

## RESEARCH ARTICLE

# Cascading effects of sand stabilization on pathogen communities: Connecting global and local processes

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## Funding information

Israel Science Foundation, Grant/Award Number: 1391/15 and 26/99; United States-Israel Binational Science Foundation-BSF, Grant/Award Number: 2012063; Horizon 2020 Framework Programme, Grant/Award Number: 871128; International Arid Lands Consortium, Grant/Award Number: 10R-12; Marie Curie Career Integration Grant, Grant/Award Number: FP7-293713

Editor: Sarah Supp

## Abstract

**Aim:** To advance our understanding of the mechanisms that mediate the relationships between global climatic and anthropogenic processes and pathogen occurrence, it is crucial to evaluate the exact pathways connecting the ecological mediators and the pathogen responses across spatial and temporal heterogeneities at various scales. We investigated the pathways connecting these two types of heterogeneities in sand stabilization that were created by contrasting forces of various human activities and long-term droughts, and pathogen occurrence in host populations. The considered candidate ecological mediators were various components of host community structure, arthropod vector traits, and the pathogen occurrence in these vectors.

**Location:** North-western Negev Desert's sands in Israel.

**Time period:** 1982–2018.

**Major taxa studied:** *Gerbillus andersoni*, *Gerbillus floweri*, *Gerbillus gerbillus*, *Mycoplasma*, *Bartonella*, *Synosternus cleopatrae*.

**Methods:** We combined information from satellite images, 36 years of rodent censuses, a natural experiment, and causal modelling.

**Results:** We found evidence that the spatial heterogeneity in sand biocrusts is largely correlated with structural differences between host communities, especially at medium spatial scales. Pathogen sampling, followed by causal modelling, suggested that the cascading effect of sand stabilization on pathogen occurrence is mainly mediated through changes in host community structure and vector burdens. Importantly, we found that structural changes in the same host community can simultaneously amplify and dilute different pathogens.

**Main conclusions:** These findings suggest that global processes can translate into local processes, where the importance of the mediation effects depend on the magnitude of environmental heterogeneity. These mediation effects can benefit some organisms while adversely affecting others.

**KEYWORDS**

anthropogenic changes, biodiversity–disease relationship, cascading effect, causal modelling, climate, dilution effect, global and local processes, remote sensing, sand stabilization, scales

## 1 | INTRODUCTION

Climatic and anthropogenic processes, such as habitat degradation, land use, and species introductions, greatly contribute to the rise of emerging infectious diseases over time (Jones et al., 2008). The global impacts of the recent outbreaks of Covid-19, Ebola, Lassa fever, SARS, and H1N1 influenza highlight the need to improve our understanding of the processes that affect pathogen occurrence. This task is challenging because the effects of global processes on the local processes that determine disease risk are mainly indirect and mediated by various ecological factors (hereafter, ecological mediators, e.g., Johnson et al., 2015; Jones et al., 2008; Titcomb et al., 2019). Therefore, identifying these ecological mediators is crucial for understanding the full impact of global processes on disease risk for wildlife and humans.

Many experiments have highlighted a suite of environmental conditions, host characteristics, and pathogen characteristics as candidate ecological mediators (e.g., Griffiths et al., 2015; Halliday, Heckman, et al., 2020; Hoverman et al., 2011; Liu et al., 2018). In these experiments, pathogen responses are quantified as a function of a single or several manipulated factors, such as abiotic conditions, resources, host community structure, host characteristics, and coinfecting pathogens. Epidemiological surveys are used to complement these studies by quantifying the relative importance of multiple factors (e.g., Borremans et al., 2011; Giraudoux et al., 2013; Tersago et al., 2011). Surveys range from the sampling of a single host population in a particular season and site (e.g., cross-sectional survey in Cohen, Einav, et al., 2015) to tracking global host communities over decades (Deyle et al., 2016; Jousimo et al., 2014; Neerinckx et al., 2008). However, owing to the challenges associated with human, wild host, and pathogen sampling, as well as to the network complexity of interactions, each survey is often conducted at a single scale, across either space or time, and only rarely across heterogeneity types, multiple scales, or both (e.g., Cohen, Einav, et al., 2015; Haas et al., 2016).

To advance our understanding of the mechanisms that mediate the relationships between the global processes and pathogen occurrence, it is crucial to evaluate the exact pathways connecting these ecological mediators and pathogen occurrence across both types of heterogeneity at various scales (Plowright et al., 2008). Revealing the exact pathways is essential as each pathway may lead to a different

pathogen response. For example, a causal analysis indicated that spillover of sudden oak death from California bay laurel, the main reservoir species, to oaks increases with reservoir density but decreases with the trees' species diversity (Dillon & Meentemeyer, 2019), suggesting that controlled removal of reservoir trees may reduce oak infection, while prescribed fire may amplify it. Likewise, considering just one type of heterogeneity at a single scale may either overlook or overemphasize scale-dependent mechanisms (e.g., Haas et al., 2016; Magnusson et al., 2020).

The level of sand stabilization is an important feature of sandy habitats (Tsoar, 2004). Its spatial and temporal heterogeneities play vital roles in shaping natural communities (e.g., Bird et al., 2017; Zhang et al., 2005). Sand stabilization heterogeneities are attributed to abiotic conditions, mainly wind power, precipitation, and topography, and their interrelated biotic factors, namely biocrust levels and vegetation patterns (Danin, 1991; Tsoar, 2004). Interestingly, the latter biotic factors feed back into the system, by modifying the soil properties, protecting it from water and wind erosion, and by increasing the soil moisture, resulting in soil stabilization (Belnap et al., 2016). In addition, accumulated evidence suggests that anthropogenic activity, which modifies the biotic components of sand stabilization, significantly influences this variability. Some human activities, such as crop production, irrigation, gardening, and afforestation, are expected to amplify sand stabilization, whereas others, such as livestock grazing, excavation, mining activities, and motorized vehicle activity, may produce the opposite effect (Hermas et al., 2019; Li et al., 2018; Ma et al., 2017). To this end, there is a growing interest in the implications of sand stabilization changes around the world and how they may affect ecosystem function (Reed et al., 2019). Here, we investigate the pathways connecting the spatial and temporal heterogeneities in sand stabilization and pathogen occurrence in the blood of wild psammophilous rodents.

Rodent communities in the sands of Israel's north-western Negev Desert offer natural experimental conditions to examine the pathways connecting multiple determinants of pathogen occurrence across both spatial and temporal heterogeneities in sand stabilization at various scales. There are several reasons why this system offers an ideal study opportunity. First, this region is characterized by remarkable spatial and temporal heterogeneities at the level of sand stabilization that are

the result of contrasting forces associated with climatic conditions and anthropogenic activity, both acting on the main biotic determinants of sand stabilization—biocrusts and vegetation (Amir et al., 2014; Qin et al., 2006; Figure 1a,b.). The closing of the border between Israel and Egypt led, on the Israeli side, to local cessation of grazing, which increased biocrust formation and, therefore, sand stabilization (e.g., Roskin et al., 2013). Ongoing agricultural activity has led to similar effects, whereas military training activity has replaced the grazers' trampling effects in part of the region. In addition, the increasing frequency of years with low precipitation, from the mid-1990s on, has led to long-term droughts that have resulted in vegetation cover reduction (Siegal et al., 2013).

Second, these sandy areas are characterized by remarkable spatial and temporal variabilities in rodent community structure, which are mainly composed of various assemblages of three resident species, *Gerbillus andersoni* (de Winton, 1920), *Gerbillus floweri* (Thomas, 1919; previously considered as *Gerbillus pyramidum* in a broad sense), and *Gerbillus gerbillus* (Olivier, 1801) (Supporting Information Appendix S1). These psammophilous communities range from those dominated by mainly one species (*G. andersoni* or *G. floweri*), through two-species (*G. andersoni* and *G. floweri* or *G. floweri* and *G. gerbillus*) to three-species communities (Figure 1a–c). Observations on the spatial distribution of these three species, combined with competition manipulations, suggest that they have a differential preference for the sand stabilization level (Supporting Information Table S1.1). This suggests that the variability in rodent community structure may be associated with the heterogeneity in sand stabilization. However, the relative contributions of biocrust and vegetation cover in determining these associations, the scale dependency of these associations, and the associations between the temporal heterogeneity in sand stabilization and the community structure are still unknown.

The third important feature of the model system is related to the pathogen community. The psammophilous rodent communities are dominated by two genera of blood-associated pathogenic bacteria, *Mycoplasma* and *Bartonella*. Both pathogens target their host's red blood cells, multiply within the vascular system, can be transmitted by flea vectors, and exhibit positive interspecific interactions (Cohen, Toh, et al., 2015; Eidelman et al., 2019). However, they are ecologically distinct, as *Mycoplasma* is mainly detected in *G. andersoni* rodents, and its main transmission route between hosts is direct, whereas *Bartonella*'s infection pattern of transmission mainly through fleas is similar among the three rodents (Cohen et al., 2018; Kedem et al., 2014; Morick et al., 2011). Thus, it is likely that these two pathogen groups are differently affected by environmental and host-related factors. Most importantly, while spatial and temporal variabilities in pathogen composition were documented among rodent communities (Cohen, Toh, et al., 2015; Gavish et al., 2014; Kedem et al., 2014; Figure 1b), there has been no attempt to connect these variabilities to the heterogeneity in sand stabilization.

Accordingly, we addressed two lines of questions:

1. Is variation in rodent (hereafter, 'host') community structure correlated with heterogeneity in sand stabilization levels, and

do these correlations depend on the type (spatial or temporal) of heterogeneity and on its scale (Figure 1)?

2. Does the heterogeneity in sand stabilization result in changes in pathogen communities, and which factors mediate this effect?

Considering the first line of questions, based on the knowledge of the three host species' differential preferences for the sand stabilization level, we hypothesized that their community structures would be correlated with either the biocrust cover, the vegetation cover, or both. We also hypothesized that the strongest correlations would be found at local scales (i.e., the plot and the site scales in Figure 1d), since the home ranges of all three species lie within these scales (Supporting Information Table S1.1), whereas at larger scales (i.e., the regional scale in Figure 1d), species-specific differences in the global distribution pattern and dispersal potential (Supporting Information Table S1.1) may obscure these environmental effects (the 'species-sorting' paradigm in metacommunity theory; Leibold et al., 2004).

Considering the second line of questions, based on the knowledge of the ecological distinction between the two pathogen groups, we hypothesized a cascading effect of sand stabilization, through structural changes in host community, on the occurrence of the host-specialist, *Mycoplasma*, and through the mediation of vector-related factors, on the occurrence of the opportunistic, vector-transmitted *Bartonella*. The suite of 13 predictions that establish the mechanistic foundation for the causal modelling analysis is summarized in Table 1 and Supporting Information Figure S5.8.

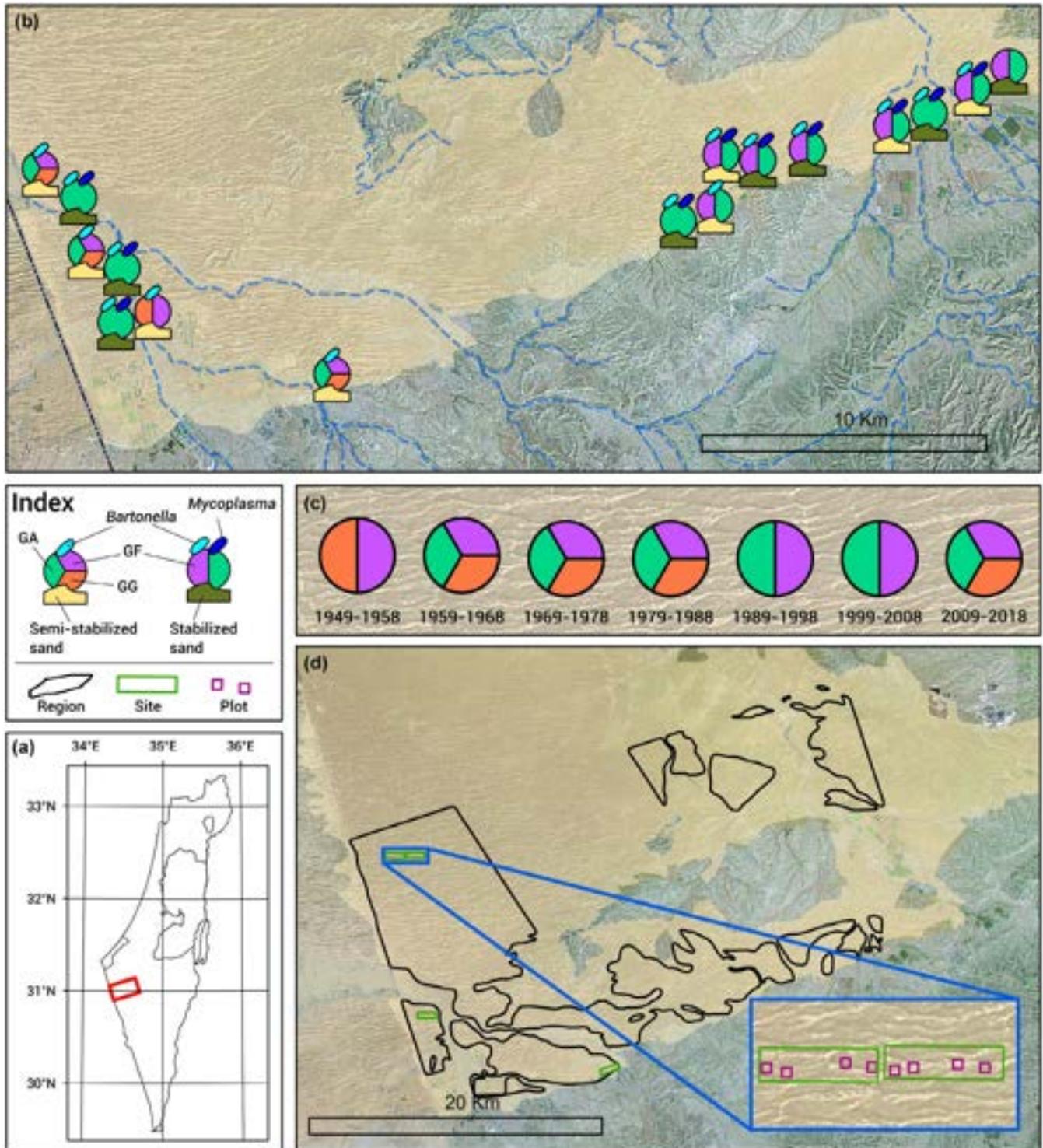
By combining remote sensing and geographical information system (GIS) procedures with data on host community structure across space and time, we found evidence that host communities respond to differences in biocrust levels. This response is related to the heterogeneity magnitude and, thus, is mainly manifested through differences between sites. Bacterial sampling, followed by causal modelling, further indicated that a cascading effect of sand stabilization on pathogen occurrence is mainly mediated through changes in host community structure and vector burdens. These results suggest that global processes, such as those amplifying the spatial heterogeneity in sand stabilization, may cascade into smaller scale processes, including those that determine disease risk in wild animals and humans.

## 2 | MATERIALS AND METHODS

### 2.1 | Question 1: is variation in host community structure correlated with heterogeneity in sand stabilization levels, and do these correlations depend on the type of heterogeneity and on its scale?

#### 2.1.1 | Study design

We combined multispectral remote sensing, GIS analyses, and data from 36 years of host censuses. First, we created three data subsets for the small, medium, and large spatial scales (Figure 1d);



**FIGURE 1** Types and scales of heterogeneity in the study area and experimental design. (a) The study areas are located in the northwestern Negev Desert, Israel (red inset). (b) A cross-sectional field survey was conducted in 2011 to test the predictions of the cascading effect hypothesis (for addressing question 2; Table 1). The sampling of paired adjacent plots differing in the level of sand stabilization demonstrates the spatial heterogeneity in sand stabilization and the corresponding heterogeneity in host and pathogen community structure. Each circle represents a site containing two to three independent 0.01-km<sup>2</sup> plots. (c) Data compilation of the dominant species, *Gerbillus andersoni* (GA), *Gerbillus floweri* (GF), and *Gerbillus gerbillus* (GG), from 1949 to 2018, showing temporal heterogeneity in host community structure (Supporting Information Table S3.3). Note that the data from before 1982 were not included in the study's analyses as there were no available satellite images until then. (d) Three spatial scales—plot, site, and region—were used in the long-term host monitoring to quantify the correlations between the sand stabilization indicators and host community structure at different temporal scales (for addressing question 1).

TABLE 1 Mechanistic foundations for the complete set of alternative cascading effects explored by causal modelling

	#	Path	Prediction	Support?
Host-related hypotheses	1	H1(A)	The habitat preferences of the hosts lie on a sand stabilization gradient, from the most sand-associated <i>Gerbillus gerbillus</i> to the least sand-associated <i>Gerbillus andersoni</i> . Thus, we predicted a positive correlation between sand stabilization and <i>G. andersoni</i> proportion.	<b>Support</b>
	2	H3ii (D); H2ii (E); H2i (F); H3i	<i>Bartonella</i> is an opportunist, and <i>Mycoplasma</i> is a <i>G. andersoni</i> -specialist; thus, we predicted a positive correlation between <i>G. andersoni</i> proportion and the presence of <i>Mycoplasma</i> in hosts and vectors but no correlation with the presence of <i>Bartonella</i> in them.	<b>Support only for <i>Mycoplasma</i> in vectors and hosts and for <i>Bartonella</i> in hosts</b>
	3	H4 (H)	Vectors reproduce better on <i>Gerbillus floweri</i> than on <i>G. andersoni</i> (Messika et al., 2017), and thus, we predicted a negative correlation between <i>G. andersoni</i> proportion and vector burden.	<b>Support</b>
	4	H5 (G)	Resource competition between the hosts is asymmetrical, with <i>G. floweri</i> the superior competitor (Abramsky et al., 1990). Thus, we predicted a positive correlation between <i>G. andersoni</i> proportion and total host density.	No support
	5	H6 (B)	The three hosts are psammophilous, and thus, we predicted a negative correlation between sand stabilization and total host density.	No support
	6	H7i-ii	<i>Bartonella</i> is mainly vector-transmitted, and <i>Mycoplasma</i> is mainly directly transmitted, but the working assumption is that <i>Mycoplasma</i> transmission occurs through <i>G. andersoni</i> hosts. Thus, no direct correlations were predicted between the total host density and the occurrence of the two pathogens.	<b>Support</b>
	7	H8 (I)	Increased host density is expected to increase the chances for vector transmission (Krasnov et al., 2002). Thus, we predicted a positive correlation between host density and vector burden.	<b>Support</b>
Vector-related hypotheses	8	V3 (C); V1 (N)	<i>Synosternus cleopatrae</i> is specialized in sandy habitats (Krasnov et al., 1999). Thus, we predicted a negative correlation between sand stabilization and vector size or vector burden.	<b>Support</b>
	9	V2i-ii	We predicted no correlation between the vector size and pathogen occurrence.	<b>Support</b>
	10	V4i (J); V4ii	<i>Bartonella</i> is mainly vector-transmitted, and <i>Mycoplasma</i> is mostly not. Thus, we predicted a positive correlation between vector burden and <i>Bartonella</i> occurrence and no correlation with <i>Mycoplasma</i> occurrence in host blood.	<b>Support</b>
Pathogen-related hypotheses	11	P1i; P1ii (K)	<i>Bartonella</i> is mainly vector-transmitted, and <i>Mycoplasma</i> is mostly not. Thus, we predicted a positive correlation between <i>Bartonella</i> occurrences in vectors and host blood, and no correlation for <i>Mycoplasma</i> .	No support
	12	P2i, P2ii (M)	<i>Bartonella</i> and <i>Mycoplasma</i> share resources within the vector haemolymph and may affect the vector behaviour and physiology. We thus predicted negative correlations between the occurrences of the two pathogens therein.	<b>Weak support</b>
	13	P3i (L), P3ii	<i>Bartonella</i> clearance time by the host is reduced in <i>Mycoplasma</i> -infected hosts, but the opposite effect does not occur (Eidelman et al., 2019). Thus, we predicted a higher <i>Bartonella</i> occurrence in <i>Mycoplasma</i> -infected hosts.	<b>Support</b>

Note: These 13 host-related (H), vector-related (V), and pathogen-related (P) predictions, which were based on previous knowledge of the model study system, were used to generate the saturated path analysis model (Supporting Information Figure S5.8), and their support by the data is indicated. 'Support' (in bold) indicates paths consistent with the prediction and appearing in at least one of the best models, and 'No support' indicates paths that are not consistent with the prediction or are not included in any of best models. Each prediction corresponds to one or several paths according to the codes ordered in Supporting Information Tables S5.6 and S5.7 and illustrated in Supporting Information Figure S5.8. The most influential paths are described in Figure 5 and Supporting Information Figure S5.9, and their codes are provided in parentheses.

each includes values from two sand stabilization indicators and host counts. These subsets were then used to produce the spatial heterogeneity and temporal heterogeneity datasets, in which the correlation coefficients—indicators for the effect size—between sand stabilization indices and the components of host community structure were calculated across spatial and temporal units, respectively. In each of these datasets, the correlation coefficients were calculated for different combinations of spatial and temporal scale units, which together allowed us to statistically test the dependency of the sand stabilization effect size on the indicator type, heterogeneity type, and its scales. The raw data are found at <https://doi.org/10.6084/m9.figshare.14847147>.

### 2.1.2 | Sand stabilization metrics

Following Karnieli (1997) and Huete (1988), we used two well-known indices to quantify sand stabilization, namely the crust index (CI) and the soil-adjusted vegetation index (SAVI). These two components characterize, respectively, the main micro- and macro-biotic properties of sand stabilization (e.g., Danin, 1991; Danin et al., 1989; Tsoar, 2004). The CI indicates the spatial extension of the biocrusts, along with their density, while the SAVI values indicate the perennial vegetation. The sand stabilization index values were extracted from satellite images of the study area for the relevant polygons (i.e., plot, site, or region; Figure 1d) and years, using remote sensing and GIS analyses (Supporting Information Appendix S2).

To confirm the assumed relationships between the stabilization level and the two indices, during 2011, we chose fourteen 0.01-km<sup>2</sup> plots that we visually characterized as stabilized and 15 adjusted plots that we characterized as semi-stabilized. Then, for these plots, we extracted the different indices as mentioned above. Our characterization best corresponded to the minimum CI and mean SAVI values (Supporting Information Figure S2.2), and thus, we used these values (hereafter, sand stabilization indicators) in the below analyses.

### 2.1.3 | Host community structure metrics

The host community structure was assessed through data of host censuses, collected between 1949 and 2018 in the north-western Negev Desert's sandy areas, Israel (hereafter, the regional scale: area enclosed by a black line in Figure 1d). A list of the data sources and details on the trapping methodology are found in Supporting Information Appendix S3. However, since satellite images only became available in 1984, the rodent data from the earlier years solely functioned as motivation for the study's aim of exploring the temporal heterogeneities in rodent communities (Figure 1c).

Data from 1949 to 1999 were compiled from museum collections, published papers, and unpublished field surveys. From 2000

to 2018, we additionally performed a hierarchical sampling design of live trappings. In this design, four distinct sandy sites of 0.5 km<sup>2</sup> were selected to represent different sand stabilization levels. Inside three of the sites, four smaller plots of 0.01 km<sup>2</sup>, at least 100 m apart, were selected, whereas in the fourth site, only three 0.01-km<sup>2</sup> plots provided suitable habitats for the psammophilous rodents and were thus selected. Since the sampling campaigns lasted from 2 to 4 sequential nights, all counts were normalized for three nights by extrapolation. From these records, we calculated the proportions of *G. andersoni*, *G. floweri*, and *G. gerbillus*, as well as the total host densities, for every scale of interest. Years and locations that did not have at least 10 rodent individuals were omitted from the analyses.

In addition to the three dominant species listed above, other rodent species were infrequently captured, namely, *Gerbillus henleyi*, *Gerbillus dasyurus*, *Meriones* spp., *Mus musculus*, *Eliomys melanurus*, and *Jaculus* spp. Accordingly, both the total host density and species proportions considered them as well.

### 2.1.4 | Assessments of spatial and temporal heterogeneities across scales

The effects of the spatial heterogeneities were assessed from the hierarchical sampling by correlating between the sand stabilization indicators and the rodent community components that were quantified across the plots (small spatial scale) and sites (medium spatial scales). We quantified them by separately analysing the data for each year (small temporal scale), and for 3-year (medium temporal scale), 6-year (large temporal scale), and 18-year intervals (extra-large temporal scale; e.g., see Figure 2e–l for the small spatial scale) (Table 2). Since all sampling events were concentrated in one region, the spatial heterogeneity at the large spatial scale (i.e., between regions) could not be tested.

The effects of the temporal heterogeneities were assessed by correlating the relevant data across single years (small temporal scale) and 3-year intervals (medium temporal scale). We quantified them by separately analysing the data for each plot (small spatial scale), site (medium spatial scale), and the entire region (large spatial scale) (Table 2). Rodent community components, at the plot and site levels, were assessed from the hierarchical sampling data, whereas those at the regional level were assessed from the full 36-year dataset, to extend the information beyond the four chosen sites. The hierarchical sampling duration (18 years) did not allow the assessment of temporal heterogeneity at the 6-year and 18-year intervals at the plot and site levels. Thus, to balance the statistical analyses, the temporal correlations at the large and extra-large temporal scales were not evaluated.

In both spatial and temporal heterogeneity calculations, the index data for each time interval were averaged between years, and the host proportions and total density were calculated from the pooled counts.

The spatial and temporal scales were chosen to balance between the dynamics in rodent communities, which reflects their natural histories (Supporting Information Table S1.1), and the sand stabilization dynamics. Accordingly, the small, medium, and large spatial scales were chosen to account for the three species' small home ranges, which cause them to be restricted to a plot-size area for most of their lives, occasional more distant movements (a few hundreds of metres) within sites, and rare, further (a few kilometres) dispersal events. The four temporal scales were chosen to consider, on the one hand, the annual fluctuations in sand stabilization (Noy et al., 2021) and rodents' high turnover rate (short longevity and single reproduction period per year), and on the other hand, the expectation that changes in sand stabilization may need to accumulate to result in a significant habitat change, as suggested by the rodents' historical records (Figure 1c).

## 2.2 | Question 2: does the heterogeneity in sand stabilization result in changes in pathogen communities, and which factors mediate this effect?

### 2.2.1 | Experimental design and host sampling

To evaluate the most likely pathways mediating the effect of sand stabilization on the probability of *Mycoplasma* and *Bartonella* occurrence in the host blood, we trapped hosts and sampled their blood and fleas (hereafter, vectors) in 31 plots differing in their sand stabilization levels (30°55' N, 34°30' E; Figure 1a–b). To isolate the effect of spatial heterogeneity in sand stabilization, we avoided annual heterogeneity by conducting all trapping in two months (July–August) in 2011. In each 0.01-km<sup>2</sup> plot, we uniformly placed 40 live Sherman traps (4 × 10 rows). To maintain independence and to avoid confounding time and treatments, all plots were located at least 40 m apart from each other, and pairs of stabilized and semi-stabilized plots within a given sampling site were sampled during the same trapping sessions. Movement of individuals between plots was never detected.

The environment-related factor was the sand stabilization level, being either semi-stabilized or stabilized (see Supporting Information Figure S2.2 for mean CI and SAVI values). Host-related factors were the *G. andersoni* proportion and the total host density. Note that in this part, we had to simplify the models, and thus we used the proportion of the most abundant species as a surrogate for community structure rather than the proportions of all species. We chose this alternative over an index of species diversity since it was previously shown that in this system, the species composition, rather than the species diversity per se, determines pathogen composition (Kedem et al., 2014). The total host density was determined as the minimum number of live individuals trapped over 3 nights (Krebs et al., 1969). All individuals were non-reproductive adults. Vector-related factors included the number of vectors collected from individual hosts (hereafter, vector burden) and the average vector size, estimated as

the tibia length to the power of three, following Messika et al. (2017). We collected vectors only from individuals on their first capture to avoid pseudo-replication. All vectors were morphologically identified as *Synosternus cleopatrae* fleas (Rothschild, 1904). Finally, the pathogen-related factors included the occurrence (presence or absence) of *Bartonella* and *Mycoplasma* in the vectors, which was assessed by extracting the DNA from one randomly selected vector per host and conducting a specific polymerase chain reaction (PCR), following Cohen, Einav, et al. (2015). The probability of *Mycoplasma* and *Bartonella* occurrence in the host blood (dependent variables) was assessed by extracting the DNA from 50 µl of blood taken from each host and conducting a specific PCR, following Cohen, Einav, et al. (2015). Sanger sequencing of 20% of the PCR-positive blood and flea samples confirmed the genus identifications. We released all the hosts at their place of capture at the end of the procedure.

## 2.3 | Statistical analyses

### 2.3.1 | Question 1

To test how the associations between sand stabilization and host community structure change as a function of the stabilization indicator type (CI or SAVI), heterogeneity type (spatial or temporal), and its scale (three spatial scales and four temporal scales), we divided the analysis into two stages. In stage 1, we calculated the Pearson *r* statistics of the correlations between the sand stabilization indicators (independent variable) and the rodent community structure (dependent variables, i.e., the proportion of each species and the total host density) for each of the heterogeneity type-scale combinations described above (Supporting Information Table S4.4 and examples in Figure 2e–l). These *r* statistics were used in stage 2 as indicators for the effect sizes of the stabilization–community structure associations (Nakagawa & Cuthill, 2007).

In stage 2, we used a model selection approach that assigns relative importance scores to the different independent variables based on the Akaike information criterion corrected for a small sample size (AICc) weight (J. B. Johnson & Omland, 2004). We first tested, over the entire dataset, whether the indicator type and the heterogeneity type (independent variables) would best predict the variability in the effect sizes calculated in stage 1 (dependent variable). To avoid confounding heterogeneity type with scale (e.g., only the temporal heterogeneity data were calculated for the large spatial scale), we omitted, from this combined dataset, the data calculated for the large spatial scale and the large and extra-large temporal scales. We then tested separately whether the spatial and temporal scales (independent variables) would best predict the variability in the effect sizes calculated across the (a) spatial heterogeneity and (b) temporal heterogeneity (dependent variables). To ensure an unbiased ranking of independent variables, each model-set included all possible combinations of additive nested generalized linear models (GLMs) with normal distribution (16 for the combined dataset and eight for each of the separated datasets). We listed a factor as important in a

TABLE 2 Sampling and analysis schemes for the long-term host monitoring

Spatial heterogeneity									
Spatial scale	Small				Medium				
Spatial unit	Plot				Site				
Temporal scale	Small	Medium	Large	Extra-large	Small	Medium	Large	Extra-large	
Temporal unit (years)	1	3	6	18	1	3	6	18	
Sample size (correlation)	15				4				
Number of independent analyses	18	6	3	1	18	6	3	1	
Temporal heterogeneity									
Temporal scale	Small			Medium			Large		
Temporal unit (years)	1			3			6		
Spatial scale	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large
Spatial unit	Plot	Site	Region	Plot	Site	Region	Plot	Site	Region
Sample size (correlation)	18	18	28 <sup>a</sup>	6	6	12	Not applicable; sample size is too low (n = 3)		<sup>b</sup> 6
Number of independent analyses	15	4	1	15	4	1			<sup>b</sup> 1

Note: A description of the various combinations of spatial and temporal scales according to which the correlations between the spatial and temporal heterogeneities in sand stabilization and the components of host community structure were analysed. The spatial heterogeneity was assessed through the hierarchical sampling campaigns conducted from 2000 to 2018, which were carried out in fifteen 0.01-km<sup>2</sup> plots, embedded in four 0.5-km<sup>2</sup> sites, within the north-western Negev Desert's sandy region in Israel (Figure 1d). The temporal heterogeneities in sand stabilization at the plot and site spatial scales were also assessed with data from the hierarchical sampling, whereas those at the regional level were assessed with the complete dataset of rodent censuses conducted from 1982 to 2018.

<sup>a</sup>Only years with at least 10 rodents were included in the analysis.

<sup>b</sup>Omitted from the statistical analyses to avoid confounding effects of spatial and temporal scales in the temporal heterogeneity analysis, and of heterogeneity type and temporal scale in the complete dataset analysis.

given model-set if its relative importance score (the sum of the AICc weights of all the models that included the focal factor) was larger than 70% (Wagner et al., 2014). These analyses were conducted separately for each of the host community components (Table 3).

To test whether the observed effects (e.g., heterogeneity type is an important predictor of the effect size) may be related to the magnitude differences between the levels of the tested factors (e.g., spatial heterogeneity in stabilization is greater than temporal heterogeneity) or rather reflect species-specific responses to them, we conducted identical analyses, with only one exception: the dependent variables were the heterogeneity magnitudes, which were evaluated by the sand stabilization's coefficient of variation (the ratio of the standard deviation to the mean; CV).

These analyses were conducted in R (R Core Team, 2013), using the car (Fox & Weisberg, 2019) and MuMIn (Barton, 2009) packages (code is provided at <https://doi.org/10.6084/m9.figshare.14847147>).

### 2.3.2 | Question 2

To evaluate the most likely pathways mediating the effect of sand stabilization (independent variable) on the probability of *Mycoplasma* and *Bartonella* occurrence in the host blood (dependent binary variables), we used a model selection approach for causal modelling on the natural experiment data from 2011

(Burnham & Anderson, 2002; Wootton, 1994). A path analysis is a powerful approach to causal modelling that evaluates alternative causal hypotheses regarding the associations between factors. The model selection approach complements the path analysis by evaluating the likelihood of the causal hypotheses, which reflect different predictions about the directions and strength of interactions, given the data and the set of models (Garrido, Hansen, et al., 2021).

The saturated path model, which integrated all biologically meaningful paths linking sand stabilization and the occurrence probability of the pathogens in host blood (the mechanistic foundations are detailed in Table 1), included all the above listed mediating factors (Supporting Information Figure S5.8). To reduce the number of competing path analysis models, we divided the analysis into two stages. In stage 1, we divided these factors into three families (i.e., host-related, vector-related, and pathogenic-related factors) and searched for the most important causal pathways within each family. This was done by keeping all pathways fixed and, each time, only manipulating the paths connecting the factors within a given family (Supporting Information Table S5.6). In stage 2, we compared all the models that showed good support for the data during the first stage ( $w_i > 10\%$ ) and their derivatives (Supporting Information Table S5.7). For both stages, we compared models while keeping the same AICc metric (i.e., using the same mediators and dependent variables), using model probabilities ( $w_i$ , where  $i$  corresponds to a specific model)

based on the AICc, which gives a measure of the plausibility, on a 0 to 1 scale, that a particular model is indeed the best model (Burnham & Anderson, 2002). The competing models were based on GLMs with a logistic distribution for the binary-dependent variables, a Poisson distribution for the count-dependent variables (vector burden), and a normal distribution for the other variables. Since the proportion of *G. andersoni* in host communities during the relevant field season had a bimodal distribution, we transformed it to a binary variable, by setting values lower than or equal to 50% to 0 and values above 50% to 1. Path analyses were conducted using Mplus (Muthén & Muthén, Los Angeles, CA). Code is provided at <https://doi.org/10.6084/m9.figshare.14847147>.

### 3 | RESULTS

#### 3.1 | Question 1: host community structure is highly correlated with the spatial heterogeneity in CI, especially at medium spatial scales

The summary of the effect sizes of the correlations between the values of the sand stabilization indicators and the components of host community structure, across space and time at multiple scales, is provided in Supporting Information Table S4.4 along with the corresponding CV values.

The indicator type was an important predictor of the effect sizes of the correlations between the sand stabilization indicators and the total host density and *G. floweri* and *G. gerbillus* proportions (Table 3), which all correlated negatively with the CI, but did not correlate negatively with the vegetation index (Figure 2b–d, f–h, and j–l). In contrast, the indicator type did not predict the correlations with the *G. andersoni* proportions (Table 3), which were positively correlated with both sand stabilization indicators (Figure 2a,e, and i). Altogether, these results suggest that in agreement with our hypothesis, all components of the rodent community structure were

correlated with the biocrust levels. Moreover, only the total host density response resembled that of the CV (Table 3, Figure 2d and 3a), suggesting that the species-specific responses are not just a result of the differences in the heterogeneity magnitude between the two sand stabilization properties.

The heterogeneity type was an important predictor of the correlations between the sand stabilization indicators and the total host density and *G. andersoni* and *G. floweri* proportions (Table 3) since they all correlated more strongly with the spatial, than with the temporal, sand stabilization heterogeneities (Figure 2a–b, and d). *Gerbillus gerbillus* showed the same trend (Figure 2c), but for this species, the relative importance of the heterogeneity type was lower (47%; Table 3). The greater effect of spatial heterogeneity accords with its higher magnitude compared to that of the temporal heterogeneity (Table 3, Figure 3b and Supporting Information Figure S4.5).

The spatial scale was an important predictor of the correlations between the spatial heterogeneity in sand stabilization and both the total host density and the *G. floweri* proportion (Table 3), which were stronger at medium than at small spatial scales (Figure 4b and d). These greater effects of sand stabilization at medium spatial scales accord with the higher heterogeneity magnitude therein, compared to that observed at small scales (Table 3 and Figure 3c). In contrast, the spatial scale did not predict the correlations between the spatial heterogeneity in sand stabilization and the *G. andersoni* and *G. gerbillus* proportions (Table 3, Figure 4a and c).

The other tested spatial predictor and the temporal scale predictors were found to be less important (Table 3). These results accord with the similar magnitude of spatial heterogeneity observed at the four temporal scales (Figure 3d) and of temporal heterogeneity observed at the three spatial scales (Table 3; Figure 3e). However, the absence of a host community response to the greater annual heterogeneity in sand stabilization, compared to that observed across the 3-year intervals (Figure 3f), may indicate time-lags between environmental changes and host responses. Altogether, these minor effects fail to support our hypotheses that the associations between sand

TABLE 3 Model selection results for the long-term monitoring

Data subset (n)	Tested effect	<i>Gerbillus andersoni</i>	<i>Gerbillus floweri</i>	<i>Gerbillus gerbillus</i>	Total host density	CV
Complete dataset (172)	Indicator type (CI or SAVI)	31	<b>100</b>	<b>100</b>	<b>100</b>	<b>100</b>
	Heterogeneity type (spatial or temporal)	<b>100</b>	<b>100</b>	47	<b>95</b>	<b>100</b>
Spatial heterogeneity (112)	Spatial scale (small or medium)	27	<b>96</b>	26	<b>95</b>	<b>77</b>
	Temporal scale (small, medium, large, or extra-large)	60	4	10	7	5
Temporal heterogeneity (80)	Spatial scale (small, medium, or large)	11	12	9	36	21
	Temporal scale (small or medium)	48	33	24	38	<b>100</b>

Note: Results illustrate the relative importance (in percentages) of the effects of the indicator type [i.e., crust index (CI) or soil-adjusted vegetation index (SAVI)], heterogeneity type (i.e., spatial or temporal), spatial scale, and the temporal scale (independent factors) on the effect sizes (dependent variable; Supporting Information Table S4.4). The two first effects were tested on the complete dataset, including small and medium spatial and temporal scales, whereas the effects of the spatial and temporal scales were evaluated separately on correlations conducted across the (a) spatial and (b) temporal heterogeneity gradients. Results are provided for each host species separately and for the total host density, along with the sand stabilization's coefficients of variation (the ratio of the standard deviation to the mean; CV) values, which indicate the corresponding magnitude of the heterogeneity in sand stabilization. Important effects >70% are emphasized in bold. n is the sample size.

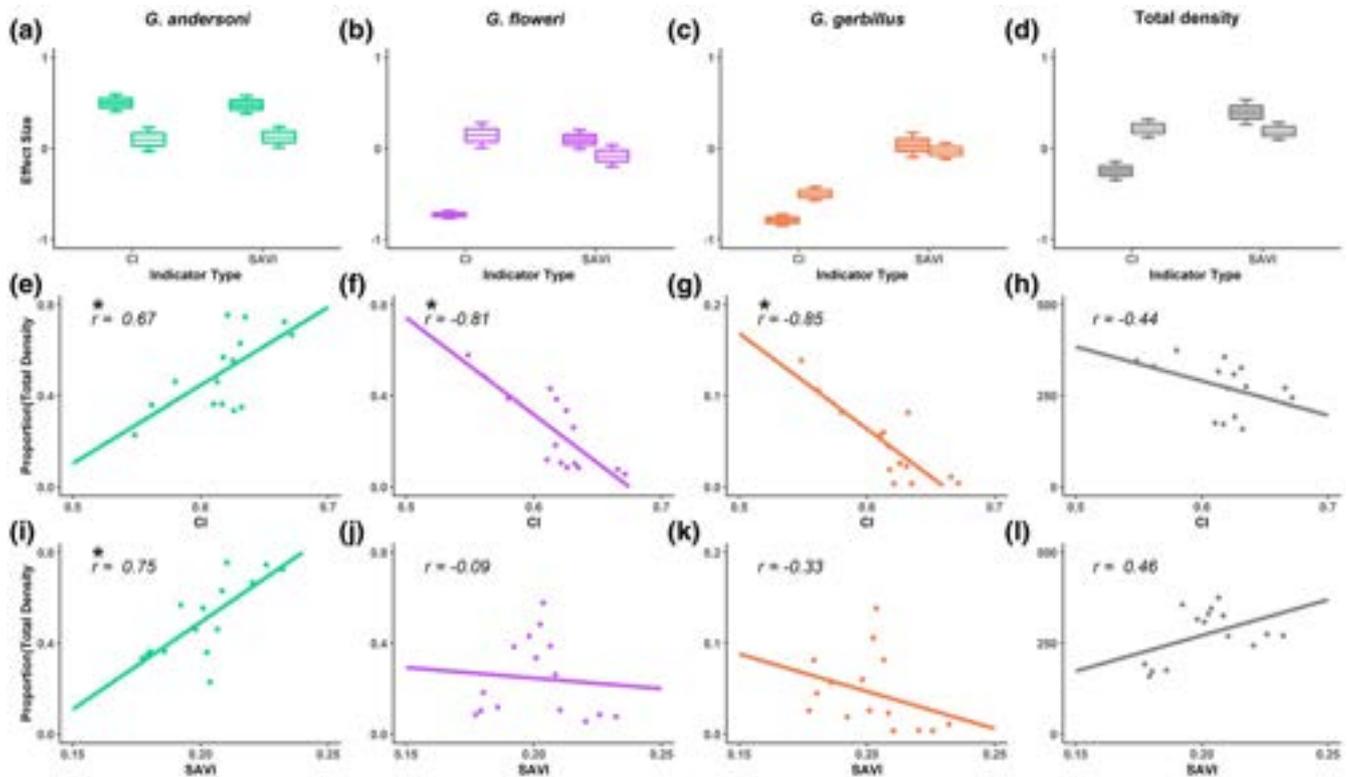


FIGURE 2 Correlations between the sand stabilization indicators and the components of the host community structure from the long-term host monitoring. (a–d) Box plots (mean  $\pm$  SE; error bars = 95% confidence intervals) of effect sizes as a function of the indicator type [crust index (CI) or soil-adjusted vegetation index (SAVI)] and heterogeneity type (filled and empty columns represent spatial and temporal heterogeneity, respectively) in predicting the proportions of *Gerbillus andersoni* (a in green), *Gerbillus floweri* (b in purple), and *Gerbillus gerbillus* (c in orange), and the total host density (d in grey). (e–l) Examples of the correlations used for quantifying the effect sizes of CI (e–h) and SAVI (i–l) in a–d. For illustration purposes, the examples are for spatial heterogeneity at the smallest spatial scale (15 plots) and the extra-large temporal scale (2000–2018). The spatial heterogeneity gradient was chosen due to its importance (Table 3), the smallest spatial scale allowed illustration of the maximum number of sampling points, whereas the extra-large temporal scale provides the most consistent data, decreasing the weight of unique fluctuations. Asterisks mark significant correlations in e–l.

stabilization and rodent community structure would depend on the temporal scale and would be greater at the local spatial scales.

### 3.2 | Question 2: cascading effects of sand stabilization on pathogen communities are mostly mediated through structural changes in host communities and vector burdens

In total, 98 rodent individuals were sampled; all were infected with fleas, resulting in a total of 1,979 fleas. The *Mycoplasma* prevalence was 38% and 34% in the host blood and fleas, respectively, whereas the *Bartonella* prevalence was 78% and 48% in the host blood and fleas, respectively.

In stage 1 of the path analyses, three out of 34 candidate models had good support from the data ( $w_i > 10\%$ ;  $\sum w_i = 91\%$ ); two represented the host-related factor family, and another represented the vector-related factor family (models 1, 2, and 3, respectively, in Supporting Information Table S5.6).

In stage 2, two derivatives of the above models were selected as the best models (models 34 and 35 in Supporting Information Table S5.7;  $w_i > 10\%$ ;  $\sum w_i = 79\%$ ). Both models had a decent fit to the data (goodness-of-fit test,  $\chi^2_{20} = 23$ ,  $p = .3$  and  $\chi^2_{22} = 22$ ,  $p = .4$ , for models 34–35, respectively), and their consistency with the specific study predictions is detailed in Table 1. In both, pathogen occurrence in the host blood was indirectly correlated with sand stabilization through its effects on the *G. andersoni* proportion (Figure 5). In agreement with our hypothesis, we found indications that the *G. andersoni* proportion increases with sand stabilization (A in Figure 5 and Supporting Information Figure S5.9) and that this increase is further translated into major changes in the host–vector–pathogen community. First, the analysis suggests that the increase in the *G. andersoni* proportion directly increases the probability of hosts to be infected by *Mycoplasma* (D in Figure 5 and Supporting Information Figure S5.9). Second, the increase is directly correlated with decreased total host density (G in Figure 5 and Supporting Information Figure S5.9), vector burden (H in Figure 5 and Supporting Information Figure S5.9), *Bartonella*

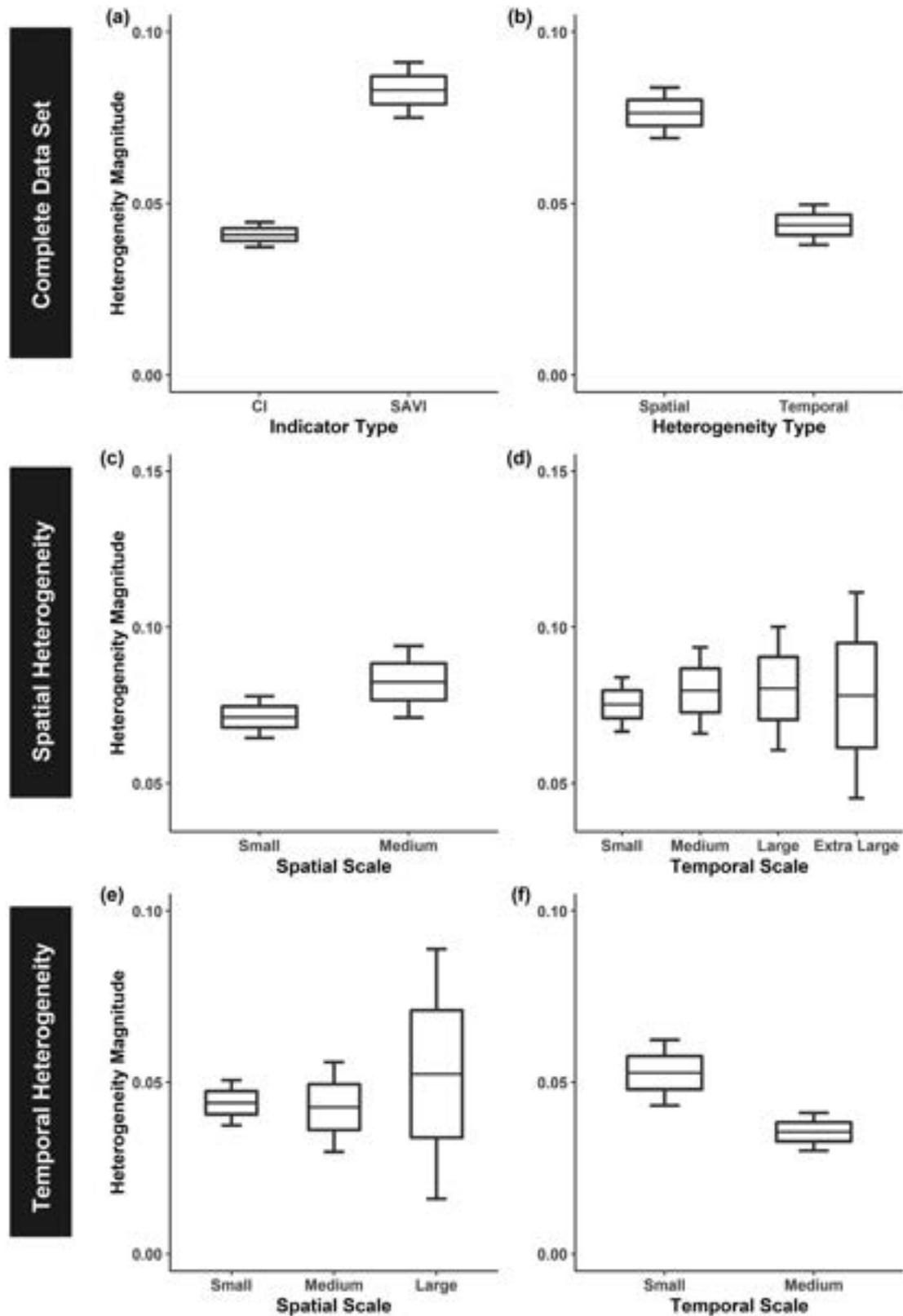


FIGURE 3 The magnitude of the heterogeneity in sand stabilization as a function of the stabilization indicator, heterogeneity type, and its scales. Box plots (mean  $\pm$  SE; error bars = 95% confidence intervals) of the sand stabilization's coefficient of variation (the ratio of the standard deviation to the mean; CV). CI = crust index; SAVI = soil-adjusted vegetation index. The values constructing the box plots in a–b are taken from the complete dataset, whereas those in c–d and e–f are taken from the spatial heterogeneity and temporal heterogeneity datasets, respectively

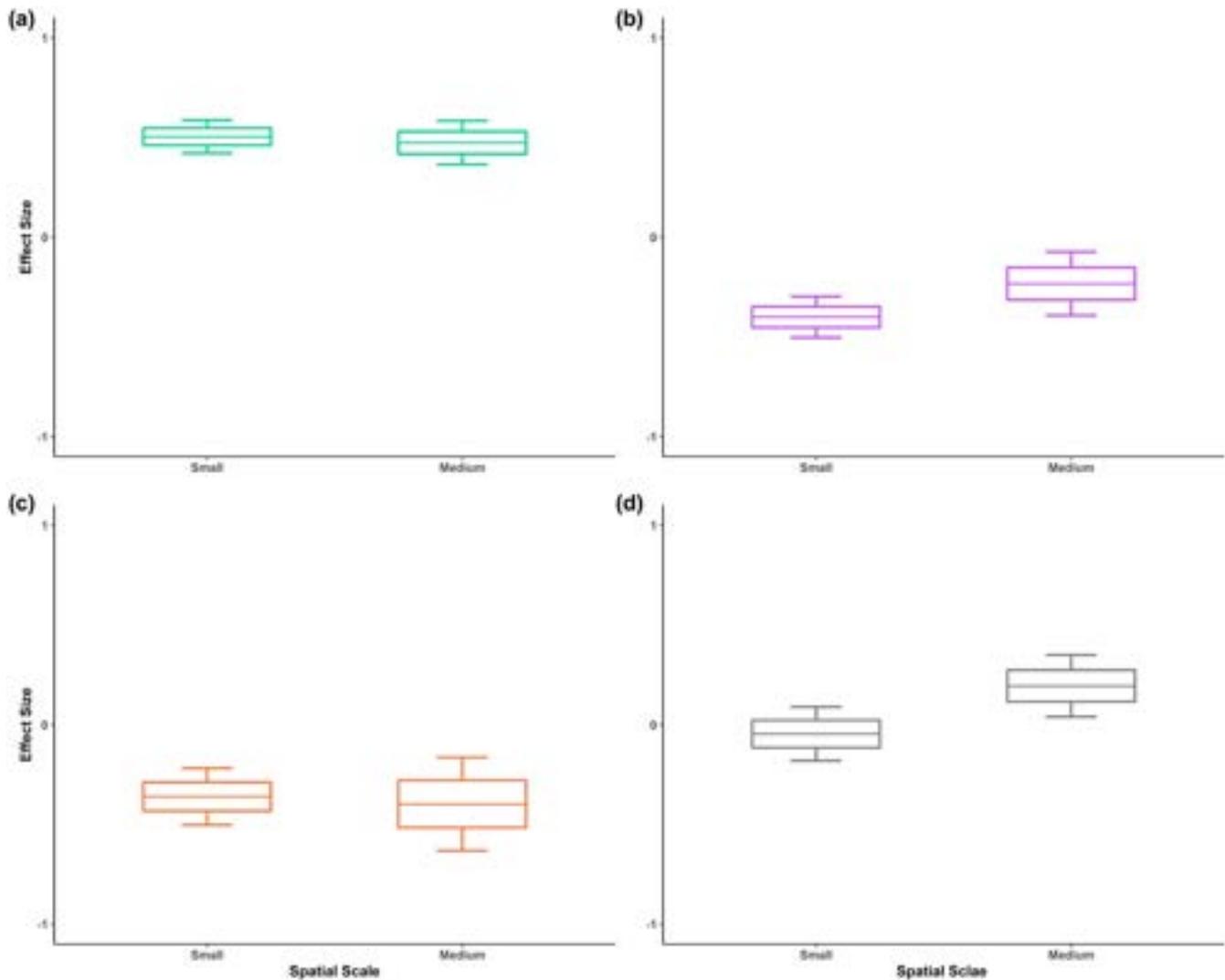
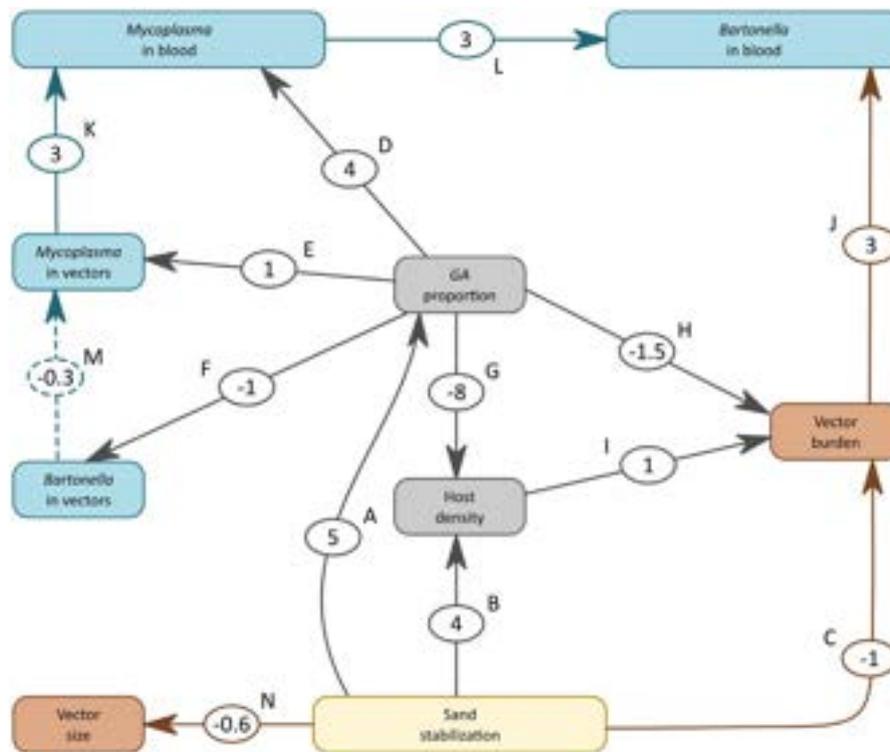


FIGURE 4 The strength of the correlations between the spatial heterogeneity in sand stabilization and the components of the host community structure as a function of the spatial scale. Box plots (mean  $\pm$  SE; error bars = 95% confidence intervals) of effect sizes as a function of the spatial scale (small for a plot level and medium for a site level) in predicting the proportions of *Gerbillus andersoni* (a in green), *Gerbillus floweri* (b in purple), and *Gerbillus gerbillus* (c in orange), and the total host density (d in grey)

occurrence in vectors (F in Figure 5 and Supporting Information Figure S5.9), and increased *Mycoplasma* in vectors (E in Figure 5 and Supporting Information Figure S5.9); all affect, either directly (J and K in Figure 5 and Supporting Information Figure S5.9) or indirectly (I and M in Figure 5), the occurrence of *Mycoplasma* or *Bartonella* in hosts. The two best models also suggest that this occurrence of *Bartonella* may be indirectly correlated with sand stabilization through its negative effects on vector burden (C and J in Figure 5 and Supporting Information Figure S5.9) and its positive effects on total host density (B in Figure 5 and Supporting Information Figure S5.9). Finally, in agreement with our prediction (prediction 13 in Table 1), *Mycoplasma* and *Bartonella* occurrences in hosts were positively correlated (L in Figure 5 and Supporting Information Figure S5.9), and we found no evidence supporting the vector size as a mediator (prediction 9 in Table 1; Figure 5).

## 4 | DISCUSSION

The complex relationships between global factors and pathogen occurrence call for mechanistic, multidisciplinary, and multiscale research in natural communities. By testing the effects of heterogeneity in sand stabilization on natural rodent–pathogen communities, our work encompasses all of these components. The interdisciplinary methodology, combined with a simultaneous consideration of spatial and temporal heterogeneities and multiple scales, allowed us to characterize a cascading effect, from global to local processes. In particular, the long-term host monitoring data suggest that in the north-western Negev Desert, where climatic and anthropogenic processes create heterogeneity in biocrust and vegetation cover, the spatial heterogeneity in biocrusts may lead to structural differences in host communities, especially at medium spatial scales. The causal modelling on the



**FIGURE 5** The best path analysis model for predicting the effects of sand stabilization on pathogen (*Bartonella* and *Mycoplasma*) occurrence in hosts. Data are taken from the cross-sectional natural experiment. Arrows represent direct and indirect influences. Numbers on the arrows are standardized effects ( $\beta$ /SEM; Sweet & Grace-Martin, 2011). The solid arrows belong to the best model (model 34 in Supporting Information Table S5.7), and the dashed arrow represents an additional relationship that is included only in the second 'best' model (M; model 35 in Supporting Information Table S5.7). Arrow E is missing from the second 'best' model (Supporting Information Table S5.7). Host-related, vector-related, and pathogen-related factors and their associated arrows are coloured in grey, brown, and light blue, respectively. Paths A–L represent the most influential direct effects as described in detail in Supporting Information Figure S5.9. GA = *Gerbillus andersoni*

natural experiment's cross-sectional data further highlights several paths through which these changes in host communities may cascade to changes in pathogen occurrence. Below, we discuss the global and local processes separately and the implications of their connections.

#### 4.1 | Global processes: from climatic and anthropogenic processes to host community structure

As detailed in the Introduction, the historical climatic and anthropogenic processes that have occurred over the years in the north-western Negev Desert region of Israel, through contrasting forces of various human activities and long-term droughts, have created a mosaic of biocrust and vegetation cover levels. Since both climatic changes and anthropogenic activity are ongoing processes, the spatial mosaic is dynamic and fluctuates through time (Noy et al., 2021). Our data suggest that this dynamic mosaic may lead to structural differences between host communities. Furthermore, the data indicate that despite the lower magnitude of biocrust heterogeneity compared to that of the vegetation cover, the hosts respond mainly to levels of the former, emphasizing both the importance of biocrusts in ecosystem functioning and the need to quantify biocrust

levels in both ecological and applied studies (Karnieli, 1997; Reed et al., 2019).

The effects of the heterogeneity in sand stabilization on natural communities usually include the replacement of psammophilous by non-psammophilous species (e.g., Bird et al., 2017; Qiao et al., 2012; Zhang et al., 2005). However, experimental data from the sand systems in both the north-western Negev and the southern coastal plain of Israel suggest that structural responses to stabilization heterogeneity may occur even within psammophilous communities. Specifically, field observations, supported by field manipulations, suggest that *G. andersoni* mainly occupies the most productive habitats, with only a low percentage of coarse sand, and *G. gerbillus* occupies the poorest and most sand-shifting habitats, whereas *G. floweri* lies in-between (Supporting Information Table S1.1). Our analyses support and complement these local-scale (within and between plots) findings. First, the positive correlations of *G. andersoni* proportions with both sand stabilization indicators and the negative correlations of the other two species with solely the biocrust index (Figure 2) offer functional explanations to the above findings. In particular, they suggest that the microhabitat separation is centred around a food-safety trade-off, where *G. andersoni*, the species least adapted to mobility in the loose sand among the three rodents (Supporting Information Table S1.1), is more

restricted to habitats with high vegetation cover, where it can be more protected from predators. In contrast, the other two species may optimize their foraging efficiency in the more open, low biocrust habitats, where they can move and detect seeds more easily.

Second, our analyses suggest that not only is the species composition correlated with the sand stabilization indicators but also the total host density. Finally, above all, our analyses suggest that the rodent community experiences greater spatial heterogeneity in sand stabilization than temporal heterogeneity, especially at medium spatial scales.

More generally, the results of the first part of the study highlight the importance of distinguishing between the heterogeneity magnitude experienced by the target organisms and the species-specific response to it. The current study system provides parallel examples in which (a) all host responses contradict the magnitude differences in heterogeneity (i.e., the higher response to biogenic crust than to vegetation cover levels), (b) only some host species responses accord with the magnitude differences they experience (i.e., species-specific response to the spatial scale), and (c) all host responses accord with the magnitude differences they experienced (i.e., the higher response to spatial than to temporal heterogeneities). Adopting this approach in future studies may extend the mechanistic insights into other global processes as well. For example, across-study comparisons suggest that biodiversity–disease relationships become more positive when evaluated across spatial than across temporal heterogeneities (Rohr et al., 2020), and it would be important to know whether this pattern is related to the biodiversity differences experienced by the organisms, or rather, to the different impacts that spatial and temporal heterogeneities impose on them.

## 4.2 | Local processes: from heterogeneity in host community structure to pathogen occurrence

The results of the long-term host monitoring suggest that heterogeneity in sand stabilization across space may lead to structural differences between host communities. The complementary natural experiment's results support our hypothesis that these community differences may be further translated into variability in pathogen occurrence. These results accord with evidence from other pathogen systems (e.g., avian influenza, plant fungi, West Nile virus, Lyme disease, and hantavirus), in which pathogen occurrence was correlated with spatial differences in host community structure (Huang et al., 2019; Jousimo et al., 2014; Kilpatrick et al., 2006; LoGiudice et al., 2008; Vadell et al., 2020, respectively).

Interestingly, while evidence from diverse disease systems that are relevant to plants, animals, and people shows either negative (termed as 'dilution effect'; e.g., Civitello et al., 2015; Liu et al., 2020; Magnusson et al., 2020) or positive (termed as 'amplification effect'; e.g., Wood et al., 2014, 2017) associations between the host species diversity and pathogen occurrence, depending on the exact effects of diversity, host specificity, scale, and community assembly (Rohr et al., 2020), our results suggest that a single host species could potentially act as both an amplifier and a diluter for different microbial pathogens in the community. In particular, the path analysis results

suggest that an increase in the *G. andersoni* proportion may simultaneously amplify the occurrence of the host specialist, *Mycoplasma*, and reduce the occurrence of the host opportunist, *Bartonella*. A recent laboratory experiment suggests that the amplification of *Mycoplasma* with increasing *G. andersoni* proportions is caused by the associated reduction in the proportions of *G. floweri* and *G. gerbillus*, who clear the infection faster than *G. andersoni* hosts (Garrido, Halle, et al., 2021). In contrast, the dilution effect of the vector-borne pathogen, *Bartonella*, is probably caused by a reduction in the vectors on *G. andersoni* hosts (paths H and J in Figure 5), which reproduces better on *G. floweri* hosts (Messika et al., 2017). This evidence for contrasting effects by the same host species has important applied aspects (see below).

To remove annual heterogeneity, the natural experiment was concentrated into two months. However, it provided a cross-sectional view that captured what appears to be the most critical sand heterogeneity type for the host community structure—spatial heterogeneity. Its causal modelling analysis provided a mechanistic explanation by suggesting that the effect of host community structure on pathogen occurrence is mostly indirect. The analyses further highlight *G. andersoni* proportion, total host density, and vector burden as the main mediators of environmental effects on pathogen composition. Importantly, in agreement with our predictions (predictions 2–3 in Table 1), we found that from the above three mediators, the *G. andersoni* proportion—a marker of host community structure—constitutes the main hub for the indirect paths (Figure 5). This finding, together with previous evidence on the widespread and common distribution of *G. andersoni* and the important role that it plays as a prey species, competitor, and host for ectoparasites and pathogens (Abramsky et al., 1994; Hawlena et al., 2006; Kedem et al., 2014; Zaitzove-Raz et al., 2020), suggests that *G. andersoni* plays a key role in structuring sandy ecosystem communities.

The network of connections offered by our best models highlighted additional hypotheses that should be experimentally verified. These include candidate mediators between community structure and *Bartonella* occurrence that were not predicted due to the opportunistic nature of these bacteria (Table 1) and would not have been revealed by traditional approaches. Importantly, our findings complement previous studies on animals and plants that highlight the important role that the vector may play in mediating these processes (e.g., Lacroix et al., 2014). Such insights should also be valuable for management decisions as they support the view that community structure, including multiple hosts and pathogen species, as well as arthropod vectors, should be considered when assessing local disease risk (Halliday et al., 2017).

## 4.3 | Cascading effect: from climatic and anthropogenic processes to pathogen occurrence

Our study highlights the importance of considering multiple pathogens and exploring the network of interactions between ecological mediators when studying complex processes in disease ecology and other interdisciplinary fields. From an applied perspective, the results caution that while a further intensification of anthropogenic land use in the studied sand dunes, such as agriculture, may decrease one

pathogen (*Bartonella*) through a decreasing vector burden, it may simultaneously increase a coexisting pathogen (*Mycoplasma*) through the cascading effects of increased biocrust and susceptible hosts.

From a basic science perspective, our study illustrates the potential of causal analysis to propose mechanistic explanations. In disease ecology, disentangling the mechanisms that mediate diversity–disease relationships is a timely endeavour (Halliday & Rohr, 2019; Rohr et al., 2020), and our path analyses, complemented by other correlative and experimental data (Garrido, Halle, et al., 2021; Messika et al., 2017), improved our mechanistic understanding of dilution by resistant hosts and amplification mediated by vectors in natural communities. Other global processes, such as climate change, biodiversity loss, latitude gradients in biotic interactions, and afforestation or deforestation, can affect pathogen occurrence (Dillon & Meentemeyer, 2019; Halliday, Rohr, et al., 2020; Liu et al., 2020), and a causal modelling approach is likely to provide new insights into them as well.

The global and local processes that are proposed by our results, as well as by other studies (e.g., Halliday, Heckman, et al., 2020; Titcomb et al., 2017; Young et al., 2014), indicate that in nature, cascading effects leading to changes in pathogen occurrence may be the rule rather than the exception. We have provided an example in which climatic and anthropogenic processes may together constitute a catalyst for a trophic cascade, resulting in variability among blood-associated pathogen communities. Similar lines of evidence suggest that El Niño-driven precipitation was the initial catalyst of a trophic cascade, which raised the risk for human hantavirus (Yates et al., 2002). These studies demonstrate that cascading effects may cross scales, emphasizing the need to study multiscale processes simultaneously.

## ACKNOWLEDGMENTS

We thank A. Tsairi, E. Maze, E. Marcus, D. Bereza, A. Lewin, T. Paz, and J. Erin for their valuable advice during the analysis phase of the study. We are grateful to R. Rabinovich and E. Maze for access to the museum collections and GIS layers.

## Author CONTRIBUTIONS

S.H., M.G., A.K., Y.Z., and H.H. designed the research; S.H., I.M., H.K., C.C., K.N., Z.S., A.K., Y.Z., Z.A., G.S., and H.H. performed the research; M.G., S.H., K.N., K.Y., and H.H. analysed the data; and H.H. wrote the paper.

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## BIOSKETCHES

**Snir Halle, Mario Garrido, Irit Messika, Hadar Kedem, and Carmit Cohen** were all students in the Hawlena group, which studies the complex interactions between hosts, vectors, and pathogens in natural communities. **Klil Noy and Koren Ytzhak** were students in the Karnieli group, which studies different aspects of remote sensing, with an emphasis on arid environments. **Zvika Abramsky, Georgy Shenbrot, Zehava Siegal, and Yaron Ziv** are interested in different aspects of rodent ecology, including community ecology (ZA), biogeography (GS), and macroecology (ZS and YZ).

## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

**How to cite this article:** Halle, S., Garrido M., Noy K., Messika I., Kedem H., Cohen C., Ytzhak K., Siegal Z., Shenbrot G., Abramsky Z., Ziv Y., Karnieli A., & Hawlena H. (2021). Cascading effects of sand stabilization on pathogen communities: Connecting global and local processes. *Global Ecology and Biogeography*, 00, 1–18. <https://doi.org/10.1111/geb.13423>