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Equilibrium dynamics of European pre-industrial populations: the evidence of carrying capacity in human agricultural societies

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Human populations tend to grow steadily, because of the ability of people to make innovations, and thus overcome and extend the limits imposed by natural resources. It is therefore questionable whether traditional concepts of population ecology, including environmental carrying capacity, can be applied to human societies. The existence of carrying capacity cannot be simply inferred from population time-series, but it can be indicated by the tendency of populations to return to a previous state after a disturbance. So far only indirect evidence at a coarse-grained scale has indicated the historical existence of human carrying capacity. We analysed unique historical population data on 88 settlements before and after the Thirty Years War (1618–1648), one the longest and most destructive conflicts in European history, which reduced the population of Central Europe by 30–50%. The recovery rate of individual settlements after the war was positively correlated with the extent of the disturbance, so that the population size of the settlements after a period of regeneration was similar to the pre-war situation, indicating an equilibrium population size (i.e. carrying capacity). The carrying capacity of individual settlements was positively determined mostly by the fertility of the soil and the area of the cadastre, and negatively by the number of other settlements in the surroundings. Pre-industrial human population sizes were thus probably controlled by negative density dependence mediated by soil fertility, which could not increase due to limited agricultural technologies.

1. Introduction

One of the fundamental principles of population ecology is negative density-dependence (i.e. population regulation via a negative feedback between population density and growth rate) [1]. Such a feedback implies that there is some level of population density above which the population growth rate is negative. We call this level the carrying capacity, and the population density is assumed to oscillate around this stable equilibrium. However, population time-series often reveal long-term trends, either decreasing or increasing. This can be interpreted either as a trajectory from a state which is far from the equilibrium towards an as yet unreached equilibrium, or, alternatively, as a continuous change in the carrying capacity itself. The latter interpretation is the most conventional in the case of human population dynamics. It is mostly assumed that people are able to overcome limitations imposed by the environment. In this way, they continually increase the carrying capacity, potentially even above the level reached by the population at any particular moment. This interpretation would imply that the carrying capacity may never actually be reached in human populations, making the very concept problematic. However, it is possible that this ability characterizes modern civilization with its advanced technologies, while pre-industrial human populations may have been relatively stable due to density-dependent effects. Human populations may therefore have been controlled by negative density dependence mediated by the environment for most of the history of mankind.

While the issue of human carrying capacity has been widely discussed in recent decades, especially in the context of the potential carrying capacity of the planet (e.g. [2–5]), there is surprisingly little evidence of its existence during human history. Most studies have either been purely theoretical, or have studied historical population changes at very coarse scales (e.g. [6,7]). There is some indirect evidence of population limitation in pre-industrial human populations: population densities of hunter–gatherers, for example, correlate well with environmental net primary productivity [8], indicating resource limitation, and human population size increased very slowly before the modern period [9] (rapid changes of human population has been reported even in the distant history, but such events occurred only occasionally [10,11]). However, these lines of evidence do not reveal whether human population dynamics did indeed have a tendency to approach stable equilibrium. Density-dependent equilibrium dynamics is characterized by the relationship between the deviation from the equilibrium population size (carrying capacity) and the change in the population growth rate. A proper demonstration of population regulation via negative density dependence should therefore include a disturbance effect that arguably moves the population out of equilibrium, and a recovery which leads back to the equilibrium density. Data of this kind are difficult to obtain, compromising our ability to reveal equilibrium density-dependent dynamics, and thus the existence of carrying capacity, in human populations.

There are a few cases that can be considered to provide evidence in this matter. At the beginning of the fifteenth century, the population of the Czech lands was reduced by the Hussite Wars (1419–1434). Since that time, the population has been growing, but at the end of the sixteenth century several famines occurred [12]. Historians have interpreted this situation as the achievement of the country's production potential (i.e. the carrying capacity) after a long period of population growth [12]. Similarly, about 100 million people died due to famines, epidemics, wars and riots in China in the eighteenth and nineteenth centuries [6]. Lee [6] has suggested that all the unrests and famines were primarily caused by overpopulation in combination with the little ice age—the population growth was faster than the growth of agricultural yields, so the *per capita* food availability decreased severely. After the famines and wars erupted, many people died, lowering the population pressure, and the situation stabilized [6]. A decrease in population size due to a disturbance and a subsequent return to the previous population level was also inferred on the basis of a simulation model of human population dynamics during the last glacial maximum (30–13 kyr BP) in Europe [13]. However, all the cases mentioned above represent *post hoc* interpretations of observed population crises. Equilibrium population dynamics has never been tested in a proper quantitative way, demonstrating that negative density dependence really led to population stabilization.

Here we use a unique historical dataset comprising population count data from 1618 to 1757 that include the Thirty Years War (1618–1648), a major disturbance in European history [14]. The war affected different settlements in central Europe differently, sometimes extirpating almost all the inhabitants directly or indirectly (due to destruction of food reserves, subsequent starvation and the spread of disease [12,15–17]), while sometimes there was only a negligible effect on population size [18]. We thus have a unique opportunity to explore quantitatively the recovery dynamics of individual settlements (figure 1) after this extensive disturbance event, and to assess which factors determined settlement population sizes. If equilibrium population size is determined by the environmental carrying capacity of a given settlement, we should expect the following three patterns: (i) the rate of recovery should be positively related to the extent of the disturbance, i.e. to the distance from the assumed equilibrium; (ii) the population size of the settlements after regeneration should be similar to the pre-war population size, and should not depend on the extent of the disturbance; (iii) the equilibrium population size of settlements should be positively related to the area of land managed by each settlement and to the soil fertility, and negatively to the number of neighbouring settlements that share the land.

2. Material and methods

(a) Data collection

Eighty-eight villages were selected within the historical borders of Bohemia [19] in the present-day Czech Republic, using geodata from the ArcČR 500 database [20]. The selection was based on a random placement of 90 points (using the random points tool in QGIS software), which were set at least 10 km apart to reduce repetition of the same attribute sets in neighbouring settlements. This requirement resulted in a relatively even spatial distribution of the tested villages in the study area (figure 1). To each of the 90 points we assigned the nearest village from the CZ RETRO database [24], which was recorded in the Tax Register of 1654 [21,22]. Two points were excluded from the dataset, as there was no village within a distance of 5 km. These steps were processed in QGIS 2.4.0, QGIS 2.6.0, QGIS 2.8.1 [25], GRASS GIS 7.0.0RC2 [26] and ArcGIS 10.2 [27].

The data for the analysis of the population dynamics were collected using two editions of historical documents, which recorded the numbers of farmers (= the numbers of farms = population size) in villages. The period immediately after the Thirty Years War is documented by the Tax Register from 1654 [21,22], while the Theresian Cadastre captures the situation in 1757, more than a hundred years after the war [28,29]. The Tax Register lists the numbers of 'abandoned' farms (which were destroyed or abandoned during the Thirty Years War). These abandoned farms were added to the number of farmers in 1654 to yield the number of farmers before the war (in 1618). In this way, we established the numbers of farmers/farms in each village in ca. 1618 (before the war), in 1654 (just after the war), and in 1757 (after the regeneration period). Additional time points were not available, as no other comparative data for the whole country were recorded until the end of eighteenth century (we checked the 'Tax Register Revisitation' from the

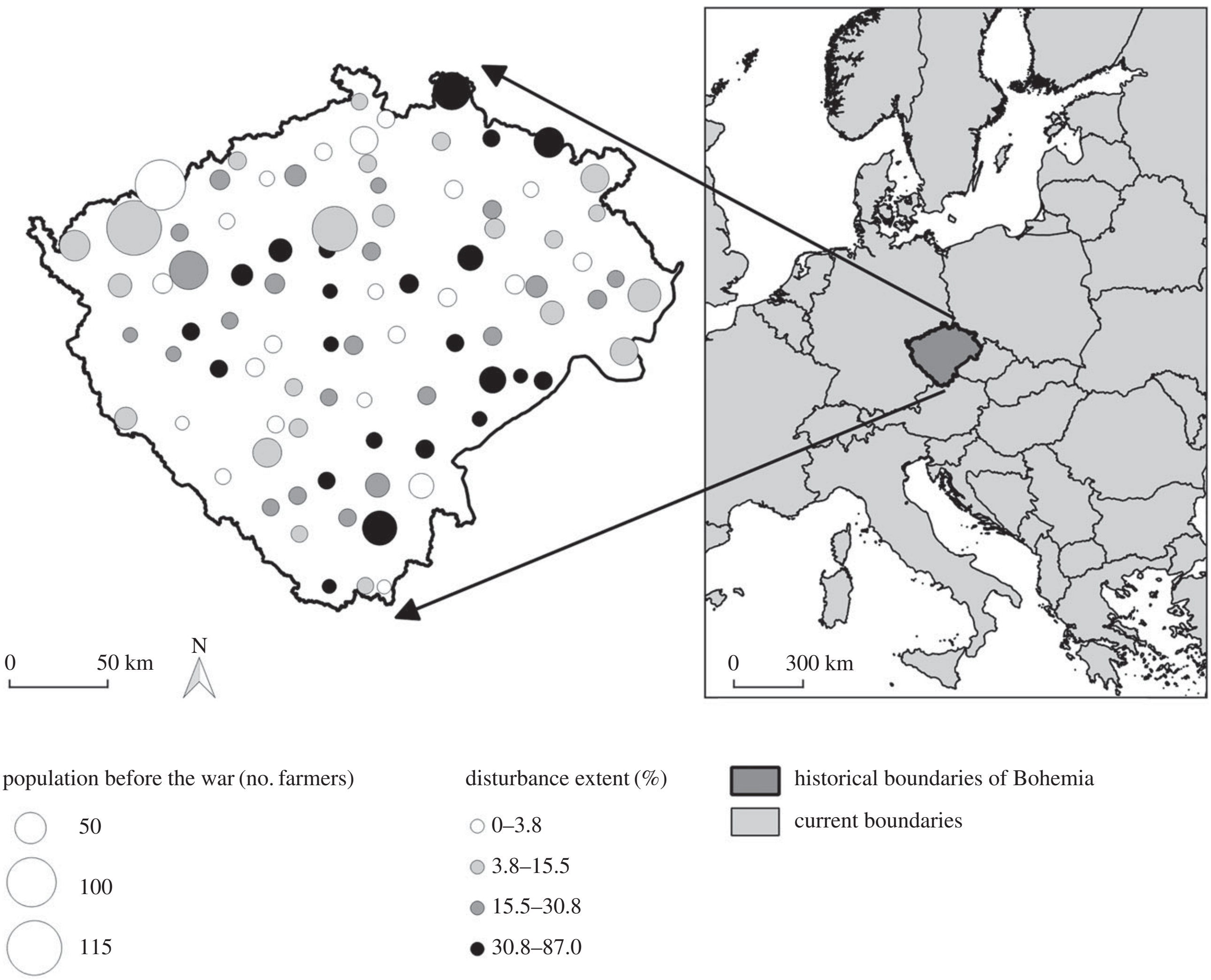

Figure 1. Position of Bohemia within Europe, the villages selected for analysis, with denoted pre-war population size and extent of disturbance. Data sources: [19–23].

1670s [30], but it covers approximately just one-third of selected villages). The Theresian Cadastre from 1757 is the only source of data covering the whole country between the end of Thirty Years War and the beginning of the Industrial Revolution.

Village characteristics were taken from several sources. The age of the settlement (referred to as *settlement age* in all tables and figures) was retrieved from the Historical Lexicon of Municipalities [31]. In the case of abandoned villages, which were not listed in this lexicon, the age was established from the database of local names in the Czech territory [32–34]. The settlement density in 1618 (*settlement density before war*) was calculated as the number of neighbouring villages within a radius of 4 km from the village. This is justified by contemporary ethnographic observations: in traditional agricultural central and eastern European societies, the majority of cultivated agricultural land is usually located within 2 km (a 30-minute walk) from the village [35]. As we were interested in the interaction with neighbouring villages, we multiplied this distance by two. The settlement density was calculated using the ArcČR 500 database [20]. The calculation included only villages actually existing in 1618 (their founding dates were obtained from the Historical Lexicon of Municipalities [31]). The size of the cadastre (*cadastre size*) was determined from current cadastres listed in the ArcČR 500 database [20]. If the cadastre belonging to the village was later incorporated into a larger unit (e.g. if it later became a part of a military training area) or if a cadastre adjacent to the studied cadastre was established after 1618, we used the size of the cadastre documented in the Stable Cadastre from the first half of the nineteenth century, the oldest available cadastral map [36]. To determine the *density of rivers and streams*, we used the current data from the HEIS database [37]. Subsequently, using the sum line lengths tool in the QGIS program, we calculated the total length of rivers and streams within a radius of 4 km from the centre of the village (as in the case of settlement density). The values describing the undulation of the terrain (*terrain undulation*) were derived from the STRM digital terrain model [38]. Terrain undulation was calculated using the roughness index tool in the QGIS software, which records the differences in elevation per unit area. For each studied settlement, we calculated the average value for a circle 4 km in radius, using the zonal statistics tool in the QGIS. *Altitude* was calculated using data from the STRM digital terrain model [38]. Data for individual villages were recorded in the GRASS GIS program, using the r.what tool. *Soil fertility* was calculated using the database of soil units in the Czech Republic [39]. Each soil unit was assigned a specific natural soil fertility value, expressed relatively as a percentage of the most productive soil unit in the Czech Republic (the values varied between 4.9% and 100%) [40]. The values were calculated as a weighted average of the soil fertility in the cadastre of the village.

With one exception, all cultural variables were derived from editions of historical documents or from historical literature, and they related directly to the time being investigated (table 1). The only exception is the size of the cadastre, which was derived from more recent maps. However, other studies have shown that the cadastre boundaries have not changed significantly over time (e.g. [41]). The analyses of environmental factors used data from current databases and maps. In some factors (density of

Table 1. List of used predictors and settlement characteristics.

variable name	data type	data sources
size of the settlements		
settlement size before war	number of farmers in the village in 1618, i.e. before the Thirty Years' War (no.)	Tax Register of 1654 [21,22]
settlement size after war	number of farmers in the village in 1654 (no.)	Tax Register of 1654 [21,22]
settlement size after regeneration period	number of farmers in the village in 1757 (no.)	Theresian cadastre [28,29]
cultural conditions		
settlement age	date of the first written note in historical documents (year)	historical lexicons [31–34]
settlement density before war	number of settlements within a radius of 4 km from the studied village in 1618 (no.)	geodatabase and historical lexicon [20,31]
cadastre size	size of cadastre (m^2)	geodatabase and historical maps [20,36]
environmental conditions		
density of rivers and streams	total length of rivers and streams within a radius of 4 km from the centre of the studied village (m)	database of rivers and streams [37]
terrain undulation	difference in elevation per unit area (m)	digital terrain model [38]
altitude	altitude (m)	digital terrain model [38]
soil fertility	weighted average of relative natural soil fertility in the cadastre (%)	database of soil units [39,40]

rivers and streams, terrain undulation and altitude), the current state can be assumed to correspond with the state in the first half of the seventeenth century. Because soil fertility could have changed with time, we decided to use a relative comparison, as is commonly used (e.g. in the study of prehistoric settlements [42]).

All data used here are available in the electronic supplementary material, dataset S1. The dataset also contains two additional variables, derived from the indicators of settlement size. *Settlement growth during regeneration period* is defined as the average annual percentage growth between 1654 and 1757, obtained from the post-war settlement size and size after the regeneration period as $100[(\textit{size after regeneration period}/\textit{size after war})^{1/(1757-1654)} - 1]$. *Extent of disturbance* measures the percentage decrease of settlement size between the pre-war and the post-war period, calculated as $100[(\textit{size before war} - \textit{size after war})/\textit{size before war}]$.

(b) Data analysis

All cultural and environmental variables were considered as potential predictors for determining the pre-war size of the settlements as an indicator of carrying capacity. Three predictors (*cadastre size*, *terrain undulation*, *settlement density before war*) exhibited substantial positive skewness; these variables were logarithmically transformed in all analyses. Collinearity among the predictors was assessed using variance inflation factors (VIFs). The maximum VIF was 2.91 (*soil fertility*), way below the usual threshold of 10; nevertheless, to check the robustness of our results, we inserted the variables into regressions in a hierarchical manner.

We applied two different modelling strategies to assess predictor effects. First, we used a nonlinear regression model that directly accounts for the discrete nature of the outcome variable, namely the Poisson count regression. To adjust for overdispersion, we used a Poisson quasi-maximum likelihood (QML) estimator with a robust sandwich estimator of the coefficient covariance matrix [43].

Second, since significant patterns of spatial autocorrelation were detected for both the dependent variable (Geary's $C = 0.953$, $p = 0.004$) and the residuals from (non-spatial) linear regressions ($C = 0.945$, $p = 0.001$ for the most saturated model), we complemented the Poisson regression with a linear model that allowed for spatially autoregressive random errors, known as the spatial error model. In order to both eliminate excessive skewness and make coefficients comparable across the two models, we logarithmically transformed the dependent variable. The spatial weighting matrix was based on Euclidean distances of the villages (obtained from latitude and longitude of the village centre), and we used Pisati's [44] implementation of the ML estimator for the spatial error model.

As the number of observations is rather small, statistical inference is not very reliable and has to be treated with caution. Therefore, we decided to complement traditional analysis of variable significance with a measure called *relative variable importance* (RVI). This measure is recommended by Arnold [45] and based on the ideas of model selection through Akaike's information criterion with small-sample correction (AIC_c). Its calculation was carried out in three steps: (i) we estimated the spatial error model for all possible subsets of the 7 predictor variables, giving us a total of $2^7 - 1 = 127$ different model specifications; (ii) for each model, we calculated the Akaike weight, see e.g. [46]; (iii) for each predictor, RVI was obtained by summing the Akaike weights across all models that included the predictor. Thus, RVI can loosely be interpreted as the probability that the predictor is contained in the most accurate model out of the 127 candidates.

An analogous analysis was carried out to study the determinants of *settlement growth during regeneration period*. Identical explanatory variables we included, with the addition of *extent of disturbance* and *size before war*. Due to the continuous nature of the dependent variable, only the spatial error model was applied.

3. Results and discussion

The regeneration rate of the settlements was positively correlated with the extent of the disturbance—the increase in the population of a settlement (numbers of inhabited farms)

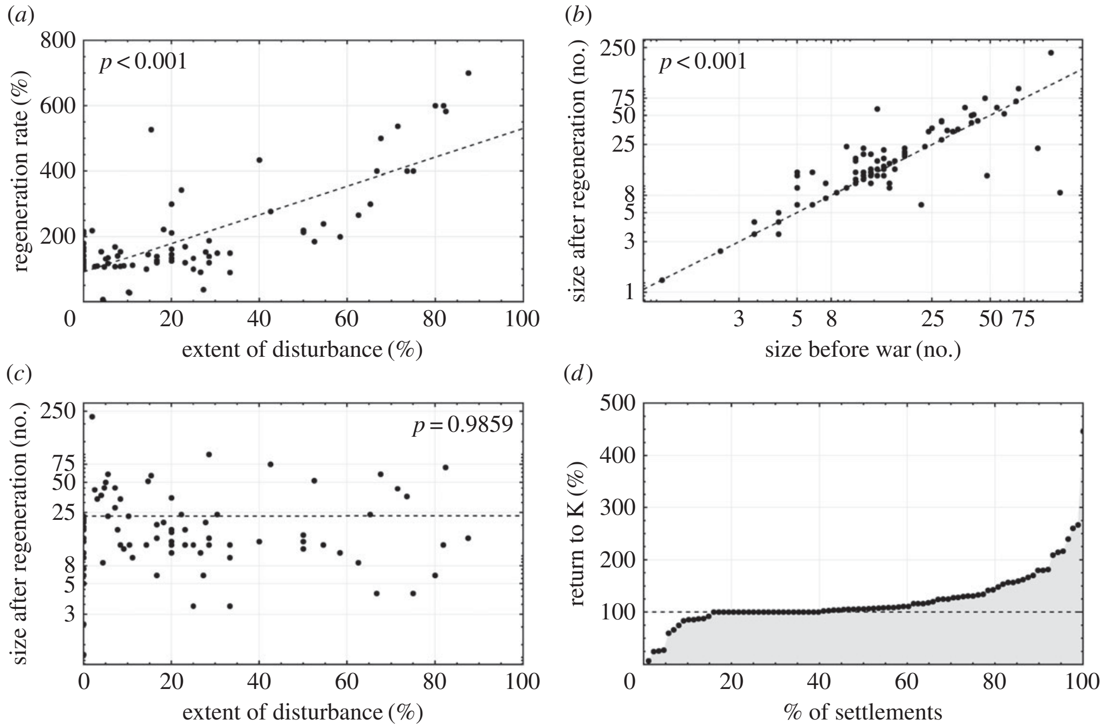

Figure 2. (*a*) Relationship between the regeneration rate and the extent of the disturbance. (*b*) Relationship between settlement size after regeneration (in 1757) and size before the war (in 1618). (*c*) Relationship between settlement size after regeneration (in 1757) and the extent of the disturbance. (*d*) Cumulative distribution of the ratio of post-war and pre-war settlement size (return to K). Legend: extent of the disturbance = percentage of farms destroyed during the war; regeneration rate = 100 × (number of farms in 1757, i.e. after regeneration)/(number of farms in 1654, i.e. after the war); return to K = 100 × (number of farms in 1757)/(number of farms in 1618, i.e. before the war). The dashed lines in panels *a* and *c* refer to linear least-squares regression, while in panel *b* to $y = x$ line. The dashed line in panel (*d*) refers to the 100% value of the return to K.

between 1654 and 1757 was proportionate to the percentage of farms within the settlement that were destroyed during the war (figure 2*a*). This is in accord with Dokoupil *et al*. [47], who argued that settlements in more damaged regions regenerated faster than settlements in less damaged regions within the region of Bohemia. In fact, the extent of disturbance was the only significant factor explaining the settlement growth during regeneration period (table 2, figure 3) and its relative variable importance almost attained the theoretical bound of 1 (RVI > 0.999). This finding represents a direct evidence of the negative density dependence at the level of individual human settlements, regardless of whether the carrying capacity (the equilibrium population size) was constant or not. However, the fact that the resulting settlement size after regeneration was similar to the settlement size before the war (figure 2*b*,*d*), irrespective of the size of the disturbance (figure 2*c*), indicates that carrying capacity did not substantially change in this period. We cannot, however, exclude the possibility that the size of the settlement increased after the study period due to changes in agricultural technologies or some other effects.

The negative density dependence was probably mediated by increasing demand for food when the number of farmers increased relative to the area of available land and the soil fertility (availability of food has been stressed as the most important population size limiting factor [7,48–51]). We therefore tested the factors affecting the pre-war settlement size with respect to the variables potentially affecting food production (table 1). The results from alternative model formulations, the Poisson model and the spatial error model, tell a reasonably consistent story. Two variables stand out in terms of relative variable importance (figure 4), *soil fertility* and *settlement density before war*, followed by *cadastre size* and *settlement age* (the latter two scoring differently in both models); the remaining variables (*altitude*, *terrain undulation*, *density of rivers and streams*) seem to be largely uninformative. In table 3, we present hierarchical regressions where predictors are entering the models in an order reflecting the relative importance of the results. In both specifications, *soil fertility*, *settlement density before war* and *cadastre size* are the significant predictors, although the former two lose their statistical significance as additional variables are included, presumably due to a combination of collinearity and small sample size.

Soil quality positively affected the pre-war size of settlements (table 3)—settlement size was higher in areas with better soil quality, irrespective of (non-significant) elevation. On the other hand, the settlement size was negatively affected by the numbers of other settlements within a radius of 4 km, suggesting a competitive effect of neighbouring settlements. Since the cadastre borders had already been delimited at that time, the competition between neighbouring settlements must have comprised an access to shared resources, e.g. to common pastures or to deposits of raw materials. Finally, cadastre size positively affected settlement size. Settlement size thus increased with soil production capacity, combined with the area available for agriculture, and it decreased due to the competitive effect of other settlements in the surroundings. Historical human populations were thus locally and regionally limited by factors affecting food availability.

Human carrying capacity may not be constant. It depends on many circumstances, including technologies for exploiting resources, patterns of production and consumption, and various exogenous factors [3,48,51,52]. We focus here on the

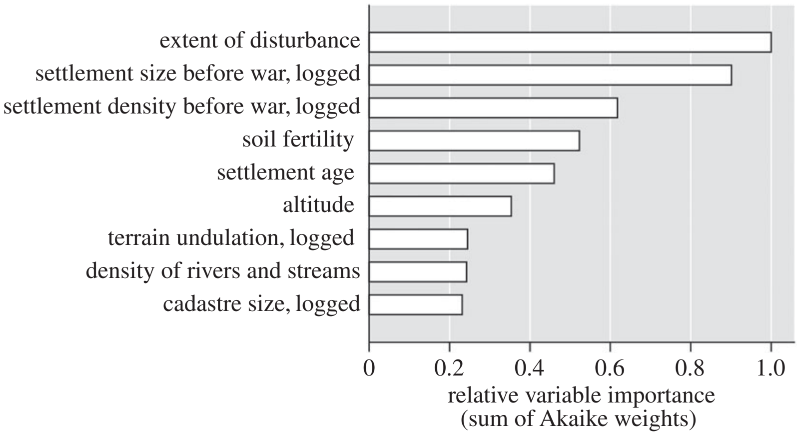

Figure 3. Relative importance of predictors of settlement growth during the regeneration period.

Table 2. Predictors of settlement growth during the regeneration period.

	dependent variable: *settlement growth during regeneration period*			
	regression model: spatial error model			
	model 1	model 2	model 3	model 4
extent of disturbance	0.0180*** (0.000)	0.0178*** (0.000)	0.0184*** (0.000)	0.0189*** (0.000)
settlement size before war, logged		−0.150 (0.131)	−0.192 (0.072)	−0.191 (0.090)
settlement density before war, logged			−0.0903 (0.366)	−0.129 (0.189)
soil fertility			−0.00210 (0.352)	−0.00432 (0.327)
settlement age				0.000545 (0.314)
altitude				−0.000531 (0.125)
terrain undulation, logged				−0.0238 (0.864)
density of rivers and streams				−0.00128 (0.549)
cadastre size, logged				0.0137 (0.928)
constant	0.0188 (0.716)	0.418 (0.077)	0.774 (0.053)	0.354 (0.890)
observations	88	88	85	84
AIC_c	134.604	130.464	128.636	137.660
max. VIF	1.000	1.001	1.105	2.961
sig. of additional terms		0.131	0.323	0.554

Notes: (i) *p*-values based on Student's *t* distribution are shown in parentheses: $*p < 0.05$, $**p < 0.01$, $***p < 0.001$; (ii) last row shows the *p*-value of a Wald test for joint significance of terms added to previous model.

near-equilibrium dynamics during the pre-industrial period. However, the subsequent industrial era brought a new dimension to human population dynamics due to the ability of humans to increase local carrying capacity much more rapidly than any time before. This era proceeded by a series of evolutionary transitions characterized by technological innovations that stimulated population growth. This in turn increased demands on the productivity of farmland, stimulating further boom in the agricultural sciences (the intensification of agriculture began in Central Europe in the

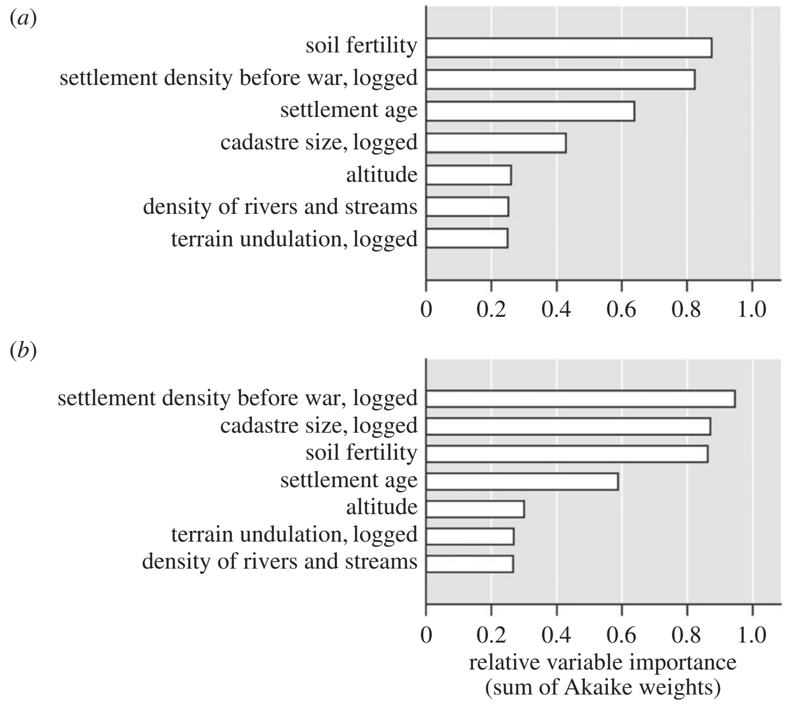

Figure 4. Relative importance of predictors of pre-war settlement size, based on (*a*) Poisson regression and (*b*) the spatial error model.

Table 3. Predictors of pre-war settlement size.

	dependent variable: *settlement size before war*			dependent variable: *settlement size before war*, logged		
	regression model: Poisson QML (robust std. errors)			regression model: spatial error model		
	model 1A	model 2A	model 3A	model 1B	model 2B	model 3B
soil fertility	0.00341*	0.00316	0.00291	0.00906*	0.00791	0.00747
	(0.020)	(0.051)	(0.224)	(0.023)	(0.111)	(0.288)
settlement density before war, logged	−0.148*	−0.0419	−0.0603	−0.385*	−0.113	−0.168
	(0.040)	(0.634)	(0.483)	(0.042)	(0.601)	(0.447)
cadastre size, logged		0.150*	0.154*		0.385*	0.389*
		(0.046)	(0.035)		(0.012)	(0.012)
settlement age		−0.000320	−0.000384		−0.000843	−0.00100
		(0.346)	(0.266)		(0.320)	(0.242)
altitude			−0.000250			−0.000640
			(0.240)			(0.382)
terrain undulation, logged			0.0708			0.192
			(0.332)			(0.385)
density of rivers and streams			−0.000411			−0.00150
			(0.812)			(0.723)
constant	1.164***	−0.958	−0.949	3.139***	−2.206	−2.091
	(0.000)	(0.534)	(0.544)	(0.000)	(0.488)	(0.538)
observations	85	84	84	85	84	84
AIC_c	268.962	268.468	275.257	216.868	211.268	217.334
max. VIF	1.076	1.427	2.908	1.076	1.427	2.908
joint sig. of additional terms		0.346	0.378		0.320	0.671

Notes: (i) *p*-values based on Student's *t* distribution are shown in parentheses: $*p < 0.05$, $**p < 0.01$, $***p < 0.001$; (ii) last row shows the *p*-value of a Wald test for joint significance of terms added to previous model.

first half of nineteenth century [53–55]), leading to the intensification of agriculture and broad changes to the ecosystem [56]. Transitions from rural and agricultural societies to urban and industrial societies may be considered as the most important global change process of the industrial age [57]. Escalating rural-to-urban migration [58], which started after the abolition of serfdom in the Czech lands in 1848 [59], makes it almost impossible to analyse the role of any potential equilibrium dynamics. The pre-industrial period that we have studied is therefore probably the last period that enabled the data to be interpreted in a straightforward way in terms of human carrying capacity. This does not necessarily preclude a role for carrying capacity even in modern times, but the concept becomes problematic whenever changes in carrying capacity take place in time scales comparable with the population growth itself (i.e. when the rate of the increase of carrying capacity is comparable with the rate at which a population itself approaches an equilibrium).

In summary, we have found that the traditional concept of environmental carrying capacity can be applied to historical human societies. Pre-industrial human population size was apparently controlled by negative density dependence mediated by soil fertility. Although there were certainly occasional increases of population carrying capacity driven by changes in subsistence technologies at least since the Neolithic revolution (e.g. the use of heavy plough and water mill or three-field crop rotation in the medieval period [60,61]), these changes were relatively rare and were followed by long periods of approximately constant population size driven by the negative density dependence mediated by limited soil fertility. Human carrying capacity is thus not just a theoretical concept, but a useful tool for understanding historical human population dynamics, even at a local scale.

Ethics. We did not perform any research on humans nor animals.

Data accessibility. All data are available in the electronic supplementary material, dataset S1.

Authors' contributions. V.F., M.Š., D.S. and P.S. designed the research, V.F. collected the data, M.Š. and J.Z. performed the data analyses, and D.S., V.F., P.S., J.Z. and M.Š. wrote the paper.

Competing interests. The authors have no competing interests.

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