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Anthropogenic disturbance and the risk of flea-borne disease transmission

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Abstract Anthropogenic disturbance may lead to the spread of vector-borne diseases through effects on pathogens, vectors, and hosts. Identifying the type and extent of vector response to habitat change will enable better and more accurate management strategies for anthropogenic disease spread. We compiled and analyzed data from published empirical studies to test for patterns among flea and small mammal diversity, abundance, several measures of flea infestation, and host specificity in 70 small mammal communities of five biomes and three levels of human disturbance: remote/wild areas, agricultural areas, and urban areas. Ten of 12 mammal and flea characteristics showed a significant effect of disturbance category (six), biome (four), or both (two). Six variables had a significant interaction effect. For mammal-flea communities in forest habitats (39 of the 70 communities), disturbance affected all 12 characteristics. Overall, flea and mammal richness were higher in remote versus urban sites. Most measures of flea infestation, including percent of infested mammals and fleas/mammal and fleas/mammal species increased with increasing disturbance or peaked at intermediate levels of disturbance. In addition, host use increased, and the number of specialist fleas decreased, as human disturbance increased. Of the three most common biomes (forest, grassland/savanna, desert), deserts were most sensitive to disturbance. Finally, sites of intermediate disturbance were most diverse and exhibited characteristics associated with increased disease spread. Anthropogenic disturbance was associated with conditions conducive to increased transmission of flea-borne diseases.

Keywords Global change · Biodiversity · Zoonotic disease · Vector · Emerging disease

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Introduction

Anthropogenic habitat disturbance disrupts ecosystem processes in ways that can affect zoonotic disease dynamics (Daszak et al. 2001; Patz et al. 2000; Wilcox and Gubler 2005 and references therein). Human population growth and coinciding increases in urbanization, agricultural intensification, and encroachment into wild areas are directly linked to the emergence of many zoonotic diseases in human populations (Wilcox and Colwell 2005). Recent increases in the incidence and severity of disease within wildlife species have been attributed to a variety of interacting factors that negatively affect wildlife health and host–pathogen interactions including habitat loss and degradation, animal and pest introductions and increased connectivity between populations (Crowl et al. 2008; Daszak et al. 2001; Deem et al. 2001). Of particular concern for both human and wildlife health, is the collective effect of anthropogenic disturbance on vector-borne diseases (Koontz and Daszak 2005). Vectors have free-living life stages and,

thus, may respond to anthropogenic changes in both environmental and host habitats.

Human activities, such as agricultural or forestry practices that change site microclimate (relative humidity, soil temperature), and anthropogenic changes in seasonal temperature and precipitation regimes directly affect vector survivorship, development and feeding rates (Harvel et al. 2002; Patz et al. 2000; Daszak et al. 2001; Keesing et al. 2006). Anthropogenic disturbances also have the potential to change the availability, density and susceptibility of hosts to pathogens and vectors, and thus indirectly influence the spread and persistence of disease within an ecosystem (Patz et al. 2000; Daszak et al. 2001; Keesing et al. 2006). Human disturbance processes have led to the recent range expansions of many vector-borne pathogens including Lyme disease, malaria, dengue fever, tick-borne encephalitis, yellow fever, West Nile fever and plague (Harvel et al. 2002).

Fleas are ubiquitous parasites of small mammals and are the primary vector for a number of diseases that affect humans including plague (*Yersinia pestis*) and *Rickettsia* spp. such as murine typhus and Rocky Mountain fever (Gage et al. 1995). Human-induced habitat change can affect small mammals (Tikhonova et al. 2006) and flea-borne mammal diseases (Azad et al. 1997) but does not always lead to increased disease incidence (Collinge et al. 2005). The presence and abundance of fleas are directly linked to the likelihood and spread of flea-borne disease like plague and are closely tied to the presence and abundance of their hosts (Lorange 2005; Eisen et al. 2006; Krasnov et al. 2006a). Disease transmission is also more likely when fleas exhibit low host specificity (i.e., parasitize a diversity of host species) (Gage and Kosoy 2005). Thus, the overall effect of disturbance on disease spread is a culmination of individual effects on host–parasite interactions, habitat dependencies of host and flea species, and host specificity of fleas. For instance, anthropogenic disturbance decreases mammal community diversity (Tikhonova et al. 2006), and should lead to decreased flea diversity. However, diversity loss may favor common host species, which tend to harbor more flea species (Egoscue 1976) and lead to an increase in overall flea abundance.

To understand how fleas and flea-borne diseases might be impacted by human disturbance, we analyze flea community dynamics and flea host utilization patterns in relation to disturbance intensity in a large sample of published studies conducted across the globe and in a variety of habitats. We interpreted the resulting correlations in the light of current theory regarding habitat change and vector parasites. Our objectives were to answer the questions: (1) does anthropogenic disturbance affect flea diversity, abundance and host specificity; and (2) what does this mean for long-term persistence of fleas and flea-borne pathogens in a changing world?

Materials and methods

Data compilation

We searched Scisearch, CSA biological abstracts, Scirus, the Defense Pest Management Information Analysis Center Literature Retrieval System (Armed Forces Pest Management Board—LRS http://lrs.afpmb.org/rlgn_app), and Google scholar using the following search terms and combination of these terms: flea(s), rodents, small mammals, vector, habitat/habitat change, parasite, flea/parasite assemblage, abiotic and biotic, anthropogenic disturbance/change, disease, plague, climate, murine typhus, flea-borne, vector borne, rickettsia. We found additional articles in the literature cited sections of these papers.

We retained only those studies that: (1) attempted to collect all fleas from animals captured in surveys that targeted the entire small mammal community, (2) live-trapped animals, (3) actively collected fleas (by brushing, etc.), (4) described the location and habitat of trapping locale, and (5) included numerical data for each flea and host species. Fleas are known to abandon dead hosts and thus studies of kill-trapped mammals are likely to underestimate true flea abundance and diversity (Murray 1957). These criteria yielded a sample of 63 studies reporting small mammal flea surveys for 70 distinct sites across the world (Table 1; Online Resource 1).

Classification schemes

We assigned each field site to one of five vegetation-based biomes and one of three disturbance levels (Table 1). We usually used latitude and longitude to identify the location of each site. If these data were not provided, we used city search engines, Google Earth, travel sites, web pages or scientific articles on other studies that used the same plots. The vegetation classifications used in this analysis were condensed versions of those presented by Olson et al. 2001. The Olson et al. (2001) terrestrial ecoregion and biome data are available in interactive form and as a GIS database from the World Wildlife Fund website (http://www.worldwildlife.org/science) and we used the latter to assign a biome to each site. We used ArcView to open the database and then saved the file as a zipped .kml (Keyhole Markup Language) file, or .kmz file, for use in Google Earth. The Olson et al. (2001) classification scheme identifies the dominant natural vegetation type based on latitude, soil conditions, elevation, and climate regime, but ignores human land use. We condensed the 14 biomes of Olsen's classification system as follows: tropical, temperate, and boreal forests were condensed into forests; temperate grassland/savannas and tropical grassland/savannas were classified into grassland/savannas, deserts, arid shrublands, and arid steppe biomes

Table 1 Continental distribution and biome classification of sites used in comparative analysis of anthropogenic disturbance and flea vector assemblage characteristics

	High impact[1–23]	Intermediate impact[24–45]	Low impact[46–70]
	23	22	25
Continent	–	–	–
Africa[8, 10, 12, 13, 18, 31, 32, 38, 40, 42, 63, 69]	5	5	2
Asia[1, 2, 4, 9, 11, 14, 16, 17, 19, 22, 24, 28, 29, 36, 37, 41, 43–46, 65]	10	9	2
Australia (Oceania)[6]	1	–	–
Europe[26, 33, 50, 62]	–	2	2
North America[3, 5, 7, 15, 20, 21, 47, 48, 52–57, 59–61, 64, 66–68,70]	6	–	16
South America[23, 49, 51, 58]	1	6	3
Biome			
Forest[3–7, 11–12, 15–17, 19, 21–25, 27–30, 33, 36–37, 43–46, 49–50, 52, 54, 58, 60–61, 64, 66]	16	12	11
Grassland/Savanna[13, 31, 32, 34–35, 39–41, 53, 63, 68]	1	7	3
Desert[1–2, 8–10, 18, 47–48, 59, 65, 67, 69, 70]	6	1	7
Chapparal[20, 42, 55, 56]	1	1	2
Tundra[26, 57, 62]	–	1	2

[1] Achuthan and Chandrahas (1971), [2]Bakr et al. (1996), [3]Carrion (1930), [4]Chenchijtikul et al. (1983), [5]Cole and Koepke (1946), [6]Cole and Koepke (1947a), [7]Deguisti and Hartley (1965), [8]Gaadoub et al. (1982), [9]Geevarghese et al. (1998), [10]Khalid et al. (1992), [11]Liat et al. (1980), [12]Linardi et al. (1994), [13]Njunwa (1989), [14]Renapurkar et al. (1971), [15]Rumreich (1945), [16]Saxena (1987), [17]Singchai et al. (2003), [18]Soliman et al. (2001), [19]Stunstov et al. (1997), [20]Trimble and Shephard (1935), [21]Vogel (1935), [22]Walton and Hong (1976), [23]Wilson de Carvalho et al. (2001), [24]Adler et al. (2001), [25]Barros-Battesti et al. (1998), [26]Bengston et al. (1986), [27]Bittencourt and Rocha (2003), [28]Chenchijtikul et al. (1983), [29]Durden and Page (1991), [30]Hastriter et al. (2004), [31] Eads and Campos (1983), [32]Heisch et al. (1953), [33]Jurik (1983), [34]Lareschi and Iori (1998), [35]Lareschi et al. (2003), [36]Liat et al. (1980), [37]Luyon and Salibay (2007), [38]Mahdi et al. (1971), [39]Nava et al. (2003), [40]Schwan (1986), [41] Shayan and Rafinejad (2006), [42]Shepard et al. (1983), [43]Stunstov et al. (1997), [44]Stunstov et al. (1997, 2nd site), [45]Woo et al. (1983), [46]Adler et al. (2001), [47]Allred (1968), [48]Anderson and Williams (1997), [49]Beaucournu et al. (1998), [50]Bengston et al. (1986), [51]Bossi et al. (2002), [52]Buckner (1964), [53]Campos et al. (1985), [54]Clark and Durden (2002), [55]Coultrip et al. (1973), [56]Davis et al. (2002), [57]Eads and Campos (1983), [58]Gettinger and Ernest (1995), [59]Grave et al. (1974), [60]Haas et al. (1973), [61]Harrison (1954), [62]Hastriter et al. (2004), [63]Heisch et al. (1953), [64]Holdenried and Morlan (1956), [65]Krasnov et al. (1997), [66]Medina et al. (2006), [67]O'Farrell (1975), [68]Poorbaugh and Gier (1961), [69]Shoukry et al. (1993), [70]US Army Env. Hygiene Agency (1978–1980). See also Online Resource 1

were classified as deserts, Mediterranean and chaparral were merged, and alpine and tundra were merged. Canopy cover was the primary characteristic used to distinguish between forest and grassland/savanna ecoregions and precipitation regime (xeric versus mesic habitats) was the primary characteristic used to distinguish between grassland/savanna and desert categories in situations where sites existed in an intermediate type biome (e.g., those described as woodland or shrubland). Five sites existed within a mosaic type landscape or had a study site description that differed from the biome classification. In these instances, we considered the size and nature of the habitat patch when assigning biome. We assigned the Olson classification to three of these studies (Achuthan and Chandrahas 1971; Nava et al. 2003; Hastriter et al. 2004) and we used the author's description or a new classification for the remaining two studies. One study in Huambo, Angola (Linardi et al. 1994) fell with the grassland/savanna biome, but was described as a forest in the paper. Angola is dominated by grasslands but has distinct forest patches at high elevations (McGinely 2008). Since these montane forests are considered relics of a moist forest biome that once dominated the region, we classified this study as a forest. Conversely, Shayan and Rafinejad (2006) conducted surveys of several sites in Iran, which encompassed three ecoregions: Zagros Mountain forest steppe, Nubo sindian desert and semi-desert, and central Persian desert basin (http://www.nationalgeographic.com—Terrestrial Ecoregions). Though the authors cite forest and meadow habitats, we categorized these surveys within grassland/savanna category to better represent the steppe like nature of most of the study sites, which for the most part lacked a continuous canopy cover.

We used the anthropocentric biome map created by Ellis and Ramankutty (2008) in Google Earth to assign disturbance level to each study site. The map shows classification assignments conducted at five arc minute ($5' = 0.0833°$ or ~ 86 km^2 at equator) and is available in interactive form from the Encyclopedia of Earth, viewable maps in Google Earth and Microsoft Virtual Earth (http://www.eoearth.org/article/Anthropogenic_biome_maps) or in GIS format (http://www.ecotope.org). Ellis and Ramankutty (2008) define four major anthropocentric biomes, namely wildlands,

rangelands, croplands and urban zones; these were further subdivided by population density and other factors to create 18 distinct habitat types. We used a simplified version of their scheme to recognize three disturbance levels: low disturbance sites were relatively *wild* or remote habitats that may include light human populations; (2) intermediate included *agricultural* areas, rural villages, and pastures, and; (3) high disturbance areas were *urban* or densely populated areas. For studies published after 1990, the disturbance class assignments were based directly on the output of the Ellis and Ramankutty (2008) map, which is projected for conditions in 2005. For studies that occurred before 1990, we used Ellis and Ramankutty (2008) for initial classification and cross checked this classification with the original study description as well as other data including census information, news articles, or other descriptions of the area near the time of the study. Using these methods, we reclassified six sites. One site characterized by Ellis and Ramankutty (2008) as intermediate (Walton and Hong 1976) was reclassified as urban and another "intermediate" site (Davis et al. 2002) was reclassified as wild because the study areas were too small to be mapped at the scale of the anthropocentric biome map. Four intermediate sites (Campos et al. 1985; Chenchijtikul et al. 1983; Coutrip et al. 1973; Graves et al. 1974; Poorbaugh and Gier 1961) were wild at the time of study but had rapidly converted to agriculture by 2005.

Most studies reported data for small mammal surveys conducted at multiple sites within an area. Where possible we pooled data from multiple surveys within a single biome and disturbance level. Seven studies (Adler et al. 2001; Bengston et al. 1986; Chenchijtikul et al. 1983; Heisch et al. 1953; Liat et al. 1980; and Stunstov et al. 1997) reported surveys from more than one disturbance class. For these studies each distinct survey was analyzed as an independent sample, yielding three sites for Heisch et al. (1953) and two sites for each of the other studies.

Hypothesis testing and statistical analysis

Small mammal and flea richness (number of species), number of small mammal or flea individuals collected, prevalence (percent of hosts parasitized), intensity of infection (mean number of fleas/parasitized mammal), flea burden (mean number of fleas/mammal) and flea species burden (mean flea species/mammal) were calculated for each host species within each site. We used the average of prevalence, intensity and flea burden values calculated for each species within a site to test for differences among communities. Though these measures are typically used to compare parasite infections between species, the average value provided a measure by which we could compare the overall infection characteristic of each community. We calculated the number and proportion (number infested/number potential host species) of host species used by each flea species within each site and averaged these values to represent the breadth of flea host selectively (niche breadth) at each site. Finally, the proportions of flea species infesting just one host or three or more host species were used as the proportion of specialist or generalist flea species present, respectively.

Relationships between log-transformed mammal and flea variables, standardized for sampling effort, were assessed with Pearson's correlation analysis using a Bonferroni adjusted α-level for multiple tests (PROC CORR, SAS 9.2). Standardizing for sampling effort (number of mammals sampled) was appropriate because many previous studies note positive associations between number of mammals captured and measures of diversity [for mammal number-flea richness (e.g., Holdenried et al. 1951; Nava et al. 2003; Vazquez et al. 2005; Stanko et al. 2002; Krasnov et al. 2004a, b, 2007; for mammal richness-flea richness relationships (Watve and Sukumar 1995; Krasnov et al. 2004b; Stanko et al. 2002; Morrone and Gutiérrez 2005)]. Previous studies suggest that the number of mammals trapped is correlated with flea burden and abundance both positively (Kotti and Kovalevskiy 1996; Krasnov et al. 2004b, 2007; and Zhonglai and Yaozing 1997) and negatively (Krasnov et al. 2006a; Stanko et al. 2002 and Schwan 1986). Similarly, in our review, total number of mammals captured was significantly ($P < 0.05$) correlated with mammal and flea richness ($r = 0.31$ and 0.44, respectively), mammal diversity ($r = -0.29$), fleas collected ($r = 0.85$), flea species burden ($r = 0.44$), and number of host species infested ($r = 0.30$; Online Resource 2). Though we did not find an association between host captured and flea prevalence, others have shown both positive (Lindsay and Galloway 1997; Bossi et al. 2002) and negative relationships (Schwan 1986). Therefore, we used hosts captured as a covariate in all analyses to minimize confounding the effect of capture effort with the effect of human disturbance and habitat.

We used generalized linear model (PROC GLIMMIX, SAS 9.2) analysis with a negative binomial distribution and log link to test for disturbance level and biome effects on number of mammal and fleas collected, richness, intensity, burden, and flea species burden. A negative binomial distribution is appropriate for count data with overdispersion (Littell et al. 2002) and was consistent with the distributions observed for our data. We only analyzed data collected from the four dominant biomes (forest, desert, grassland/savanna, and Mediterranean) because alpine/tundra habitats were not represented in all disturbance classes. We used PROC GLIMMIX analysis with a binomial distribution and logit link to test for disturbance and biome effects on prevalence of hosts infested, proportion of spe-

cialists, generalists and host species infested. Tukey adjusted tests of means were used to identify pair-wise differences between disturbance classes or biomes for significant model variables. We also ran an analysis as described above to test for differences among disturbance classes within the most prevalent biome, forest, as well as to look for specific differences among biomes within each disturbance level.

Results

Our sample of 63 studies included 70 sites (Table 1; Online Resource 1). These studies described flea communities from 23 high (urban) disturbance, 22 intermediate (agricultural), and 25 low (wild) disturbance sites. Sites were located on six continents with Asia and North America hosting the majority of study locations. Forest (both deciduous and rainforest) was the most well-represented biome, followed by deserts and grasslands.

Mammal and flea richness were positively correlated with each other (Fig. 1). Flea number was positively correlated with flea burden, prevalence and intensity of infestation. Measures of flea infection (prevalence, intensity, flea burden) were positively correlated with one another (Fig. 1). Proportion of host specialist at each site was negatively correlated with the proportion of generalists ($r = -0.50$) and the average number of hosts/flea species ($r = -0.59$).

Disturbance level

Disturbance was a significant predictor for six variables; a significant interaction between disturbance class and biome also affected six variables (Table 2). Disturbance class had a stronger influence than biome on all small mammal community variables, whereas flea community variables were more commonly explained by biome or by the interaction term (Table 2). Averaged across biome, richness peaked in intermediate disturbance (agricultural) classes. Two of three abundance measures (number of fleas, flea burden) were greatest in urban sites, whereas number of mammals captured was significantly greater in wild locations (Figs. 2, 3). Two measures of infection, prevalence and proportion of host species used, were significantly higher in urban sites and three measures, number of host species used, intensity,

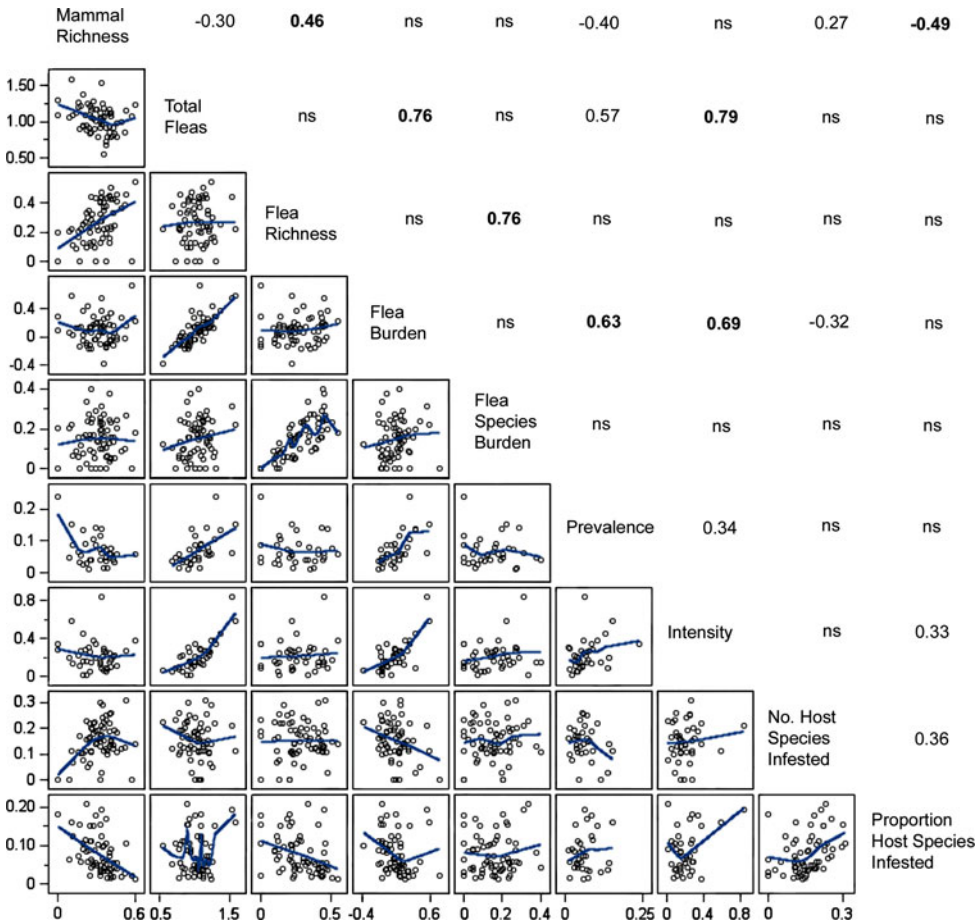

Fig. 1 Pearson correlation analysis for variables calculated from 63 studies conducted around the world. Scatter plots with loess (locally weighted scatterplot smoothing) lines are displayed below the diagonal (border emphasized on plots displaying significant interactions) and *r* values for significant associations. Variables are standardized for sampling effort. Descriptions of variables can be found in the text. $P < 0.0001$ (values in *bold*), otherwise $0.0009 < P < 0.03$ (displayed above the diagonal), *ns* non-significance

Table 2 Significant ($P \leq 0.05$) effects (X) for mixed model analysis of disturbance level (low, intermediate and high disturbance) and biome (forest, desert, grassland/savanna and Mediterranean) on mammal and flea communities surveyed in 63 studies (A–C). Significant difference across disturbance classes within forest biomes (D); significant differences (X) among biomes within each level of disturbance class (E–G)

Variable (no. obs.)	Overall model			Disturbance in forest habitat (D)	Biome within disturbance class[b]		
	Disturbance (A)	Biome (B)	Interaction (C)		Low (E)	Intermediate (F)	High (G)
No. mammals captured (67)	X	–	X	X		X	X
No. mammal spp.[a] (67)	X	–	–	X	–	–	–
Prevalence[a] (40)	X	X	X	X	X	X	X
Intensity[a] (41)	X	–	–	X	–	–	–
Flea burden[a] (63)	–	–	X	X	–	X	X
Flea spp. burden[a] (65)	–	–	–	X		–	–
Proportion infested host spp. (65)	X	X	X	X	–	–	X
No. Fleas[a] (67)	–	X	–	X	–	–	X
No. Flea spp.[a] (67)	–	–	–	X	–	–	–
Number host spp./Flea spp.[a] (65)	X	–	–	X	–	–	–
Proportion flea specialists (67)	–	X	X	X	X	X	X
Proportion flea generalists (67)	–	–	X	X	–	–	X

[a] Log of the number of mammals captured/site was used as an offset variable

[b] Tukey's least significant difference was used to control for Type I error

and flea species burden, were greatest in agricultural sites (Figs. 2, 3). Mean proportions of generalist and specialist fleas were greatest in agricultural sites (Fig. 3).

Within forest biomes, all 12 variables differed significantly among disturbance classes (Table 2). Number of mammals and fleas collected were significantly higher in urban sites, whereas most other variables were significantly greater in agricultural sites (Figs. 2, 3).

Biome

Biome was the primary factor explaining observed changes in the total fleas collected at a site and significantly affected prevalence, proportion of host species infested, and proportion of host specialists at a site (Table 2). Most measures of infestation were relatively low with little variation across biomes for low disturbance sites, but as disturbance increased, infestation increased also, with great variation among biomes (Figs. 2, 3; Table 2). The prevalence of infested mammals showed the greatest degree of significant divergence across biomes. Forests had a significantly greater number of mammals and proportion of specialists in wild sites and higher flea burden in agricultural sites, as compared to other habitats (Figs. 2, 3). Deserts had a significantly higher number of fleas and higher prevalence than any other biome, and fleas infested a greater proportion of available host species in deserts versus other biomes (Figs. 2, 3). Deserts also had a much lower proportion of specialists, particularly in high disturbance sites. Mediterranean sites had the greatest flea diversity and showed distinct trends with respect to the proportion of generalist, specialists and flea burden (Fig. 2).

Discussion

There were clear and statistically significant associations between anthropogenic disturbance and mammal and flea community structure. Most measures of flea infestation increased with increasing disturbance (Figs. 2, 3) and variables associated with increased risk of disease spread and transmission, in particular number of mammals and fleas collected, prevalence and intensity of infestation (Nieto et al. 2007; Krasnov et al. 2006a; Hawlena et al. 2007), increased significantly as disturbance increased. Because we used "total mammals" as an offset (covariate) in linear model analysis, the variable "total fleas" is equivalent to the flea index (fleas/capture), a measure commonly used to quantify flea infestation levels and associated with an increased likelihood of plague outbreaks (Hawlena et al. 2007). The influence of disturbance on mammal and flea characteristics was most evident in analyses restricted to the forest biome (Table 2), probably reflecting greater statistical power as sample size increased. Like Wilcox and Gubler (2005) and Tikhonova et al. (2006), we found that richness and diversity (Shannon's H; data not shown but trends and significance tests mirrored those produced with

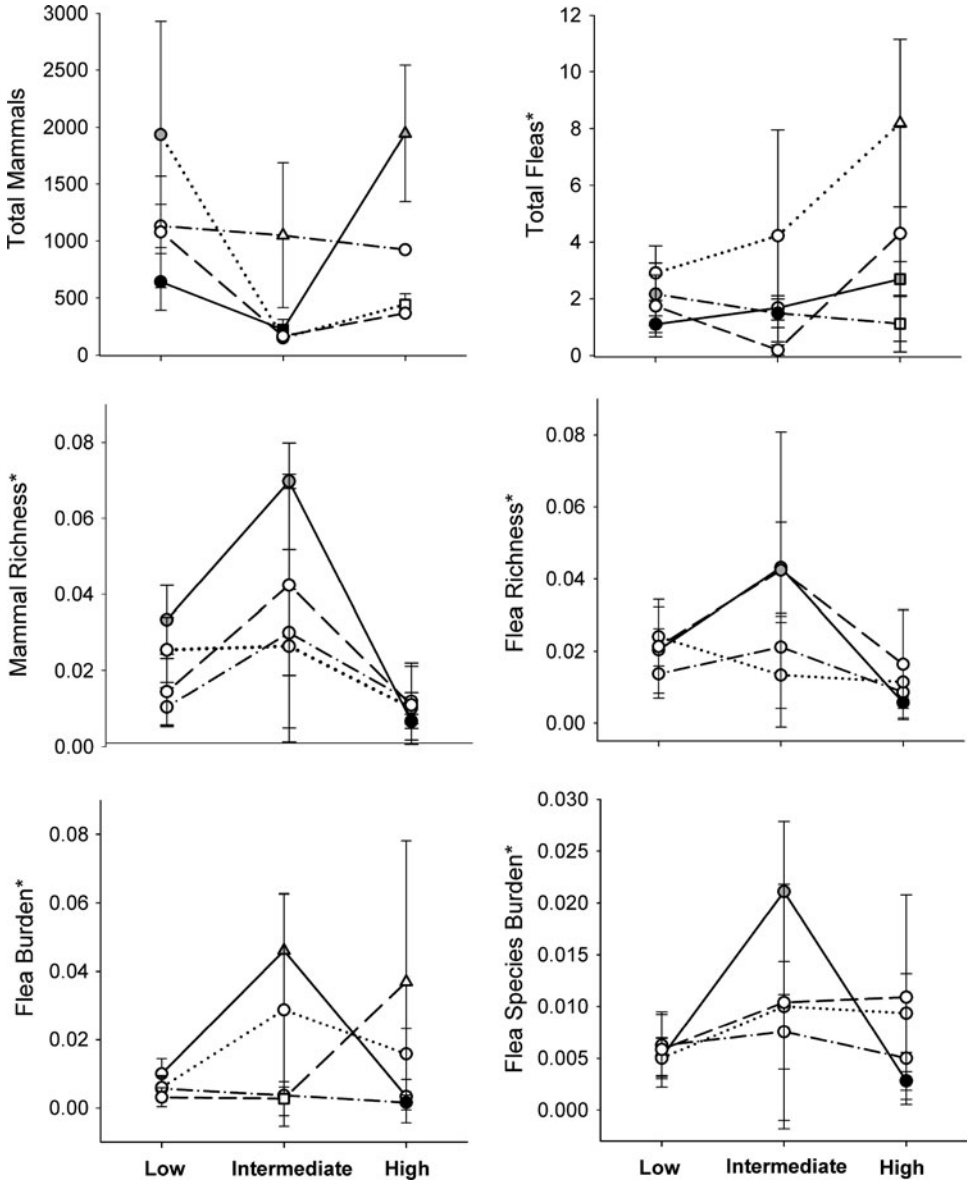

Fig. 2 Mean values for small mammal and flea variables from 63 studies categorized into three anthropogenic disturbance classes (low, intermediate, high) and four biomes (*solid line* forest, *dash and dotted line* grassland/savanna, *dotted line* desert, *dashed line* Mediterranean). *Bars* indicate SE. *Open circles* are default markers and indicate no significant difference. Biomes which are significantly different ($P \leq 0.05$ using Tukey–Kramer multiple comparison methods) from one another are indicated by *triangles* and *squares*. Significant differences between disturbance classes for each biome ($P \leq 0.05$ using Tukey–Kramer multiple comparison methods) are indicated by *gray and black shading*. Significant differences as determined by F tests from generalized linear model (GLM) analysis of the overall model (y is a function of disturbance class and biome, not depicted on graph) are as follows: total mammals (low > intermediate, $P = 0.01$); mammal richness (intermediate > high, $P = 0.02$); remaining variables are not significantly different

richness measures) of mammal communities decreased with increasing anthropogenic disturbance. Our analysis extends this pattern, in that human disturbance also reduces richness and diversity of flea communities when comparing wild and urban sites.

It is generally accepted that increased anthropogenic activity leads to decreased ecosystem heterogeneity and stability (sensu Wilcox and Gubler 2005; Bradley and Altizer 2006), which has several repercussions for disease transmission. In particular, changes in diversity can have many consequences for flea community structure with direct implications for disease spread. First, ecosystem simplification can favor host species that are natural reservoirs or good intermediate hosts for zoonotic disease (LoGuidice et al. 2003). Commonly, these host species are habitat generalists that benefit from disturbance-related declines in abundance of habitat specialists (Keesing et al. 2006). In addition, these generalist host species often carry more diverse flea communities and higher flea loads (number of fleas/host), both of which are associated with increased disease transmission (Egoscue 1976). Second, increases in the densities of generalist host species favors transmission of vectors and their pathogens (Egoscue 1976; Keesing et al. 2006; Wilcox and Gubler 2005). Third, disturbance can also favor generalist vector species, which are important determinants for the spread of zoonotic disease among wildlife populations due to their tendency to feed from a variety of taxa (Molyneux 2003; Gettinger and Ernest 1995). For this reason, increased abundance of generalist vectors is strongly associated with increased parasite transmission (Gettinger and Ernest 1995) and incidence of disease outbreaks in both human and wildlife population

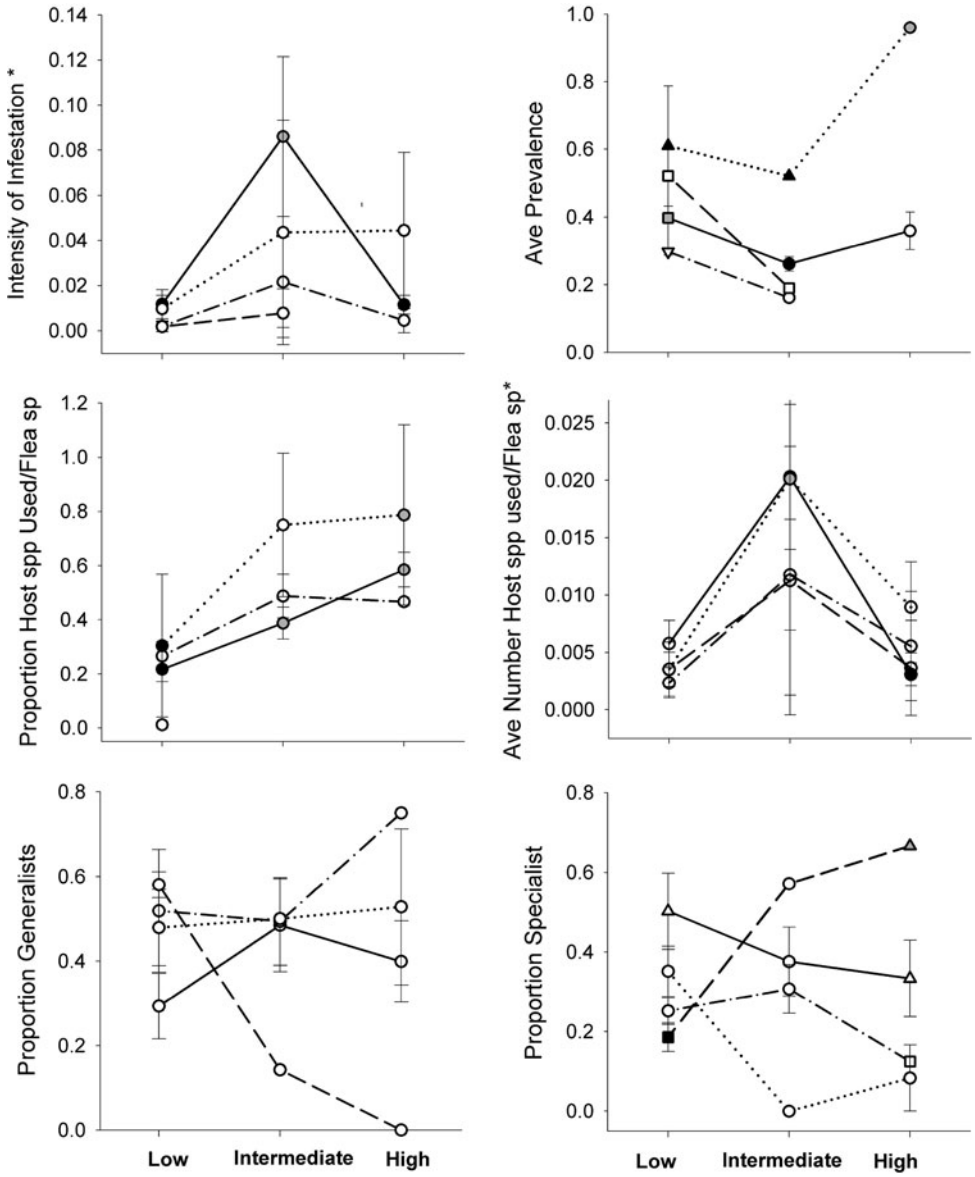

Fig. 3 Mean values for flea measures in small mammal communities from 63 studies categorized into three anthropogenic disturbance classes (low, intermediate, high) and four biomes (*solid line* forest, *dash and dotted line* grassland/savanna, *dotted line* desert, *dashed line* Mediterranean). *Bars* indicate SE. *Open circles* are default markers and indicate no significant difference. Biomes which are significantly different ($P \leq 0.05$ using Tukey–Kramer multiple comparison methods) from one another are indicated by *triangles* and *squares*. Significant differences between disturbance classes for each biome ($P \leq 0.05$ using Tukey–Kramer multiple comparison methods) are indicated by *gray and black shading*. Significant differences as determined by *F* tests from GLM analysis of the overall model (*y* is a function of disturbance class and biome, not depicted on graph) are as follows: intensity of infection (intermediate > low, $P = 0.036$), prevalence (intermediate < low, $P < 0.0001$), proportion host spp. used by each flea species (high and intermediate > low, $P = 0.00013$), Average number of host species used by each flea species (intermediate > low, $P = 0.0009$). Remaining variables are not significantly different

(Nieto et al. 2007; Hawlena et al. 2007). In addition, at least one study found that fleas with broad host spectrums (infest multiple host species) tended to be good plague vectors (Krasnov et al. 2006a, b, c), and thus there could be additional inherent characteristics of a generalist species that predispose them to be good disease vectors.

Overall, this study showed trends of diversity that might be related to ecosystem simplification (when comparing remote and urban sites), and flea host use became more generalized as disturbance increased. Specifically, the proportion of generalist flea species (excluding Mediterranean communities) and the average number and proportion of host species infested by each flea species increased with increasing disturbance (Fig. 3), whereas the number of specialists decreased (except in Mediterranean communities). Our analysis cannot suggest whether these trends reflect an evolutionary mechanism (generalists are better adapted for dealing with disturbance), or an ecological mechanism (specialist lost with loss of their host species). Nonetheless, it is clear that fleas in more disturbed sites tend to infect a greater number of species. In addition, flea exchange among hosts is known to increase with the percentage of hosts infested (Bossard 2006), and prevalence increased with greater disturbance in this study. Clearly anthropogenic activity can potentially increase disease risk through changes in flea host utilization patterns.

Flea host specificity was measured in two ways in this study: by quantifying individual flea species host utilization or the number or host species used versus available at each site, and by classifying flea species according to the number (one or greater than three) of host species parasitized. A number of studies have examined the relationship between

various measures of host specificity and environmental or host community characteristics. Many found that habitat type and the physical characteristics of habitat affect how fleas use hosts (Cole and Koepke 1947; Krasnov et al. 2004a; Trpis 1994; Chandrahas and Krishnaswami 1971; Castleberry et al. 1983). In contrast, Poulin (1998), in his review of specificity patterns of small mammal parasites, considered host traits such as density, lifespan, diversity of habitats used, and social structure most important in determining the host breadth of parasite species (e.g., Poulin et al. 2006). Poulin's view is supported by Krasnov et al. (2004c, 2006c) who found specialization negatively related to host body size and abundance. Our analysis only found a significant relationship between flea specificity and disturbance or host variables when measuring the number or proportion of host species used rather than quantifying fleas as specialists or generalist. It may be that our definition of specialists and generalist were limited (raw species counts versus an index). Host phylogeny, which was not addressed in this review, may have also affected our results (e.g., Felsenstein 1985; but see Guègan et al. 2005). The proportion of hosts used by a flea species was significantly and negatively related to the host availability (mammal richness; Fig. 1) indicating that fleas did not increase their host species spectrum linearly with host species availability. In analysis of disturbance effects, average number of host species used and mammal richness trends correspond, but the proportion of host species used is clearly tied to disturbance (Fig. 3). Thus, the trend for broader host species utilization with increasing disturbance does not relate solely to host or flea diversity.

Many infection parameters peaked at sites of intermediate disturbance (Figs. 2, 3). Most notably, the intensity of infestation, average number of hosts species utilized by flea species, and flea burden were significantly higher in intermediate disturbance sites (Figs. 2, 3). Sites of intermediate disturbance can be important areas for disease exchange and emergence because they contain peridomestic mammal species which readily carry disease between wild reservoir hosts and the commensal mammal species that live in proximity to humans. Indeed, plague in humans is commonly associated with the presence of peridomestic mammal species (Perry and Fetherston 1997). In this study, intermediate disturbance sites contained the greatest number of host and flea species, which may reflect the merging of domestic, peridomestic and wild mammal communities. Therefore, these sites provide not only greater opportunity for vector exchange between reservoir and commensal mammals, but also exhibit characteristics commonly associated with both increase vector exchange and disease transmission.

Biome was associated with both the magnitude and direction of the observed effects of disturbance on flea communities (Figs. 2, 3). Forest and Mediterranean sites were most diverse, whereas grassland/savanna and desert sites contained the fewest species, which may reflect a relationship between habitat complexity and species richness. Deserts appeared to be more sensitive to disturbance than other biomes (Figs. 2, 3). Mammals in deserts also had higher prevalence and carried more fleas per individual than other sites. The tendency for high flea burden may be a result of the relatively low diversity and richness of fleas in desert sites, which could lead to a predominance of generalist species that tend to be more abundant within communities (Krasnov et al. 2004c). This tendency is also reflected in a much lower proportion of specialists in deserts relative to other habitats (Fig. 3). The degree and type of disturbance may be an important factor in how a system responds to disturbance. For instance, grassland to agriculture transitions are less dramatic than forest to agriculture transitions with respect to overstory structure and species exchange and, therefore, grassland communities may be more tolerant of this particular change. These differences might explain why grassland/savanna communities appear to be the less susceptible to disturbance related changes in host and flea community characteristics (Figs. 2, 3). Agricultural systems also provide a source of water that may influence small mammal and thereby flea populations and may counter the negative consequences of disturbance. Whatever the mechanism, biome is an important consideration when assessing the ultimate response of a community to anthropogenic disturbance.

Though this analysis was able to identify a number of trends that were invariant to location or habitat type, two sources of variation may have influenced our capacity to identify trends for and between all habitat types explored in this analysis. First, each of our broad biomes included diverse systems. For instance, the forest biome included tropical rainforest, temperate mixed conifer and boreal forests each of which differs with respect to historic disturbance regimes, range of variability, and characteristics of host and flea communities. If these differences are strongly related to the impact of anthropogenic disturbance on an ecosystem, then we could have failed to detect some important effects of human disturbance, which could be unmasked in a future study with a larger sample size within each biome. A second source of variation not included in this analysis is time since disturbance. Once disturbance occurs, ecosystems begin to move towards a new equilibrium. It is unknown whether some of our observations pertained to systems still in flux. It may be that there is no equilibrium once a natural system is disturbed. Though we did not quantify variation attributable to ecosystem classification scheme or time since disturbance, the high degree and number of significant interactions observed despite these sources of variation point to the ubiquitous nature of

disturbance effects on flea communities of a diversity of small mammal species across the globe.

Global warming is predicted to lead to range expansions of many arthropod vector species (particularly in regions of reduced frost occurrence) and increase the frequency of vector-borne disease outbreaks (Githeko et al. 2000; Epstein 2001; Harvel et al. 2002). However, because higher temperatures reduce adult survivorship, population density of vector species could decrease and lead to lower disease transmission rates (Harvel et al. 2002). Also, local climatic conditions (or biome) are likely to play an important role in determining disease emergence (Lafferty 2009). While the ultimate effects of global warming remain to be seen, this study presents clear evidence for the important role of habitat disturbance in increasing flea-borne disease risk.

Anthropogenic disturbance favors several conditions conducive to flea-borne disease spread, namely higher infestation levels, greater flea abundance, and greater host utilization. Disturbance also facilitates greater flea exchange and higher flea infestation levels through its effect on diversity, which may favor generalist host and vector species. Disturbed habitats may play an important role in facilitating the range expansion of vectors predicted by global warming scenarios (Cumming and Van Vuuren 2006). Those regions which are already destabilized are most prone to the negative consequences of such expansion, whereas range expansions will be more limited in areas less affected by disturbance due to the presence of natural checks and balances which reduce the conditions that promote flea exchange. Thus, preservation of functional and diverse ecosystems may be an effective strategy for limiting zoonotic disease spread.

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