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There is little evidence that spicy food in hot countries is an adaptation to reducing infection risk

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Spicier food in hot countries has been explained in terms of natural selection on human cultures, with spices with antimicrobial effects considered to be an adaptation to increased risk of foodborne infection. However, correlations between culture and environment are difficult to interpret, because many cultural traits are inherited together from shared ancestors, neighbouring cultures are exposed to similar conditions, and many cultural and environmental variables show strong covariation. Here, using a global dataset of 33,750 recipes from 70 cuisines containing 93 different spices, we demonstrate that variation in spice use is not explained by temperature and that spice use cannot be accounted for by diversity of cultures, plants, crops or naturally occurring spices. Patterns of spice use are not consistent with an infection-mitigation mechanism, but are part of a broader association between spice, health, and poverty. This study highlights the challenges inherent in interpreting patterns of human cultural variation in terms of evolutionary pressures.

Human culture evolves, but it is not always clear which aspects of culture have been shaped by selection on benefits to survival and reproduction. Cuisine is a notable aspect of cultural variation that is flexible in response to both dietary need and available ingredients, and diet has an obvious impact on survival and success. We might therefore expect cuisine to have been shaped by selection, as appropriate use of foods (whether consciously or unconsciously) could increase the chances of people surviving and thriving. Since optimal diet might vary between environments, such a mechanism could generate variation in cuisine between cultures. The use of spices provides a key case study in 'Darwinian gastronomy'[1], or the adaptive benefit of culturally inherited food preferences. Rather than providing direct nutritional benefits, spices may act as antimicrobial agents, reducing the risk of foodborne illness. It has been suggested that cuisines from hot regions use more spices to counteract the greater risk of food spoilage[1,2]. One of the key pieces of evidence supporting this hypothesis is a positive correlation between spice use and average temperature[1] (Fig. 1).

The search for evolutionary explanations of human cultural diversity is as old as evolutionary theory, but it has always been problematic[3]: relatedness between cultures can generate patterns of association that can be misinterpreted as a functional relationship when they may be driven simply by shared inheritance of suites of causally unconnected traits. Shared features due to inheritance violate the assumptions of statistical tests because related cultures tend to be similar in many respects, causing many aspects of culture to be correlated even if they are not directly connected. This common statistical problem, known as Galton's problem or phylogenetic non-independence[4,5], was acknowledged in previous studies of adaptive cuisine, but the authors lacked suitable means of correction[1,2].

In this Article, we make three important advances in testing the adaptive cuisine hypothesis for spice use. First, we assemble a global dataset of recipe data for cuisines recorded for a wide range of national, sub-national and super-national areas (Table 1), along with environmental and socioeconomic data associated with each cuisine. Second, we use analytical techniques developed in macroevolutionary biology to account for statistical non-independence due to shared ancestry and proximity[6,7]. Third, we use statistical analyses to explicitly compare the explanatory power of different hypotheses for higher spice use, considering infection risk mitigation, shared history, proximity, socioeconomic factors, cultural diversity and botanical and agricultural diversity. Our approach consists of a series of tests, each designed to probe a possible explanation for the observed relationship between spice use, temperature and infection risk.

Results

The goal of this study is to investigate whether the geographic pattern of use of spices is consistent with adaptive evolution of cuisine in response to variation in risk of foodborne infection. This hypothesis has been supported by a correlation between the average number of spices per recipe and temperature[1,2,8], and between the use of spices and historical disease prevalence[9]. However, previous studies did not account for similarities in cuisines due to spatial proximity (because nearby cultures are subject to similar environmental conditions) or relatedness (because related cultures tend to have similar cuisines as well as similar environments), nor did they evaluate the degree to which the significant correlations reported were driven by covariation between environmental and socioeconomic factors. We used a series of tests to explicitly model the effect of relatedness, proximity and covariation on the association between spice and infection risk. Each test asks whether spice use is related to a particular environmental or socioeconomic variable, and if it is, whether that relationship might be explained by covariation with another relevant variable. In this way, we evaluate the explanatory power of each variable in a stepwise manner, rather than including all possible variables in a single multivariate analysis. Below and in Table 2, we summarize our analyses step by step, with all tests described in Supplementary Data 1. All results explicitly demonstrated model autocorrelation due to spatial proximity and relatedness.

Spice use is correlated with average temperature (Fig. 1). However, we demonstrate that this relationship is largely an indirect result of

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Fig. 1 | Spice and temperature. Mean spice use per recipe is correlated with average temperature, but this is driven largely by geographic clustering. Neighbouring cuisines tend to have both similar spice use and similar temperatures. When spatial and phylogenetic non-independence is taken into account, there is no significant association between temperature and spice use in the combined dataset ($t_{68} = 0.45$, $P = 0.658$), supported by a Bayes factor of 6.6, suggesting that temperature does not predict spice use above and beyond association through relatedness and proximity of cultures. DACH refers to Austria, Germany and Switzerland. Details of the cuisines are provided in the Supplementary Information.

closely related and nearby cultures experiencing similar temperatures and also having similar patterns of spice use, rather than a direct connection between spice and temperature. In our dataset (45 cuisines, variables estimated directly from available recipe data; "Total" in Table 1), autocorrelation due to proximity and relatedness of cuisines accounts for 53% of variation in mean spice use. If this autocorrelation is taken into account, there is no significant relationship between mean spice use per recipe and temperature (regression coefficient (β) = 0.03, $t_{43} = 0.20$, $p = 0.844$). We found that the data supported the null model (no association between temperature and spice) over the alternative model (spice is related to temperature) with a Bayes factor for the null result (BF_{null}) of 5.9. Similarly, spice use

is correlated with historical pathogen load (Supplementary Data 1), but the association is not supported after accounting for autocorrelation, given the marginal p value and low Bayes factor ($\beta = 0.35$, $t_{43} = 1.99$, $p = 0.053$, $BF_{null} = 2.6$). The evidence for lack of direct associations between spice, temperature and historical pathogen load is even stronger in the combined dataset (70 cuisines, including data[2] from Billing and Sherman; "Combined" in Table 1; Supplementary Data 1) and is not due to low statistical power. We demonstrate that the analysis on both datasets provided sufficient power (>0.8) to detect any effect on mean spice use with $\beta \geq 0.15$ (that is, equivalent to one s.d. change in the independent variable leading to more than 0.15×s.d. in mean spice use: Supplementary Fig. 1).

Table 1 | Recipe datasets included in this study, including the original data used in a previous study of adaptive cuisine[2] and data from four published recipe datasets[3-5]

	Dataset	Cuisines	Recipes	Spices	Source
1	B&S	38	4,578	41	ref. [2]
2	Global	10	18,868	62	ref. [37]
3	China	19	8,498	54	ref. [35]
4	India	8	2,761	45	ref. [34]
5	Japan	8	825	19	ref. [8]
6	Total	45	31,108	93	refs. [2-5]
7	Combined	70	33,750	93	refs. [1-5]

"Total" refers to the combination of datasets 2, 3, 4, and 5. The "combined" dataset consists of unique cuisines in datasets 1–5 (using data from 2–5 for any cuisine present in both B&S and the other datasets; numbering is according to Table 1). Further details are provided in the Methods and Supplementary Information.

However, for the adaptive cuisine hypothesis, temperature is a proxy measure for the proposed causal factor, which is risk of infection from contaminated food[2,9,10] (Fig. 2). Mean spice use is associated with incidence of foodborne illness, averaged at regional level[11] ($\beta = 0.43$, $t_{43} = 2.78$, $p = 0.008$; $BF_{null} = 3.7$), even when autocorrelation is accounted for. However, the evidence for the relationship between spice use and foodborne illness is substantially weaker for the combined dataset of 70 cuisines ($\beta = 0.23$, $t_{68} = 2.27$, $p = 0.027$, $BF = 0.9$). Given that most of the relationships between spice use and other factors are weaker for the combined data, we report statistics for our data (Table 1); statistics for the same tests conducted on the combined dataset (our data plus data from ref. [2]) are available in the Supplementary Information and in Supplementary Data 1. Similarly, we report tests for mean spice per recipe, but we include results for median spice per recipe in the Supplementary Information. All results reported here explicitly model autocorrelation due to relatedness and proximity.

Can we interpret the association between foodborne illness and average number of spices per recipe as evidence for the adaptive cuisine hypothesis that more spices are added for their antimicrobial properties in areas where risks of foodborne infection are greatest? Mean spice also correlates with incidence of diarrhoea from all causes in young children ($\beta = 0.41$, $t_{40} = 2.20$, $p = 0.034$) and the evidence for this correlation ($BF = 1.4$) is stronger than for foodborne illness ($BF = 0.9$). However, this variable measures a specific health outcome—reported diarrhoea for children under the age of 23 months—regardless of the cause, which may include foodborne infection, environmental contamination or contact-based infections[12]. Similarly, spice use has been reported to be associated with historical pathogen load[9], which includes diseases transmitted by vectors, contact and environment rather than through food (although we find little evidence of a significant relationship between spice and historical pathogen load in this analysis). This points to a potential problem when seeking correlations between cultural variables (such as spice use), health outcomes (such as foodborne illness) and environment (such as temperature or pathogen prevalence). Poor health outcomes tend to correlate together on a global scale, such that areas with a high risk of foodborne infection also have a high risk of infection from vectors, contact and environment (Fig. 2).

In fact, other indicators of poor health outcomes provide a better prediction of spice use than foodborne illness or other infectious diseases. Life expectancy, which reflects poor health outcomes not only from infectious disease but also non-infectious diseases such as lung cancer, poverty-related illness such as malnutrition, and traumatic deaths including war and accidents, is associated with spice use ($\beta = -0.31$, $t_{43} = -2.90$, $p = 0.006$, $BF = 1.0$). Poor health outcomes

that are associated with low socioeconomic development but not connected to infection risk are also associated with patterns of spice use. For example, road traffic deaths per capita predict mean spice use significantly better than foodborne illness does at the country level ($BF = 3.6$) and predict mean spice use as well as foodborne illness does in the combined dataset ($BF = 1.0$). The association between spice and a range of poor health outcomes suggests that the relationship might not be entirely due to risk of infection.

Patterns of poor health outcomes have strong geographic and socioeconomic patterns[13,14]. Given that cultural factors can also show marked geographic and socioeconomic patterns, this raises the possibility that many different measures of poor health outcome, including foodborne disease and childhood diarrhoea, will be indirectly associated with patterns in cultural variables, including aspects of cuisine[4]. Indicators of socioeconomic development provide a link between many different aspects of human culture, population and health. For example, gross domestic product per capita (GDPpc), a general indicator of relative poverty, predicts mean spice use as well as foodborne illness does ($BF = 1.8$; Fig. 3). There is some support for GDPpc having greater predictive power for variation in mean spice use than foodborne infection: adding GDPpc to a model with foodborne illness significantly increases model fit to mean spice use for our dataset ($LR = 4.33$, $p = 0.037$; $BF = 1.7$). By contrast, adding foodborne illness does not increase the fit of a model of GDPpc predicting mean spice use ($LR = 3.31$, $p = 0.069$; $BF = 1.0$). This result is not due to the coarse resolution of the foodborne illness variable measured at regional level, because after reducing the resolution of GDPpc to regional level, GDPpc is still a significantly better predictor of mean spice use than foodborne illness ($BF = 2.7$) and adding foodborne illness does not significantly increase the fit of a model of GDPpc predicting mean spice use ($LR = 0.32$, $p = 0.569$; $BF = 0.4$). These results suggest that foodborne infection has little additional explanatory power for spice use above its association with poverty in general.

Why is spice use associated with poor health outcomes and poverty? One possible explanation is through poor diet or low food availability. Prevalence of malnutrition (as reflected in rates of child stunting) is significantly associated with mean spice use ($\beta = 0.40$, $t_{43} = 2.86$, $p = 0.007$, $BF = 3.3$) and, unlike foodborne illness, adding GDPpc to a model with malnutrition does not significantly increase model fit to mean spice use ($LR = 1.42$, $p = 0.20$; $BF = 0.7$). Another possible explanation is that places where spices grow naturally were the target of European colonial occupation and exploitation. This pattern of aggressive resource capitalisation in the 'Spice Islands' by predominantly Dutch, English, Spanish and Portuguese traders resulted in an increase in wealth in the European countries but may have come at the expense of wealth accumulation in the source countries for spices (represented in our dataset by Indonesia and Malaysia). However, the association between spice use and GDPpc is still significant after removing cuisines associated with the spice trade, both the colonizers and the colonized ($\beta = -0.39$, $t_{41} = -4.13$, $p < 0.001$, $BF = 11.8$), so the pattern of colonial exploitation association with the spice trade cannot provide a general explanation for the negative relationship between GDP and spice use. Furthermore, the relationship between spice use and GDPpc holds for a dataset consisting only of cuisines from areas that were never under colonial rule ($\beta = -0.39$, $t_{31} = -3.07$, $p = 0.004$, $BF = 5.7$), so patterns of colonization seem unlikely to provide a general explanation of the association between spice use and poverty.

Whatever its cause, the association between spice use and GDPpc generates the potential for many indirect associations with other cultural and environmental variables. GDP is a broad-brush measure of economic development and it has strong geographic patterning, thus GDP is expected to correlate with other variables that show similar spatial patterns, even in the absence of any direct causal connection. For example, GDP has a latitudinal gradient[15] (Fig. 2,

Table 2 | Summary of main results corresponding to links in Fig. 2

Link	Response	Predictors	t	d.f.	LR	BF
1	Mean spice use	Temperature	0.20	43		0.2
3	Mean spice use	Foodborne illness	**2.78**	43		**3.7**
	Mean spice use	Childhood diarrhoea	**2.20**	40		**1.4**
	Mean spice use	Historical pathogen	1.99	43		0.4
	Spice in meat vs non-meat dishes	Foodborne illness	−1.51	40		0.7
	Alcohol and vinegar	Foodborne illness	−1.23	43		0.4
	Chilli	Foodborne illness	−0.94	43		0.2
	Mean spice use	Life expectancy	**−2.90**	43		**1.0**
	Mean spice use	Road traffic deaths	1.26	33		0.3
	Mean spice use	Malnutrition	**2.86**	43		**3.3**
	Mean spice use	GDPpc	**−3.50**	43		**6.6**
	Mean spice use	Foodborne illness			3.31	1.0
		+ GDPpc			**4.33**	**1.7**
6	Mean spice use	Latitude	−1.76	43		0.8
	Mean spice use	Foodborne illness			3.80	**1.3**
		+ Latitude			0.10	0.3
11	Mean spice use	Population density	−1.59	43		0.3
	Mean spice use	Cuisine area	1.35	43		0.2
	Mean spice use	Language diversity	0.80	43		0.2
12	Mean ingredients	Population density	−1.46	43		0.2
	Mean ingredients	Cuisine area	**2.03**	43		0.5
	Mean ingredients	Language diversity	−0.47	43		0.1
13	Mean spice use	Vertebrate diversity	0.17	43		0.1
	Mean spice use	Plant diversity	−0.11	43		0.2
	Mean spice use	Crop diversity	−0.53	43		0.2
	Mean spice use	Spice diversity	−0.31	43		0.2
15	Mean ingredients	Vertebrate diversity	−1.16	43		0.2
	Mean ingredients	Plant diversity	−0.83	43		0.2
	Mean ingredients	Crop diversity	−1.04	43		0.2
	Mean ingredients	Spice diversity	1.01	43		0.2
16	Mean spice use	Mean ingredients	**7.86**	43		**>10⁷**

For each link, a regression is first done for each predictor within each category of variables, and the t statistic, degrees of freedom (d.f.) and Bayes factor against the null hypothesis (BF) are reported. A predictor has significant effect on the response variable if its t statistic is significant at a 0.05 significance level (in bold) and its BF value is larger than 1 (in bold). If any predictor has significant effect, then a likelihood ratio (LR) test is performed to test if the predictor in the indirect link gives significant predictive power to mean spice use above and beyond foodborne illness. This is done by comparing the likelihood of a model with foodborne illness and the significant predictor in the indirect link and the likelihood of a model with only foodborne illness. Similarly, we also test whether foodborne illness gives significant predictive power to mean spice use above and beyond the predictor in the indirect link. This is done by comparing the likelihood of a model with foodborne illness and the predictor and the likelihood of a model with only the predictor in the indirect link. Significant results are indicated by LR and BF values in bold: all reported analyses account for non-independence due to proximity and relatedness (Methods). GDPpc, gross domestic product per capita.

link 4), and so GDP will tend to correlate with other variables that show a latitudinal gradient, including a range of health outcomes such as hip fractures[16,17], blood infections[18], breast cancer[19], multiple sclerosis[20], traffic accidents[21] and risk of infectious disease[22] (link 5). The latitudinal gradient in infection risk offers a possible explanation for the association between spice and foodborne illness. After accounting for latitude, we find that foodborne illness no longer has significant association with spice use: adding foodborne illness to a model with latitude does not significantly increase model fit to mean spice use (LR = 3.80, $p = 0.051$; BF = 1.3). By contrast, adding GDPpc significantly increases the fit of a model of foodborne illness and latitude predicting mean spice use (LR = 4.30, $p = 0.038$; BF = 1.5), suggesting that the extra predictive power of poverty on mean spice above and beyond risk of foodborne infection is not due to covariation of GDP with latitude.

Socioeconomic factors such as GDP correlate with aspects of human population that also show strong spatial patterns, such as population density. Areas of high population density tend to have lower GDP[15] and higher risk of pathogen infection[23] (Fig. 2, links 7 and 8). Population density also varies with climatic variables[4,15] and biodiversity[24] (links 9 and 10), creating potential indirect links between human cultural variation and risk of infection, because the regions that support higher population densities also have greater cultural diversity, as measured by the number of autochthonous languages in an area[7]. If areas with higher cultural diversity use more spices in their cooking (link 11) due to exposure to a greater diversity of local cuisines, then this could drive an indirect link between spices and infection risk via population density (link 8). Since high population density regions also tend to have lower GDP[15] (link 7), population density and cultural diversity could also create a potential
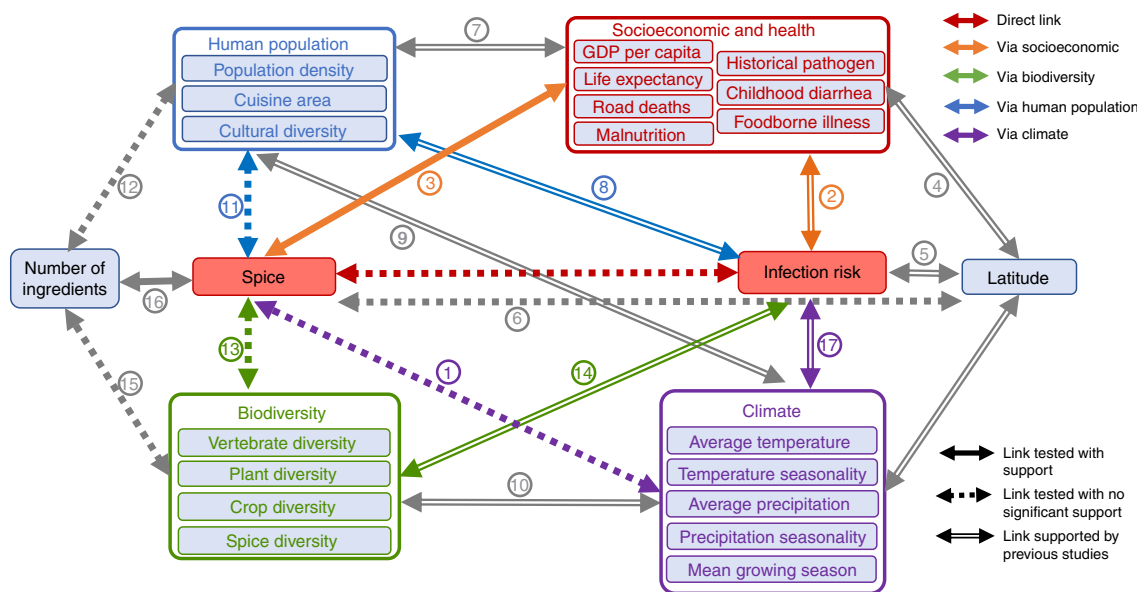
Fig. 2 | Horrendogram of proposed links between spice use and infection risk. Variables are grouped by covariation; for example, it is difficult to separate socioeconomic variables from health outcomes, because they are all functionally interrelated and statistically correlated. The links in this diagram are all discussed in the text and statistical results given in Table 2; all statistical tests reported model autocorrelation due to proximity and relatedness. In summary: (1) spice use is not significantly related to temperature; (2) infection risk correlates with socioeconomic factors, such as GDP[13,14,68]; (3) spice use is related to foodborne illness, has a weak association with childhood diarrhoea, but is not significantly associated with historical pathogen load; spice use is related to life expectancy, malnutrition, road traffic deaths, and GDPpc, and it has a stronger association with GDPpc than infection risk; (4) GDP is associated with latitude[15]; (5) infectious diseases have a latitudinal gradient[22]; (6) spice use is not significantly correlated with latitude; (7) GDP is associated with population density[15]; (8) population density is associated with higher risk of infectious disease[23]; (9) population density varies with climate[4,15]; cultural diversity, as reflected in number of languages, varies with climate[7]; (10) biodiversity varies with climate[24]; (11) cuisine areas with greater cultural diversity do not use more spices per recipe; (12) average number of ingredients per recipe is not significantly associated with cultural diversity, population density or cuisine area; (13) spice use is not associated with biodiversity; (14) infection risk increases with biodiversity[26]; (15) number of ingredients per recipe is not associated with biodiversity; (16) spice use is related to number of ingredients per recipe; and (17) human pathogen diversity varies with climate[22].

indirect link to health outcomes and infection risk. However, we find that cuisine areas that contain more language groups do not have significantly higher mean spice use ($\beta = 0.09$, $t_{43} = 0.80$, $p = 0.427$, $BF_{null} = 5.9$), nor is mean spice use significantly associated with population density ($\beta = 0.09$, $t_{43} = -1.59$, $p = 0.118$, $BF_{null} = 4.0$) or cuisine area ($\beta = 0.09$, $t_{43} = 1.35$, $p = 0.184$, $BF_{null} = 5.4$). The mean number of ingredients per recipe and the total number of spices included in a regional cuisine are also not significantly related to language diversity, population density or area (link 12; Table 2 and Supplementary Data 1).

Spatial patterns of biodiversity provide an alternative indirect link between spice use and infection risk. Higher biodiversity might increase spice use due to the greater diversity of plants available for inclusion in recipes (Fig. 2, link 13). Plant biodiversity shows similar global patterns to bird and mammal diversity, largely due to their covariation with climate[25] (link 10), and diversity of vertebrate hosts increases the risk of infection through zoonotic events and by acting as a reservoir for human diseases[26] (link 14). Biodiversity could also drive an indirect association between spice use and poverty, because GDP is correlated with many aspects of biodiversity[27,28], including pathogen diversity[29] and infectious disease[30]. However, we find no evidence of a significant association between mean spice use and the diversity of plant species or crop plants in the cuisine area (Table 2); nor do we find evidence of association between mean spice per recipe and the number of spices growing within the cuisine area (link 13: $\beta = -0.04$, $t_{43} = -0.31$, $p = 0.757$, $BF_{null} = 6.6$). Mean spice use is not significantly associated with vertebrate diversity (Table 2). Biodiversity could indirectly influence spice use via

overall recipe complexity, if biodiverse regions have a greater range of available ingredients. While recipes with more ingredients tend to include more spices (link 16: $\beta = 0.83$, $t_{43} = 7.86$, $p < 0.001$), there is no evidence of a connection between any measures of biodiversity and the number of ingredients per recipe (Table 2, link 15), nor is there a link with the total number of spices used in a cuisine (Supplementary Data 1). Although biodiversity is correlated with climatic variation, we find that none of the climatic variables that are known to have significant association with biodiversity and cultural diversity—including temperature seasonality, average precipitation, precipitation seasonality and mean growing season[7]—are significantly associated with mean spice use, mean number of ingredients per recipe or the total number of spices included in a cuisine (Fig. 2, link 1 and Supplementary Data 1).

When we trace the possible links in Fig. 2, taking only those paths that have significant support from these data or from previous studies, the only solid connections between spice and infection risk run via general indicators of health and poverty. Of these, indicators of poverty and poor health outcome, including GDP and road traffic deaths, provide equally strong (and, in some datasets, stronger) explanatory power for variation in spice use than indicators of risk of infection, including foodborne infection, early childhood diarrhoea and historical disease prevalence. However, the covariation between socioeconomic and cultural parameters makes it difficult to ascertain the causes of the patterns with any great certainty. We can never include all relevant cultural, socioeconomic or environmental variables, so we cannot be certain that observed correlations between variables are not an indirect result of covariation
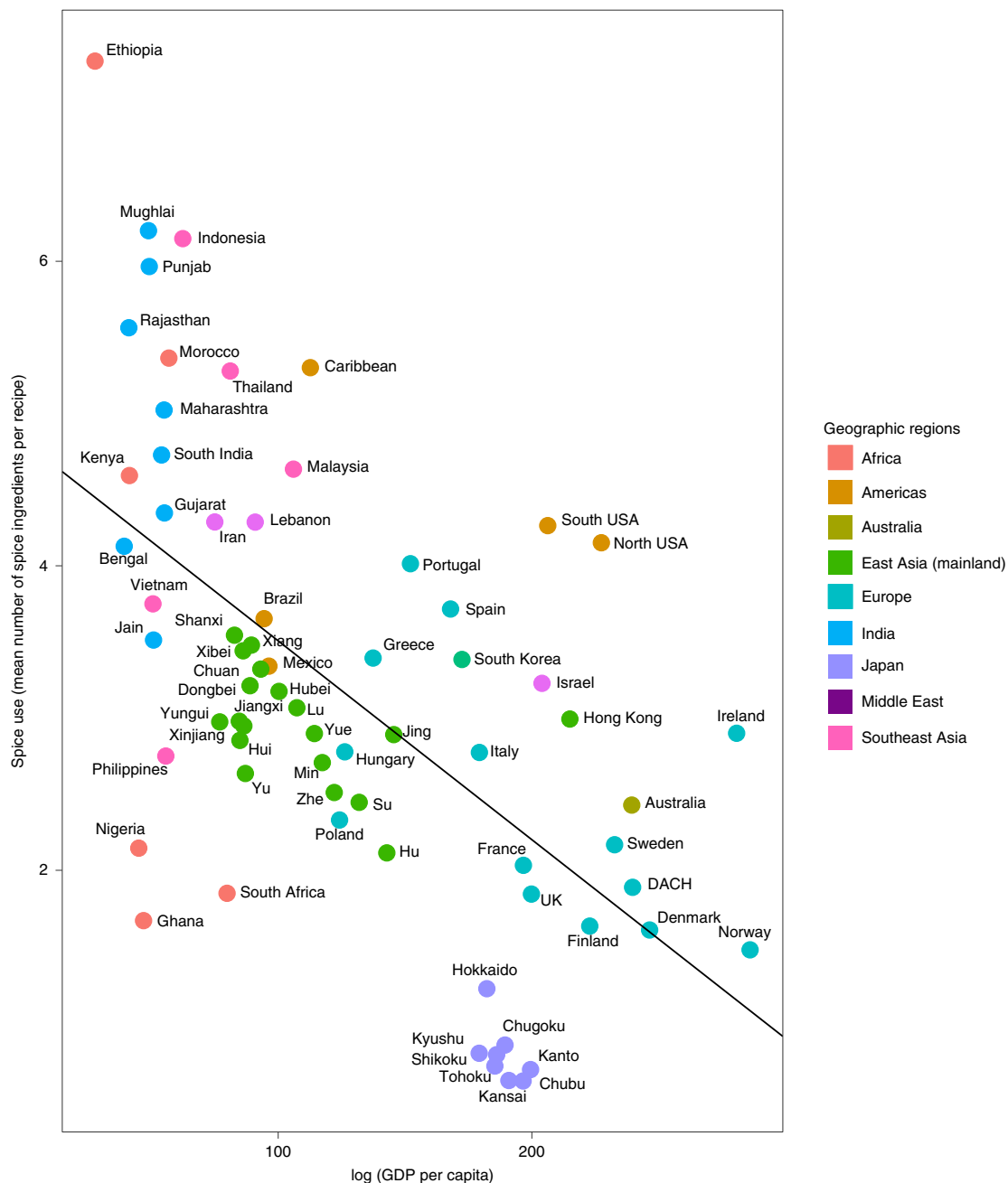
Fig. 3 | Spice and GDP. Mean spice use per recipe is significantly associated with GDP per capita of the cuisine area ($t_{68} = -2.73$, $p = 0.008$, Bayes factor = 3.6) in the combined dataset, after accounting for spatial and phylogenetic non-independence.

with an unmeasured quantity. Even though road traffic deaths are often a better predictor of spice use than infectious disease, we do not expect there to be a direct causal relationship between traffic accidents and spice use. Instead, it seems likely that we could find additional socioeconomic or cultural variables that provide even stronger correlation with spice use, but if we attempted to include all relevant cultural and socioeconomic parameters, the number of variables would eventually outnumber the number of cuisines, increasing the risk of spurious correlations.

As a way of cutting through the jungle of entangled variables that covary with culture, history and geography, we can test three additional predictions of the adaptive cuisine hypothesis that are at least potentially independent of the association between spice use and poverty: (1) higher spice use should be associated with foods

with greater risk of foodborne illness, such as meat-based dishes[8,10]; (2) spices that show greater antimicrobial effects that survive cooking, such as chilli, should show the strongest relationship with infection risk[2,10]; and (3) greater infection risk should also promote inclusion of other antimicrobial ingredients in cuisines, such as vinegar and alcohol[8].

Mean spice use in recipes containing meat or seafood is significantly higher than in recipes with no meat-based ingredients ($t_{40} = 6.51$, $p < 0.001$). However, vegetarian cuisines that contain no meat recipes do not have lower average spice levels than cuisines containing meat ($t_{44} = -0.68$, $p = 0.502$), and areas with higher incidence of foodborne disease do not have a larger difference in spice use between meat and non-meat recipes ($t_{39} = -1.51$, $p = 0.138$). The higher spice use in meat recipes may reflect greater recipe
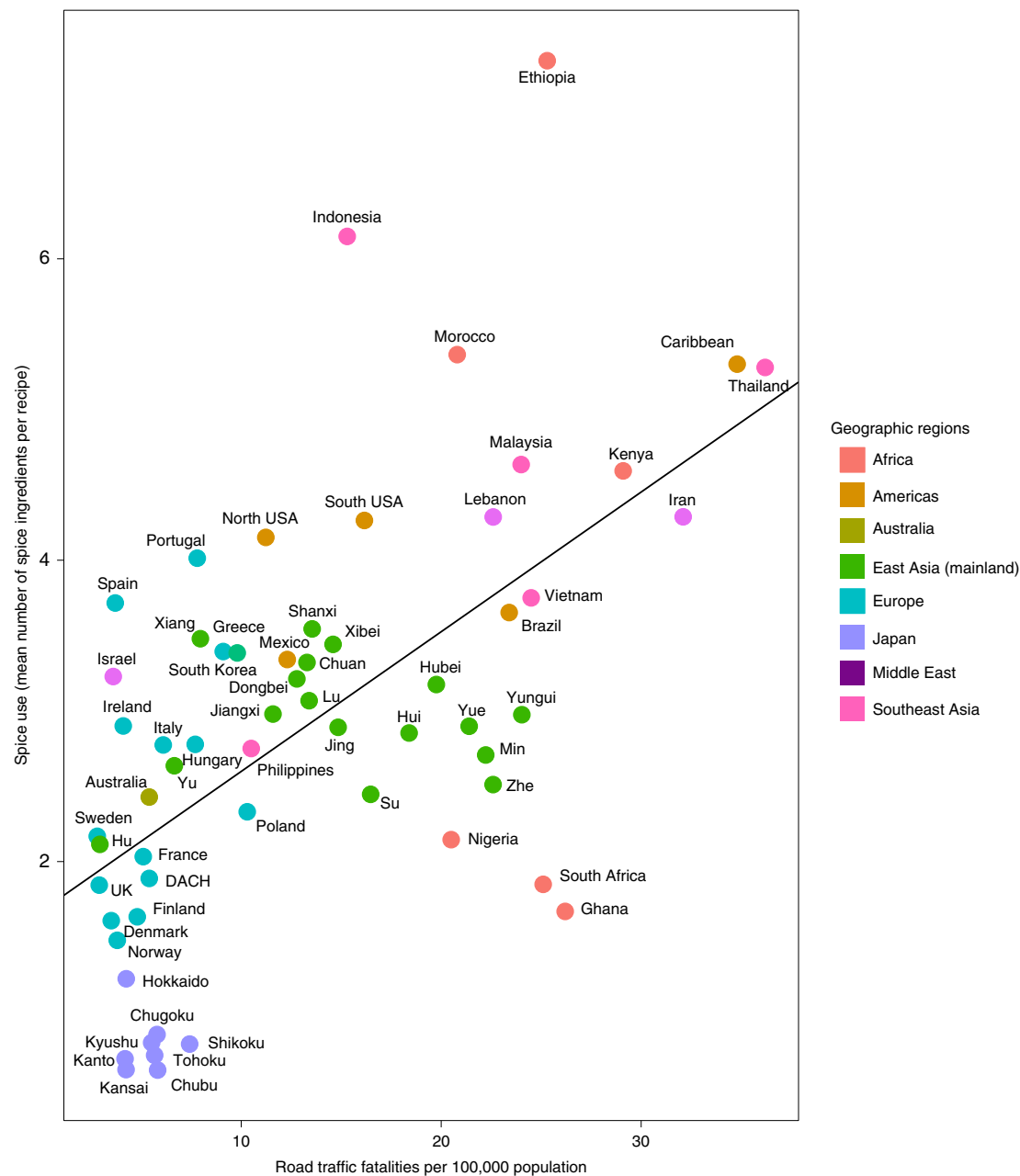
Fig. 4 | Spice and traffic accidents. Mean spice use is related to poor health outcomes that are not attributable to infection, such as road traffic fatalities per 100,000 population (from World Health Organization Global Health Observatory data repository, 2013 figures). Road deaths predict mean spice use as well as foodborne illness in the combined dataset (BF = 1.0), taking into account non-independence due to proximity and relatedness.

complexity, since meat recipes tend to have more ingredients ($t_{40} = 4.97$, p < 0.001), and number of ingredients correlates with number of spices (Fig. 2, link 16). However, the number of ingredients does not fully explain the difference in mean spices in meat-containing recipes compared with non-meat recipes (LR = 4.65, p < 0.031; BF = 10.2).

Using chillies as a test case, we find no evidence for the prediction that highly antimicrobial spices should show stronger association with infection risk. Incidence of foodborne illness is not significantly associated either with inclusion of all *Capsicum*-derived ingredients ($t_{43} = -0.52$, p = 0.604) or hot chillies ($t_{43} = -0.94$, p = 0.353). Similarly, inclusion of vinegar is not significantly associated with prevalence of foodborne illness ($t_{43} = 1.31$, p = 0.196). Alcohol is also not significantly associated with foodborne illness, whether we analyse all alcoholic ingredients ($t_{43} = -0.48$, p = 0.633) or alcohol

excluding beer ($t_{43} = -0.50$, p = 0.619). In case the regional incidence of foodborne illness is not fine-grained enough to pick up these relationships, we also tested the three predictions using cuisine-level socioeconomic variables that show a correlation with risk of foodborne infection, but we get the same results: difference in spice use between meat and non-meat recipes, inclusion of chilli or vinegar, or alcohol use are not significantly associated with life expectancy (Supplementary Data 1).

Discussion
In summary, we find that, contrary to the predictions of the adaptive cuisine hypothesis, patterns of spice use are better predicted using socioeconomic variables that reflect global patterns of poverty and health outcomes than by temperature or risk of infection. There is also no evidence that the use of other ingredients with antimicrobial

Table 3 | List of spices counted in this study

Spice	B&S	China	India	Japan	Global	Notes
Ajwain	−	−	+	−	−	Carom, fruit of *Trachyspermum ammi*
Allspice	+	+	−	−	+	Dried berries of *Pimenta dioica*
Amaranth	−	+	−	−	+	Leaves or seeds of *Amaranthus*
Amchoor	−	−	+	−	−	Dried unripe mango, *Mangifera*
Anise	+	+	+	−	+	Aniseed, *Pimpinella anisum*
Anjelica	−	−	−	−	+	Leaves or roots of *Angelica archangelica*
Artemisia	−	+	−	−	−	Wormwood, *Artemisia annua*
Asafoetida	−	−	+	−	−	Hing powder, dried gum of *Ferula*
Basil	+	−	+	−	+	Leaves of *Ocimum*
Bay	+	+	+	−	+	Leaves of *Laurus nobilis*
Camphor	−	+	+	−	−	Substance from *Cinnamomum camphora*
Capers	+	−	−	−	+	Pickled fruit or flowers of *Capparis spinosa*
Capsicum	+	+	+	−	−	Bell peppers, *Capsicum annum* or *Capsicum grossum*
Caraway	+	−	+	−	+	Fruits of *Carum carvi*
Cardamom	+	+	+	−	+	Seeds of *Elleteria* or *Amomum*
Celery	+	+	−	−	+	Seeds, stalks or leaves of *Apium graveolens*
Chilli	+	+	+	+	+	Small spicy *Capsicum*, including cayenne
Chamomile	−	−	−	−	+	Flower of *Chamaemelum nobile*
Chervil	−	−	−	−	+	Leaves of *Anthriscus cerefolium*
Chrysantheum	−	+	−	+	−	Flower of *Chrysantheum* sp.
Cinnamon	+	+	+	−	+	Bark of *Cinnamomum*
Citrus	+	+	+	+	+	All citrus including juice, peel, oil or extract
Cloves	+	+	+	−	+	Flowers of *Syzygium aromaticum*
Coriander	+	+	+	−	+	Leaves, seeds or roots of *Coriandrum sativum*
Cumin	+	+	+	−	+	Seeds of *Cuminum cyminum*
Curry leaf	−	−	+	−	+	Leaves of *Murraya koenigii*
Dill	+	−	+	−	+	Leaves or seeds of *Anethum graveolens*
Drumstick leaves	−	−	+	−	−	Leaves of *Moringa oleifera*
Epazote	−	−	−	−	+	Leaves of *Levisticum officinale*
Fennel	+	+	+	−	+	Seeds of *Foeniculum vulgare*
Fenugreek	+	+	+	−	+	Seeds and leaves of *Trigonella foenum-graecum*
Fuki	−	−	−	+	−	Giant butterbur, *Petasites japonicus*
Galangal	+	+	−	−	−	Laos, root of *Alpina*
Garlic	+	+	+	−	+	Roots and shoots of *Allium sativum*
Garcinia indica	−	−	+	−	−	Kokum, dried fruit of *Garcinia indica*
Gardenia	−	−	−	+	−	Seed of *Gardenia augusta* or *Gardenia jasminoides*
Ginger	+	+	+	+	+	Root of *Zingiber officinale*
Hemp	−	+	−	+	−	Seed or oil of *Cannabis sativa*
Horseradish	+	+	−	−	+	Root of *Armoracia rusticana*
Hyssop	−	−	−	−	+	Leaves or oil extract from *Hyssopus officinalis*
Japanese horseradish	−	+	−	−	+	Wasabi, *Eutrema* (*Wasabia*) *japonica*
Japanese parsley	−	−	−	+	−	Leaves of *Oenanthe javanica*
Japanese pepper	−	+	−	+	−	Sansho, *Zanthoxylum piperitum*
Juniper	+	−	−	−	−	Berries of *Juniperus*
Lavender	−	+	−	−	−	Flowers of *Lavandula*
Lemon balm	−	−	−	−	+	Leaves of *Melissa officinalis*
Lemon verbena	−	−	−	−	+	Leaves of *Lippia citriodora*
Lemongrass	+	+	+	−	+	Leaves or oil of *Cymbopogon*

Table 3 | List of spices counted in this study (continued)

Spice	B&S	China	India	Japan	Global	Notes
Licorice	−	+	−	−	−	Root of *Glycyrrhiza glabra* or *Glycyrrhiza uralensis*
Lilium	−	+	−	+	−	Bulb or root of *Lilium*
Long pepper	−	+	−	−	−	Fruit of *Piper longum*
Lovage	−	−	−	−	+	Seeds or leaves of *Levisticum officinale*
Marjoram	+	−	−	−	+	Leaves of *Origanum majorana*
Mastic	−	−	−	−	+	Resin of *Pistacia lentiscus*
Mate	−	−	−	−	+	Leaves of *Ilex paraguariensis*
Mexican oregano	−	−	−	−	+	Leaves of *Lippia graveolens*
Mint	+	+	+	−	+	Leaves of *Mentha*
Myoga	−	−	−	+	−	Japanese ginger, *Zingiber mioga*
Mitsuba	−	−	−	+	−	Leaves of *Cryptotaenia*
Mountain pepper	−	+	−	−	−	Fruit of *Lindera glauca*
Mustard	+	+	+	+	+	Seeds or oil of *Brassica alba*, *Brassica juncea* or *Brassica nigra*
Nigella	−	−	+	−	−	Seeds of *Nigella sativa*
Nutmeg	+	+	+	−	+	Fruit of *Myristica fragrans* including mace
Onion	+	+	+	+	+	*Allium*: includes chives, leeks, shallots
Oregano	+	−	+	−	+	Leaves of *Origanum vulgare*
Paprika	+	+	−	−	+	Dried, powdered *Capsicum annum*
Parsley	+	+	−	−	+	Leaves of *Petroselinum crispum*
Peony	−	+	−	−	−	Root of *Paeonia* (paeonol)
Pepper	+	+	+	−	+	Black and white pepper, *Piper nigrum*
Peppermint	−	−	−	−	+	Leaves of *Mentha piperita*
Perilla	−	+	−	+	−	*Perilla frutescens var. crispa*
Poppy	−	−	+	−	+	Seeds of *Papaver somniferum*
Pomegranate	−	−	+	−	+	Including anaardana (dried pomegranate seeds)
Radish	−	+	+	+	+	Roots of *Raphanus*, including daikon (*Raphanus sativus*), mu (*Raphanus raphanistrum*)
Rose	−	+	+	−	+	Extract from flowers or buds of *Rosa indica*
Rosemary	+	+	−	−	+	Leaves of *Rosmarinus officinalis*
Sage	+	+	−	−	+	Leaves of *Salvia officinalis*
Saffron	−	−	+	−	+	Flower of *Crocus sativus*
Sandalwood	−	−	+	−	−	Extract from wood of *Santalum* sp.
Savory	+	−	−	−	+	Leaves of *Satureja*
Seaweed	−	+	−	+	+	Includes kelp, nori, carageenen
Sesame	+	+	+	+	+	Seeds and oil from *Sesamum indicum*
Sichuan pepper	−	+	−	−	−	*Zanthoxylum simulans* or *Zanthoxylum bungeanum*
Star anise	−	+	+	−	+	*Illicium verum*
Tamarind	+	+	+	−	+	Fruit of *Tamarindus indica*
Tarragon	+	−	−	−	+	Leaves of *Artemisia dracunculus*
Tea	−	+	+	−	+	Leaves or oil of *Camellia sinensis*
Thyme	+	−	−	−	+	Leaves of *Thymus*
Toon	−	+	−	−	−	Chunya, *Toona sinensis*
Tumeric	+	+	+	+	+	Root of *Curcuma longa*
Vanilla	−	+	+	−	+	Fruit, oil or extract of *Vanilla*
Vetiver	−	−	+	−	−	Extract or oil from *Chrysopogon zizanioides*
Wild tumeric	−	+	−	−	−	Root of *Curcuma aromatica*

We began by including all of the ingredients categorized as 'spice' in ref. [2], then added other ingredients that meet the definition of spice in other cuisines. The five sources of recipe data are described in Table 1, and how spices were defined and counted are described in Methods and Supplementary Information.
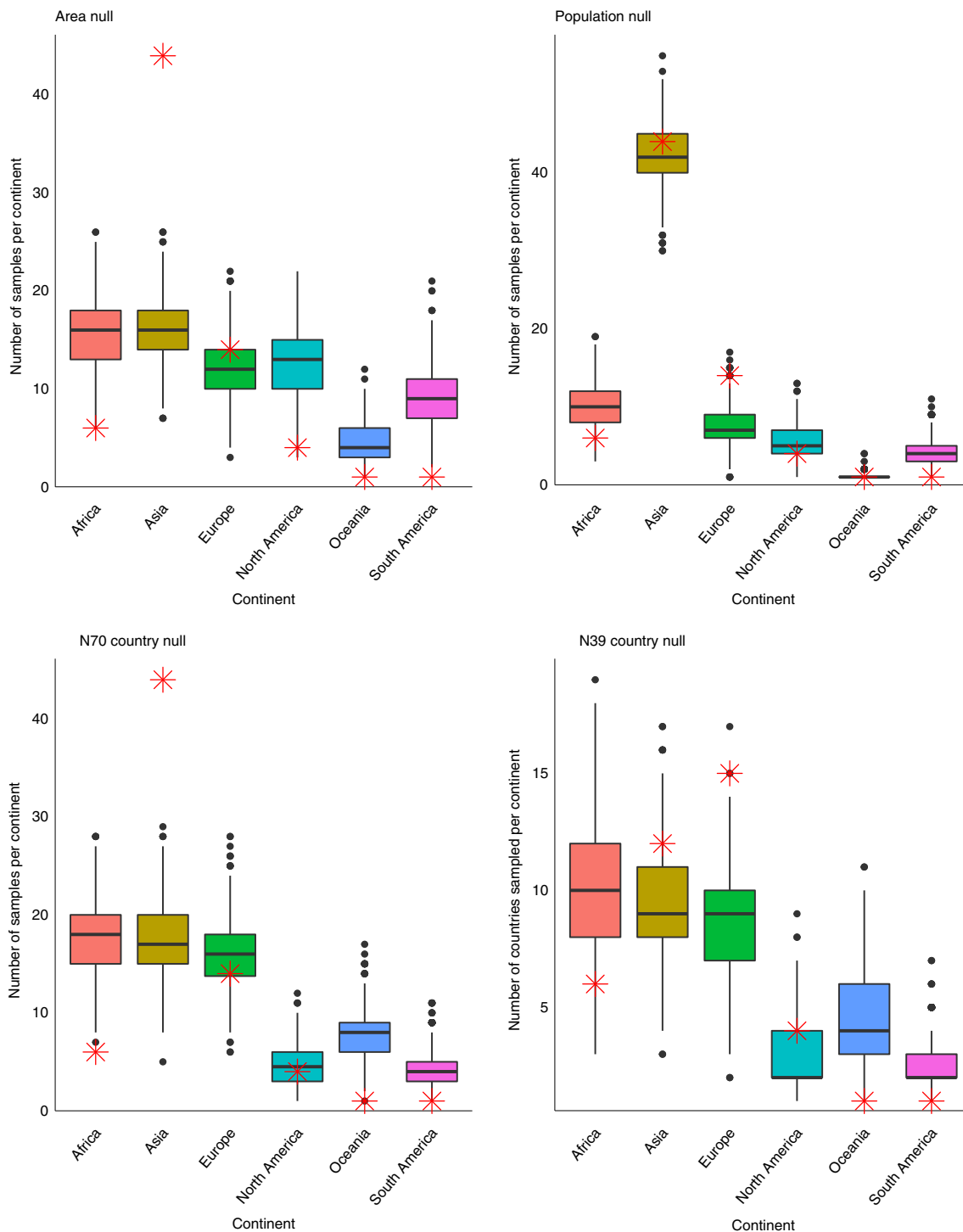
Fig. 5 | Geographic sampling bias. To detect sampling bias in our global cuisine database, we compared the distribution of our data across continents with four different null models to determine whether our observations were more biased toward some regions than would be expected from a random sample of world cuisines. For the first three null models, we sampled 70 countries with replacement (to match our combined dataset) in proportion to their total geographic area (area null), in proportion to their population size (population null) or in equal proportion across all countries (N70 country null). We then tallied these sampled points by continent. For the fourth null model, we sampled 39 countries (matching our country-level dataset) without replacement in equal proportion and then tallied by continent (N39 country null). This plot shows the distribution of expected samples per continent if sampling is unbiased. For each plot, a red star marks the value for our database for comparison. The central line in each box is the median value, the box edges are the 25th and 75th percent quartiles, the lines extend to 1.5 times the interquartile range, and dots represent outlying points beyond that range.

properties, such as vinegar, alcohol or chilli, is associated with risk of infection from foodborne pathogens or with health outcomes in general. While meat dishes have more spices on average than non-meat dishes, this pattern does not seem to be influenced by the incidence of foodborne illness or poor health outcomes. There are no convincing paths of association connecting spice to temperature

or infection risk via patterns of biodiversity (spice use is not higher where more spices grow), via cultural diversity (more culturally diverse areas do not use more spices) or via climate (Fig. 2).

These results do not suggest that poverty causes higher spice use, just as they do not suggest that car accidents increase spice use (Fig. 4). Instead, they demonstrate that correlations between aspects of human cultural groups that show distinct spatial and historical patterns, such as infection risk and spice use, should be interpreted with caution. Correlates of poverty that are not associated with infection (such as malnutrition and road deaths) are equally good predictors of spice use as variables that reflect infection risk (foodborne illness, early childhood diarrhoea and historical disease prevalence). There is also a lack of evidence that other potential antimicrobial ingredients, including chilli, alcohol and vinegar, are associated with risk of infection. These results demonstrate that there is currently no compelling evidence to assign a special explanatory role to risk of infection in variation in the spiciness of cuisines, above and beyond any other socioeconomic indicators. Spice use has a stronger association with GDP and poor health outcomes from a range of causes. The correlation between infection risk and spice appears to be an indirect effect of relatively higher spice use in regions with traditionally lower socioeconomic indicators. It is not possible to isolate a cause of this association from these cross-cultural data, but this pattern should allow researchers to generate additional explanatory hypotheses and collect appropriate variables to test them.

Socioeconomic factors are highly labile, for example, many countries have shown rapid increases in GDP and improvement in general health outcomes within the past few decades, so it may be argued that they are the wrong targets for investigating the role of evolutionary forces that may have shaped cultural variation over centuries or millennia. However, cuisine is also highly labile, and spice use responds rapidly to changing fashions, availability and economics[31]. Commonly used spices are often products of fluctuating global trade patterns, and many are relatively recent additions to many contemporary cuisines. For example, the widespread use of chilli in global cuisines (Table 3) postdates patterns of global conquest and trade that spread the domesticated chilli from its origins in Mexico[32,33]. Indeed, the economic power of spices is in part driven by their transportability, being typically able to be stored for long periods, and sold in relatively small quantities for high value. The transportability of spices may explain why we find no association between the diversity of spices growing within the cuisine area and the mean spice per recipe: spices are often used far from where they are grown. Associations between spice use, temperature and pathogen load have been noted both for contemporary recipes taken from internet databases and traditional recipes from cookbooks or interviews[1,8,34,35], and many of these include spices that are a relative recent addition to the cuisine. If the observed associations between spice use and pathogen load are due to the role of spices in mitigating infection risk[9], spice use must reflect an ongoing response to levels of threat, not simply historical inertia. Furthermore, foodborne illness continues to apply strong mortality pressure on modern cultures[11]. If spice use is under selection for infection risk mitigation, then the lability of culture and cuisine should allow a nimble response to adjust levels of spice use in response to infection threat.

Like many global studies of cultural evolution, our study is biased by the available data[36]. Previous tests of the hypothesis that spicy food is a response to higher temperature have either focussed on a single region (such as China[35] or Japan[8]), or used a global dataset that contained an overrepresentation of recipes from European cuisines (for example 30% of the cuisines from Europe, even though it represents only 10% of the world's population[2]). We have greatly expanded global representation: in particular, our dataset is less biased toward European cultures, and the sampling of cuisines from mainland Asia is more in line with global population (Fig. 5). However, cuisines from Africa and South America are relatively

underrepresented in our combined database. We hope future studies will fill in these large gaps, and provide more detailed sampling in underrepresented regions.

Spicier food tends to be found in hotter countries (Fig. 1), but analysis of variation in global cuisines does not provide support for the hypothesis that spice use patterns represent cultural adaptation to infection risk mitigation. This study has highlighted how an apparently simple question—why do hot countries have spicy food?—is very difficult to answer clearly because of the intertwined nature of cultural, environmental and socioeconomic variables. However, we can use statistical analyses to test the relative strengths of association between variables and we can generate additional predictions that provide independent tests of hypotheses connecting those variables. Here we show that the relationship between temperature and spice use is an artefact of spatial and phylogenetic autocorrelation—that is, the association between temperature and spice is largely driven by similarities between neighbours and relatives, which tend to have both similar cuisines and similar climates, causing an incidental correlation between spiciness of food and the average temperature. When we account for variation between cuisines taking distance and relationships into account, there is no evidence that temperature explains variation in spice use. We demonstrate that spice use and infection risk are related through socioeconomic variables, such as poverty and poor health outcomes, with no convincing evidence that variation in spice use is best explained as a direct association between infection risk and inclusion of antimicrobial ingredients. This conclusion is supported by a lack of relationship between other antimicrobial ingredients and infection risk. The association between temperature and spice use highlights that, as databases grow and studies of cultural evolution undergo a growth in popularity, we need to develop more sophisticated ways to evaluate the relative support for different explanatory hypotheses using comparative analyses, without risking being led astray by incidental cross-cultural correlations.

Methods

Cuisines. We aimed to test whether the relationship between spice use and average temperature supports the hypothesis that higher risk of infection from foodborne pathogens selects for increased spice use[1,2,10]. In addition to analysing the original dataset[2] of Billing and Sherman (1998), we constructed a dataset consisting of cuisines from 31 national, 2 super-national and 37 sub-national regions[2,8,34,35,37] (Table 1). These data provide greater power to test the adaptive cuisine hypothesis, in a number of key ways. First, the expanded dataset has nearly twice as many cuisines, more than double the number of different spices and over six times as many recipes as the original study (Table 1). Second, we increase both the coverage and resolution of the data, with a greater global coverage, including 37 sub-national cuisines. In particular, this allows us to bring a finer level of resolution to India and China, which cover a very large geographic extent, are environmentally heterogeneous and have diverse cuisines, and contain a substantial proportion of the world population (Fig. 5). Third, by using large databases of recipes, we are able to derive a finer level of detail on cuisines, including not only mean spices but also the presence of specific ingredients such as meat-based ingredients, alcohol, vinegar, and chilli. We are also able to control for number of ingredients per recipe as a measure of overall recipe complexity. Fourth, we use the geographic area covered by the cuisine to derive a range of spatial, environmental and socioeconomic variables, and to account for spatial autocorrelation in the data. Fifth, we use inferred relationships between cuisines to account for phylogenetic non-independence in the data.

We analyse three measures of spice use for each cuisine: mean number of spices per recipe, median number of spices per recipe, and the total number of spices used in a cuisine (that is, the list of all spices included in any recipe assigned to that cuisine). Spice does not have an unambiguous definition, but here we take it to mean an ingredient added to a dish in relatively small quantities, primarily for flavour, colour or smell, rather than for bulk, nutrition or pharmaceutical effects. This definition follows Billing and Sherman, but while they only count plant products as spices[2], we extend the category to natural food additives derived from seaweed (Table 3). There are many other spices included in regional cuisines that are not listed in Billing and Sherman[2]. For example, asafoetida (hing powder) was not included in Billing and Sherman[2], but it is used as a spice in many cuisines, and is considered to have antimicrobial properties[38]. Given that the adaptive cuisine hypothesis concerns the antimicrobial effects of spices as food additives, it is important to include relevant region-specific spices in addition to those recorded

in the Billing and Sherman dataset[8,35]. Therefore we expanded the list of spices (Table 3) to include ingredients from the regional cuisines that are added to recipes in relatively small quantities for taste or other properties, as long as we could find published studies suggesting that they had antimicrobial activity (Supplementary Table 1).

Some ingredients could be considered either a vegetable in their own right or as a spice additive. For example, onion and sweet pepper were included in the spice list in Billing and Sherman[2], whether they were used as a flavour additive or a main ingredient, on the grounds that they contribute antimicrobial phytochemicals to the dishes. For the same reason, we include Japanese radish as a spice, because radish can contain antimicrobial compounds, although the amount depends both on the variety of radish and the mode of preparation[8,39]. We also count seaweed, whether used as a main ingredient or as an additive (for example, as included in Japanese seven spice), as it has reported antimicrobial properties and can be used to protect food against spoilage[40–42]. When in doubt as to whether to include an ingredient as a spice or not, we looked for evidence in the scientific literature that the ingredient has antimicrobial or preservative properties (some examples are presented in Supplementary Table 1).

Because the hypothesis being tested is that spices help to protect food from spoilage due to their antimicrobial activities and therefore reduce risk of food poisoning on consumption, we only count those additives that may have an antimicrobial effect on the food itself, not ingredients considered to have pharmaceutical benefits to the consumer of the food. For example, we include amaranth leaf as a spice because, in addition to being been used as a traditional medicine in many cultures, it has been shown to have antimicrobial activity[43,44]. Similarly, we count peony root (paeonol), lily roots (*Lilium brownii*), licorice (*G. glabra* and chinese licorice *G. uralensis*), toon (*Toona sinensis*) and artemisia (*Artemisia annua*) as spices: these are traditional medicines that have also been reported to have broad antimicrobial effect[45–51]. However, we do not include ingredients added as aspects of traditional medicine if there is no additional evidence of antimicrobial effects on foods. For example, while Zhu et al.[35] count fundamental medicinal herbs such as *Rehmannia glutinosa* (地黄) and safflower (*Carthamus tinctorius*; 红花) as spices, they are not included in our list due to lack of documentation of antimicrobial activity, but we do include fundamental herbs that have documented antimicrobial effects such as tea (茶叶) and *Cannabis sativa* (大麻; counted as hemp (Table 3)).

For the purposes of counting spices per recipe, multiple ingredients from the same category in one recipe are counted as a single spice. Following Billing and Sherman[2], we count leeks, chives and onions in a single category (onion). We use single category of spice derived from *Capsicum* species: chilli (including cayenne), capsicum (bell peppers) and paprika, however for the separate analysis of chilli we have two categories, all *Capsicum* and hot chilli only. Garlic sprouts are counted as garlic as they contain some of the key antimicrobial chemicals from garlic[52]. Similarly, we record different varieties of the same spice in the same category: for example, a recipe calling for black, white and green cardamom would have cardamom counted as one spice not three. Following Ohtsubo (2009), we combine all kinds of citrus (including lemon, lime, yuzu and orange peel) into a single category[8]. Sesame oil is counted as sesame[53]. In general, we grouped together spices that are closely related and have the same active chemical components. Black and white pepper are both from *Piper nigrum*, and so are counted as a single category, but different pepper species are counted as separate categories; for example, long pepper (*P. longum*), mountain pepper (*Lindera glauca*), Japanese pepper (*Zanthoxylum piperitum*) and Sichuan pepper (*Z. simulans* and *Z. bungeanum*),

Many recipes call for a premixed blend of spices—for example, curry powders in Indian cuisines and cooking sauces in Chinese cuisine—so we record the spices typically included in that mix. Supplementary Table 2 lists the spice mixes recorded in any of the recipes included in our analyses. The precise ingredients for each spice mix may vary between households or between commercially available powders and sauces, but we aimed to include the spices typically associated with each mix. For example, a typical garam masala spice mix might contain eight spices (coriander seeds, cumin seeds, cardamom seeds, peppercorns, fennel seeds, mustard seeds, cloves and red chillies), but the number and type of spices might vary between particular blends.

The relationship between temperature and spice has been suggested to apply more strongly to meat-based dishes than to vegetable dishes[10], so where possible we have recorded spices for both meat and vegetable recipes separately. For this purpose, seafood, meat-based soups and stocks are counted as meat. Four of the regional Indian cuisines are vegetarian so have no meat recipes listed.

Following Ohtsubu[8] and Zhu et al.[35], we record the use of vinegar and alcohol in recipes because it is proposed to have antimicrobial benefits in food preparation[54]. Although salt also has food preservative properties, it has not been included as a spice in previous studies[2,8,35], and is not consistently recorded in the recipe databases, so cannot be included in this analysis.

Where possible, we used all listed ingredients from each recipe (including both spice and non-spice ingredients) to calculate the average number of ingredients per recipe, and the total for the cuisine. This was not possible for the Billing and Sherman data[2], for which only average values for spice are provided, nor for the Ohtsubo data[8], which records only general categories of ingredients such as 'vegetable'. However, for the Chinese, Indian and global (CulinaryDB) databases,

we had lists of all ingredients for each recipe (Table 1). We removed any obvious duplicates—for example, if several different kinds of chicken meat were included in a recipe, we counted it once as 'chicken'. We also excluded items listed in the ingredients that were not foods, such as paper. We excluded a small number of Chinese ingredients that did not have a clear translation into English. The number of ingredients may therefore contain some errors but given the size of the databases for which we have ingredient lists (28,347 recipes), we think that the mean number of ingredients per recipe will give an approximate indication of recipe complexity.

Autocorrelation between cuisines. We need to identify cuisines with a defined area on the global map in order to correct for spatial autocorrelation in the analysis and to estimate climate, biodiversity and population data. This does not need to be a perfect representation of the spatial location of different cuisines: we expect that in reality cuisines will not have hard borders, will overlap in space and may change location over time. But an approximate location allows some correction for spatial proximity and provides a way of estimating environmental data for each cuisine. For country-level data, R polygons describing the national borders were retrieved from the R package rworldmap[55,56]. For sub-national regions, we used the Global Administrative Areas database[57] to produce a map file that can be read in R. We record the area of each cuisine based on these distributions (in m²). Once each cuisine was represented by a map polygon, we used an equal area projection and the gCentroid function in R (RGeos package[58]) to produce a geographic midpoint for each of these polygons and record the latitude and longitude of this midpoint. The association between each cuisine and a map area allows us to calculate a number of variables that represent environmental factors of those regions. Clearly, for cuisines with a large geographical extent, we expect that the average environmental data will not be an accurate representation of conditions in every part of that area, instead it will be a reflection of the typical conditions the cuisine is found in. Most published studies identifying environmental or biological correlates of cuisine have used average temperature for a country or region to represent the climate, even for countries with a wide range of climatic variability such as Australia[2]. Details of cuisine areas definitions and environmental variables are given in the Supplementary Information.

To correct for covariation due to the relatedness of cultures, we need a way to express the expected level of similarity between cuisines due to common descent. For the purposes of this analysis, we use a hierarchical classification of the dominant language for each region to give an indication of likely patterns of cultural similarity (details in the Supplementary Information). This classification does not represent an evolutionary history, as we do not expect cultural histories to exactly follow a bifurcating pattern of diversification and divergence, nor do we expect dominant language to be a perfect representation of the patterns of relatedness among cuisines (for example, in some cases this approach may group cuisines that have related dominant languages through shared colonial history). However, the requirement for phylogenetic correction in cross-cultural comparisons does not depend on having a perfect representation of these patterns of covariation: any information we can provide on covariation due to historical relationships is better than using no information on relatedness at all[5,21,59–62]. We test the robustness of our conclusions to assumptions made about relationships between cuisines by conducting analyses on an alternative classification (see Supplementary Information).

Infection risk. We include data from the World Health Organization on foodborne illness, which is summarized for 14 world regions[11]: we gave each cuisine the value for the region it is found in. We used the median number of foodborne illnesses per 100,000 people from diarrhoeal disease agents, invasive infectious disease agents, helminths, chemicals and toxins, from the 2010 figures provided in ref. [11]. We include country-specific estimates of the incidence of diarrhoea in children under the age of 2 yr (per 100 children)[12], estimated from household survey data which records all instances of diarrhoea from any cause. We also include a measure of historical pathogen load which has been proposed as a predictor of spice use[9]. Historical disease prevalence (P2_9) is a combined index based on past epidemiological impact of nine human diseases on a normalized averaged scale[9]: leishmanias (transmitted by sandfly bites), schistosomes (infection through skin), trypanosomes (insect bite), leprosy (human contact), malaria (mosquito bite), typhus (lice, fleas, mites and ticks), filariae (mosquito), dengue (mosquito) and tuberculosis (contact)[9]. These diseases are spread by environmental contamination, contact between humans or by vector rather than by contaminated food (though the possibility of foodborne infection cannot be discounted for tuberculosis[63] and some trypanosomes; for example, Chagas disease[64]). Historical pathogen load is available at country level, so we gave sub-national cuisines the value recorded for the whole country.

Climate and biodiversity. We recorded temperature, latitude, precipitation, temperature seasonality, precipitation seasonality, and mean growing season for every cuisine area as well as the biological and cultural diversity of each area (details are in Supplementary Information). Spices are not necessarily used where they grow: in fact, spices have been both a driver and an indicator of global patterns of trade[31]. However, many spices and herbs are used in the area they are grown in, so we aimed to control for the possibility that the relationship between

number of spices and temperature is an indirect result of the biodiversity of a region influencing the variety of ingredients available to be incorporated into recipes. To represent spatial patterns of plant diversity, we estimated the average number of plant species and crop species found per unit area in each region, and used the Global Biodiversity Information Facility to extract occurrence records for each spice plant in Table 3 (details in Supplementary Information).

Socioeconomic and human population variables. Many aspects of culture covary, generating a rich potential for correlations between cultural variables even if they have no direct causal connection[4,21]. Therefore, we included a number of broad-brush socioeconomic measures as a way of detecting and controlling for covariation, including population density, life expectancy and GDPpc. Population density was estimated for cuisine areas, and GDPpc and life expectancy are available for many sub-national regions (See Supplementary Table 1). In addition to analysing this national and sub-national level data, we generated regional level averages to test whether differences in their predictive power were due to different resolutions. To represent food availability and diet, we estimated rates of child malnutrition for each cuisine area. To represent poor health outcomes that are not connected to disease or malnutrition, we included number of road traffic fatalities per head of population. Cultural diversity within a cuisine area is represented by the number of autochthonous languages found within that area. We also recorded whether each cuisine is in a country that has been a colony. Details of sources of all variables are given in the Supplementary Information.

Statistical analysis. *Modelling autocorrelation.* We used the method of Hua et al.[9], which is based on Freckleton and Jetz[8], to model autocorrelation due to proximity and relationship between cuisines. In brief, the method constrains the residual correlation in spice use as a linear function of their spatial proximity and phylogenetic similarity and estimates the overall contribution of autocorrelation to residual correlation and the relative proportion of autocorrelation due to spatial proximity versus phylogenetic similarity, using a maximum likelihood approach. This method allows us to model how much of the similarity between cuisines can be explained by the spatial location and similarity to relatives, so that we can look for evidence of meaningful associations between variables above and beyond the patterns of similarity due to proximity and relatedness[4,65]. Full details of the method are given in the Supplementary Information. The maximum likelihood estimates of the intercept and β are derived by generalized least squares. Some variables are right skewed, so we applied log transformation to each of these variables if transforming the variable increased the maximum likelihood of the model that includes the variable, because increasing likelihood suggests a better fit of residuals in the response variable to a multivariate normal distribution. Transformed variables are named with suffix '_tr' in Supplementary Data 1. All variables were scaled to have mean of zero and variance of one before the analyses, so the value of regression coefficient can be interpreted as the amount of change in standard deviations in the response variable with a 1 s.d. change in the independent variable.

Power analysis. Simulation has been widely applied to assess the power of a generalized least squares analysis[66]. To assess the power of our method, we simulated 1,000 datasets with the same size as the observed dataset and with a specific regression coefficient as effect size. Then, we applied our method with significance level 0.05 to each simulated dataset and estimated the power of the method as the proportion of simulated datasets from which the method detects the effect. For each dataset, we simulated the independent variable from a standard normal distribution, and simulated the residual in response variable from a multivariate normal distribution with covariance matrix fixed to its maximum likelihood estimate from the observed dataset under a regression model including only intercept. The final response variable is the independent variable multiplied by the regression coefficient plus the residual. As a result, the regression coefficient in the simulation is comparable to the regression coefficient estimated from the observed dataset (Supplementary Fig. 1).

Model comparisons. We applied likelihood ratio tests and Bayes factors to test if adding an independent variable to a model significantly increased the model fit. Bayes factor for the null result (the absence of a relationship) is calculated as the marginal likelihood of the null model (without the relationship) over the alternative model (with the relationship). Conversely, Bayes factor for the presence of a relationship is calculated as the marginal likelihood of the alternative model over the null model.

A significant likelihood ratio test with level 0.05 and a Bayes factor larger than 1 were considered evidence that the addition of the independent variable increases model fit, with Bayes factor larger than 3 suggesting strong evidence. This was used to test if spice use is significantly associated with an independent variable or if the link between spice use and foodborne illness can be fully explained by their covariation with a third variable. For example, if adding foodborne illness to a model including a measure of poverty significantly increases the model fit, then we conclude that the link between spice use and foodborne illness cannot be fully explained by their covariation with the measure of poverty. To avoid numerically evaluating the Bayes factor, we used multivariate normal inverse gamma distribution as the conjugate prior for regression coefficients and residual

variance[67] and analytically derived the marginal likelihood of a model conditional on the best fit correlation structure in the model (Supplementary Information).

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability
This study uses only previously published data and all published sources are given in the Methods and Supplementary Information (Table 1). All variables analysed are provided in Supplementary Tables 4 and 5.

Code availability
All code used is available by request.

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Acknowledgements

Author contributions
A.S., H.S., L.B. and R.D. collected data, X.H. and A.S. analysed the data and L.B. wrote the paper. All authors designed the analysis, interpreted results and approved the manuscript.

Competing interests
The authors declare no competing interests.

Additional information
Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41562-020-01039-8.

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Peer review information Nature Human Behaviour thanks Ranier Gutierrez, Caitlyn Placek and Roland Sookias for their contribution to the peer review of this work. Primary Handling Editor: Charlotte Payne.

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Software and code

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Data collection	None
Data analysis	Ushey, K., Allaire, J. J. & Tang, Y. reticulate: Interface to 'Python'. R package version 1.14. https://cran.r-project.org/package=reticulate. (2019).; Zizka, A. et al. CoordinateCleaner: Standardized cleaning of occurrence records from biological collection databases. Methods in Ecology and Evolution 10, 744-751 (2019); rgeos: Interface to Geometry Engine - Open Source (GEOS) v. 0.3-21 (R package, 2016). Vavrek, M. J. fossil: palaeoecological and palaeogeographical analysis tools. Palaeontologia Electronica 14:1T (2011).

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