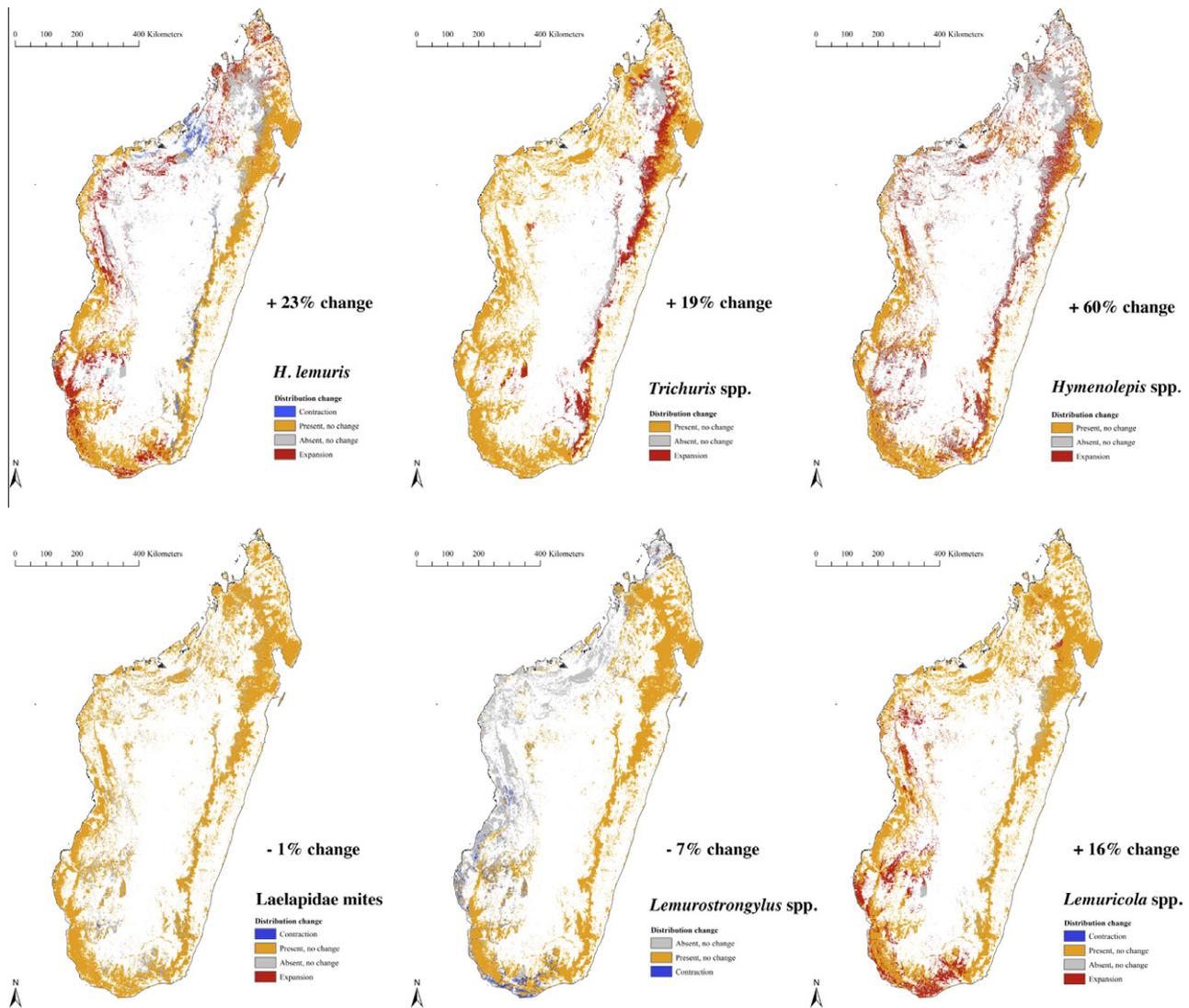
Fig. 3. Predicted expansion and contraction of *H. lemuris*, *Trichuris* spp., *Hymenolepis* spp., Laelapidae mites, *Lemurostrongylus* spp. and *Lemuricola* spp. distributions under projected changes in climate. The total percentage change from area of current distributions to the future distribution area, accounting for both expansion and contraction, is also presented.

fects, including *Hymenolepis* spp., *Trichuris* spp. and *H. lemuris*, may experience the most expansion in range. In our models, the helminths, which can cause dehydration and weight loss, exhibited an average range expansion of 22% with climate change. In particular, *Hymenolepis* spp., which have led to nausea, abdominal pain and diarrhea in human hosts, were expected to expand their range by 60%. Helminths are predicted to expand upward along the elevational gradient, which may be possible due to increasing temperatures and precipitation through much of the country.

Ectoparasites in this study are predicted to expand in their ranges by 11% on average. In previous studies, fleas and ticks tended to be sensitive to subtle changes in temperature, precipitation and humidity (Haines and Patz, 2004). Other studies of ticks demonstrated an expansion northward and upward into higher elevations, an extension of their host-seeking activity periods, an increase in their abundance and an enhancement of their developmental rate (Diuk Wasser et al., 2010; Gray et al., 2009; Kardol et al., 2010; Moller, 2010; Ogden et al., 2005, 2004, 2006). Ectoparasites are of primary concern for their potential to decrease fitness, damage the skin and act as vectors for infectious disease. For example, milder winters and an earlier spring enhanced development and extended activity levels in ticks in Sweden, leading to

a direct increase in the incidence of tick-borne encephalitis in humans (Lindgren and Gustafson, 2001).

4.1. Environmental influences on parasites

To better understand the mechanisms for how climate change might affect parasite distributions, we explore the ways in which seasonally varying temperature and precipitation can influence parasites, both in lemurs and non-lemur hosts. A study of *Microcebus murinus* found that both gastrointestinal parasite richness and abundance were higher in the warmer, wetter season (Raharivololona and Ganzhorn, 2010). Similarly, ectoparasite richness within a *Propithecus edwardsi* population was higher in the wet season (Wright et al., 2009) and gastrointestinal parasite prevalence was higher within *Eulemur flavifrons* during the warm, wet season (Schwitzer et al., 2010). This pattern also holds true for the prevalence of a strongyle nematode in chimpanzees during the rainy season (Huffman et al., 1997). Another study in Uganda found that wetter habitats predicted the elevated prevalence of *Trichuris* spp. in colobine monkeys (Chapman et al., 2010). Even for parasites with indirect life cycles within insect hosts, parasite reproduction is enhanced when ambient temperatures are elevated (Pascual

Table 3
Shifts in predicted distributions for the six focal parasite species in response to climate change. Current and future distribution ranges in both square kilometers and in percentage of Madagascar's land area and forested area are presented. Expansion and contraction area, total change area and percentage change are presented. Parasites are ranked in order of the largest to the smallest changes.

Type	Parasite	Current (km2)	Current coverage (%)[a]	Current coverage, forested area (%)[b]	Future (km²)	Future coverage (%)	Future coverage, forested area (%)	Expansion (km²)	Contraction (km²)	Change with climate shifts (km²)	Change with climate shifts (%)
Ectoparasites	Laelapidae mites	151,011	26	86	149,823	25	85	325	1513	−1188	−1
	H. lemuris	109,596	19	62	134,512	23	76	31,916	7000	24,916	23
Helminths	*Hymenolepis* spp.	69,791	12	40	111,875	19	64	42,084	0	42,084	60
	Lemurostrongylus spp.	128,511	22	73	118,943	20	68	0	9569	−9569	−7
	Lemuricola spp.	144,022	24	82	167,674	28	95	24,232	579	23,653	16
	Trichuris spp.	132,277	22	75	157,860	27	90	25,583	0	25,583	19
Mean		122,535	21	70	140,114	23.7	80	20,690	3,110	17,580	18
Maximum		151,011	26	86	167,674	28.3	95	42,084	9,569	42,084	60
Minimum		69,791	12	40	111,875	18.9	64	0	0	−9,569	−7
Helminth mean		118,650	20	67	139,088	23	79	22,975	2,537	20,438	22
Ectoparasite mean		130,304	22	74	142,168	24	81	16,120	4,257	11,864	11

[a] Total area = 591,930 km².
[b] Total forested area = 176,156 km².

and Dobson, 2005). That said, this trend does not hold true across all species. For example, some helminths, such as *Enterobius* spp., prefer cooler temperatures and will expire in very warm temperatures (Caldwell, 1982).

When examining studies of parasites within non-lemur hosts, the environment continues to be to an important influence. Warmer temperatures, in particular, should support the faster reproduction and longer transmissibility of parasites with environmental reservoirs and stages; therefore, one would expect higher parasite species richness and infection rates with increasing temperature (Allen et al., 2002; Hoberg et al., 2008; Larsen and Roepstorff, 1999; Rogers and Sommerville, 1963). For some vector borne disease, such as malaria, climate may extend the length of the transmission season (Lafferty, 2009b), and the distribution of human bacteria and helminths exhibited a positive correlation with monthly temperature ranges (Guernier et al., 2004).

Precipitation is also important to consider. Guernier et al. (2004) found that the maximum annual range of precipitation corresponded positively with human parasite richness, indicating that regions with distinct dry and wet seasons may harbor more parasites. Additionally, Froeschke et al. (2010) determined a significant positive correlation between mean annual precipitation and nematode infestation. Many parasites require water or humid conditions to complete their life cycle (Guernier et al., 2004), and will respond to increasing precipitation. Many helminths produce fragile eggs that cannot withstand harsh arid conditions (Roberts and Janovy, 2000), therefore drier climates can interfere with ova development. Seasonal rains can create microhabitats for parasite larva and protozoal parasites and can extend the duration of environmental stages by delaying desiccation (Nunn and Altizer, 2006). However, some parasites are able to enter a state of hypobiosis during harsh climatic periods (Brooker et al., 2006). It is important to understand the unique effects of temperature and precipitation on each parasite of interest, which will vary by life stage and duration. We call for field and laboratory-based studies to further our knowledge of the effect of environmental change on lemur parasites.

4.2. The complex effects of climate change on disease

A comprehensive view of the climate change literature shows that not all parasites will respond similarly to warming temperatures (Hoberg et al., 2008). Numerical changes could include shifts in abundances of parasites, increasing development rates, reduced parasite generation time, extended seasonal periods for parasite growth and transmission, enhanced survival rates and, ultimately, amplification of parasite abundance and prevalence. Functional changes could include: shifting patterns of geographic and altitudinal ranges for both parasites and hosts, alterations in the size of parasite ranges including novel habitats and hosts, changing phenologies and local extinctions. Micro-evolutionary responses may include local adaptation through selection and changes in gene frequencies. Lastly, synergistic responses may lead to increasing interactions among novel hosts and parasites and unpredictable cascading changes within ecosystems (Hoberg et al., 2008). Host switching events will be important and widespread consequences of climate change, and can stimulate several downstream effects in ecosystems (Brooks and Hoberg, 2007; Froeschke et al., 2010; Kutz et al., 2005).

While it is worthwhile to address these potential consequences of climate change, the actual effects are complex and difficult to predict. Lafferty (2009b) and Randolph (2009) present some important and contrasting perspectives on the effects of climate change that should also be considered. For example, it will be important to disentangle seasonal effects of temperature and precipitation with those of host reproduction, host density and other factors on transmission risk. Additionally, even with increasing temperatures, the rate of parasite growth and development should slow eventually due to their high resource demands (Lafferty, 2009b). Lastly, Lafferty (2009b) proposes that pathogen distributions may shift in latitude or elevation but not necessarily expand in total distributional area. In Madagascar, the contrasting shifts in increased precipitation throughout the country, yet further aridification in the south, may temper the expansion of lemur parasite distributions.

4.3. Species distribution modeling: limitations and utility

While these models are built from real data, caution should still be taken as they are primarily designed for predictive purposes. Model predictions should be incorporated and utilized in decision-making with a full understanding of the assumptions and inherent uncertainty. Many papers have discussed the subject of whether presence-only data are sufficient to accurately predict dis-

tributions. Model realism depends upon the quantity and quality of the data, the ecological relevance of the environmental variables included, the scale of the analysis, and the dispersal and biotic interactions of the modeled species (Ward et al., 2008). Presence data tend to be biased towards those areas easier to sample, such as near roads, towns, field sites or waterways (Phillips and Dudik, 2008; Reddy and Dávalos, 2003). Despite its ability to improve model fit, presence-absence data also present their own complications with issues of detectability and false absences (Elith et al., 2011; Pearson et al., 2006). Lastly, other important information, such as biotic interactions, geographic barriers and history also influence the distributions of species, but are not included in the development of these models (Pearson et al., 2007). Other considerations include: habitat patch size and connectivity, abundance of parasites and hosts, and other landscape barriers (Ostfeld et al., 2005). Caution should also be taken in interpreting distributions based upon projected climate data, as there is uncertainly in the future climate scenarios, in the future presence of species, and in how species will react to changing climate, including adaptation and migration (Rodríguez et al., 2007; Thuiller, 2004; Thuiller et al., 2008; Vaughan and Ormerod, 2005). Lastly, the inherent variability in parasite seasonality, life cycles and life stage vulnerability to environmental influences could not be addressed explicitly in these models.

To ground-truth these models and improve their accuracy, parasite-specific information should be investigated at a site level as well. Continued wildlife health monitoring can provide data on the seasonality, environmental vulnerability, virulence, transmissibility and distribution of each parasite to assess inter-species and inter-annual variation (Dudaniec et al., 2007). Such monitoring should take place among a diversity of hosts, including humans, domestic animals, rodents and wildlife populations in order to assess cross-species transmission risk. Within-host variability should also be addressed as innate immune function can fluctuate, as seen in birds (Zylberberg et al., 2012). With improved data, researchers can employ other disease models to understand the transmission patterns of parasite within a population.

Despite limitations, species distribution models have been shown to be a useful and rapid tool for research and applied needs in biogeography, conservation biology and ecology, as described in a number of studies (Elith and Leathwick, 2009; Elith et al., 2011; Kumar and Stohlgren, 2009; Pearson et al., 2006; Rodríguez et al., 2007). SDMs have been utilized to prioritize conservation action, to determine range filling, to assess niche evolution, to identify habitat limiting factors, to predict the geographical ecology of invasive species, and to assess landscape hazards (Ayalew and Yamagishi, 2005; Chang et al., 2007; Dai and Lee, 2003; Ohlmacher and Davis, 2003; Pearson et al., 2007, 2006; Richmond et al., 2010). Several studies have successfully utilized SDMs to assess the distributions and regulating environmental conditions relevant to parasites and diseases. SDMs have been used to assess hosts, parasites and their vectors in a number of environments (Bethony et al., 2006; Brooker et al., 2002, 2006; Brooker and Clements, 2009; Brooker and Michael, 2000; de Silva et al., 2003; Froeschke et al., 2010; Holt et al., 2009; Jewell et al., 2007; Levine et al., 2004, 2007; Neerinckx et al., 2008; Noor et al., 2008; Peterson et al., 2004, 2002; Peterson and Martinez-Meyer, 2007; Peterson and Shaw, 2003; Ron, 2005; Simoonga et al., 2009).

5. Conclusions

Global biodiversity is under serious threat due to anthropogenic disturbance and climate change (Bellard et al., 2012; Hannah et al., 2008; Irwin et al., 2010b; Şekercioğlu et al., 2012; Thomas et al., 2004). Changes in climate have affected spatial and temporal pat-

terns of disease globally, with these alterations identified as the biggest threat to global health for the 21st century (Costello et al., 2009; Patz et al., 2005). In Madagascar, human-mediated deforestation and a changing climate are threatening to eradicate the unparalleled species richness that has evolved in Madagascar over millions of years.

In order to address the viability of lemur populations in Madagascar, conservation planners should address their health, including efforts to estimate current and future spatial patterns of disease. Consistent wildlife health monitoring provides a number of benefits, including the documentation of parasite communities within lemur populations, the establishment of baseline health levels, the improved understanding of ecological and spatial patterns of parasite infection, the enhanced power of disease modeling and prediction, and the improved management of vulnerable lemur populations and their habitats. The PBSP and other lemur health studies have made essential progress in first documenting, and now analyzing, spatial patterns of parasites within lemurs throughout Madagascar.

In this study, we have expanded upon these data to explore spatial patterns of parasitism on broader, ecological scales and under shifting environmental conditions due to climate change. We predicted that lemur parasites could expand in their distribution by as much as 60%, which may result in the exposure of these parasites to new lemur populations and novel hosts, such as domestic animals and humans. Such an expansion could have profound effects on the health of both lemurs and humans. As land-use change in Madagascar increases the frequency of contact between humans and wildlife, the risk of zoonotic disease transmission demands further study.

We recommend collaboration among the Madagascar National Parks agency, active environmental organizations, the Ministry of Health and researchers to target areas of highest disease risk with enhanced human, lemur and domestic animal health monitoring. Improved education of these partners about wildlife parasites would provide useful professional training (Nichols and Gómez, 2011). We also recommend prioritizing conservation efforts within forested areas projected to experience the most dramatic shifts due to climate change. To mitigate climate change and maintain sufficient wildlife habitat, networks of protected areas should incorporate topographic and elevational diversity, as well as maintain high connectivity (Şekercioğlu et al., 2012).

Glossary

Ectoparasite: a parasite that lives on the exterior of its host.
Helminth: a parasitic worm.
Species distribution model: A model that uses a species' observed distribution to predict its potential distribution based upon environmental conditions.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2012.09.003.

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