Global patterns of environmental synchrony and the Moran effect

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There is considerable debate over the relative importance of dispersal and environmental disturbances (the Moran effect) as causes of spatial synchrony in fluctuations of animal populations. If environmental factors generally exhibit high levels of spatial autocorrelation, they may be playing a more important role in synchronizing animal populations than sometimes recognized. Here I examine this issue by analyzing spatial autocorrelation in annual rainfall and mean annual temperatures from sites throughout the world using the database maintained by the Global Historical Climatology Network. Both annual precipitation and mean annual temperatures exhibit high synchrony declining with distance and are statistically significant over large distance, often on a continental scale. In general, synchrony was slightly higher in annual precipitation at short distances, but greater in mean annual temperatures at long distances. No latitudinal gradient in synchrony of either variable was detected. The high overall synchrony observed in these environmental variables combined with a pattern of decline with distance similar to that observed in many animal populations suggest that the Moran effect can potentially play an important role in driving synchrony in a wide variety of ecological phenomena regardless of scale.

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Many populations fluctuate in synchrony over what in at least some cases are strikingly large areas. Potential driving forces behind such patterns of spatial autocorrelation include predation and predator switching (Ydenberg 1987, Ims and Steen 1990, Ims and Andreassen 2000), dispersal (Ranta et al. 1995), and environmental synchrony, or the Moran effect (Moran 1953, Ranta et al. 1997a, b, 1999). Although the potential importance of the Moran effect has been demonstrated theoretically (Ranta et al. 1995, Haydon and Steen 1997, Heino et al. 1997, Lambin et al. 1998, Ripa 2000) and empirically (Grenfell et al. 1998, Ranta et al. 1999), its relative importance remains unclear, in part because climatic perturbations are not generally believed to be a potential cause of the decline in synchrony with distance commonly observed in natural populations (Ranta et al. 1995, 1999, Lindström et al. 1996, Swanson and Johnson 1999).

In two populations synchronized entirely by the Moran effect, spatial autocorrelation in the environmental factor driving synchrony is predicted to match that observed between the two populations if both have the same density-dependent structure (Moran 1953, Hudson and Cattadori 1999). However, to the extent that the populations either do not share the same pattern of density dependence or are subject to nonlinear dynamics, synchrony in the environmental factor must be greater than that between the populations (Grenfell et al. 1998, 2000). Thus, a critical issue in the debate over the relative importance of the Moran effect versus dispersal in synchronizing populations is the pattern of autocorrelation exhibited by the environmental variables potentially driving the Moran effect. Are they synchronized over large distances, and do they exhibit a decline with distance comparable to that observed in animal populations (Ranta et al. 1999)? If so, environmental factors are potentially the primary cause of synchrony in many animal populations and of other ecological phenomena.

Despite the importance of annual variability in environmental conditions to understanding the causes of synchrony in population dynamics, no comparative analysis of a large-scale spatial synchrony in annual weather conditions has been conducted. This is surprising given the current interest in large-scale weather patterns affecting global climate, the most prominent of which is the el Niño-Southern Oscillation which is known to be a principal cause of global interannual climate variability (Cane 1986, Linthicum et al. 1999). Here I analyze spatial autocorrelation in the two most commonly measured climatic variables, annual rainfall and mean temperature, over various areas ranging from several relatively small countries with areas $< 10^6$ km^2 to entire continents with areas $> 10^7$ km^2. I also consider whether patterns vary latitudinally and compare patterns to two recently reported examples of synchrony in animal populations.

Methods

Monthly precipitation and mean temperature data were downloaded from the Global Historical Climatology Network ⟨ftp://ftp.ncdc.noaa.gov/pub/data/ghcn/⟩, a repository of weather records from 20790 sites (for rainfall) and 3126 (mean temperature) worldwide. Data going back as far as 1900 were used in the analyses.

For each site, total annual precipitation and the sum of the mean monthly temperatures were determined for each year, where years were defined both on a January–December calendar and July–June fiscal year basis. However, results were similar for the two sets of analyses, and thus only analyses for the January–December calendar year are discussed here. Any year with missing data for one or more months was discarded.

Analyses were conducted for seven continents or large geographic regions (Africa, Asia, Australia, Europe [west of the Urals], North America, South America and Oceania [including New Zealand]) and eight representative countries (Canada, Finland, France, India, Japan, New Zealand, United States [excluding Alaska and Hawaii], and the United Kingdom). Insufficient sites were available from Finland, France, and New Zealand to warrant analysis for mean annual temperature. To test for latitudinal differences, I divided the Western Hemisphere, near Eastern Hemisphere (west of 60°E longitude) and the far Eastern Hemisphere (east of 60°E longitude) into seven 20° latitudinal bands between 60°S and 80°N latitude. Mean values were then tested using ANCOVAs in which hemisphere and distance category were controlled for as main factors prior to consideration of latitude (the covariate), where the latter was ordered by distance from the equator (1–4, where 1 = 0° to 20°N or S and 4 = 60° to 80°N or S latitude).

Spatial autocorrelation was assessed using the modified correlogram technique of Koenig and Knops (1998a). Briefly, data sets were standardized by replacing environmental values (x) with the residuals obtained from a regression of year on x. This eliminates long-term trends due to global change or other factors not of direct interest in these analyses. After calculating residuals, Pearson correlation coefficients (r) and great-circle distances were determined between all pairwise combinations of sites within each geographic region of interest for which the appropriate environmental data were available. Due to analytical limitations, the number of pairwise correlations was limited to 10^6. When a larger number was available (i.e., when the number of sites in the region exceeded 1414), the 10^6 values used were randomly chosen from the full set of pairwise correlations.

This process yields two related n × n matrices, one with the distances between the n sites and the other containing the correlation coefficients between the standardized weather variables measured at the sites. For statistical analysis, correlation coefficients were divided into seven categories, depending on the geographic distance between sites: < 100 km, $100– < 250$ km, $250– < 500$ km, $500– < 1000$ km, $1000– < 2500$ km, $2500– < 5000$ km, and ≥ 5000 km. Pairs of sites falling into the larger distance categories were only present for the larger geographic regions analyzed.

Within each distance category, 100 randomization trials were conducted in which sets of correlation coefficients were chosen from the pool such that individual sites were used only once. Once a set of such correlations using all available sites once was chosen, the mean r value for the trial was determined and the number of positive and negative correlation coefficients present in the chosen subset of values counted. Means ($\pm$ SE) were calculated from the set of 100 mean r values generated by the randomization trials. Statistical significance was based on the number of trials in which positive correlations outnumbered negative correlations. In as much as 5–7 tests were conducted (one for each distance category) for each region, I used a conservative alpha level of $p \leq 0.01$; thus, in order to be significant, ≥ 99 out of 100 trials had to consist of more positive than negative correlation coefficients. For other tests, I used an alpha level of $p < 0.05$.

Results

Regardless of the geographic region, spatial synchrony for annual precipitation started high and declined more or less log-linearly with distance, remaining statistically significant up to distances of 500 (for New Zealand) to 5000 (for Australia) km (Fig. 1). Mean ($\pm$ SD) synchrony (Pearson r values) for the continents and large

geographic areas analyzed (n = 7) were 0.613 ± 0.106 (<100 km), 0.472 ± 0.100 (100– <250 km), 0.360 ± 0.095 (250– <500 km), 0.229 ± 0.088 (500– <1000 km), 0.079 ± 0.063 (1000– <2500 km), 0.016 ± 0.035 (2500– <5000 km), and 0.011 ± 0.020 (≥5000 km). Thus, on average, values were statistically greater than zero up to distances of 1000 km.

Synchrony in mean annual temperature also usually decreased with distance, but tended to do so less quickly than annual precipitation, often remaining statistically significant up to 2500 km and even 5000 km or more (Fig. 2). Mean ($\pm$ SD) r values for the continents and large geographic areas analyzed (n = 7) were 0.525 ± 0.087 (<100 km), 0.450 ± 0.056 (100– <250 km), 0.422 ± 0.049 (250– <500 km), 0.338 ± 0.046 (500– <1000 km), 0.187 ± 0.065 (1000– <2500 km), 0.058 ± 0.076 (2500– <5000 km), and 0.053 ± 0.070 (≥5000 km). Thus, on average, values were statistically greater than zero up to distances of 2500 km.

The primary difference between patterns of synchrony in annual precipitation and temperature is that the latter tended to be lower than annual precipitation at close distances but greater at large distances (Fig. 3). Considering the seven large geographic regions, five (71%) had higher synchrony in rainfall than temperature at distances of <100 km (Wilcoxon test, z = 1.2, p = 0.24), whereas the reverse was true for six out of seven sites (86%) at all three distance categories between 500 and 5000 km (Wilcoxon tests, z = 2.02, 2.20, and 1.69 for distance categories 500– <1000 km, 1000– <2500 km, 2500– <5000 km; p = 0.04, 0.03, and 0.09, respectively).

In the ANCOVAs testing for latitudinal trends in synchrony of annual rainfall there was no difference among hemispheres ($F_{2,109} = 0.4$, p = 0.7) or latitude ($F_{1,109} = 2.0$, p = 0.16) when controlling for distance category. There was also no difference in synchrony with latitude in annual mean temperature ($F_{1,103} = 1.8$,

Fig. 1. Mean spatial autocorrelation, as measured by Pearson correlations, in annual precipitation (January–December) for a) seven continents and/or large geographic areas and b) eight representative countries. Values are statistically significant (p ≤ 0.01) up to distances of 500 km (New Zealand), 1000 km (Oceania, Canada, Finland, Japan, and the United Kingdom), 2500 km (Africa, Asia, Europe, North and South America, France, India, and continental USA), and 5000 km (Australia); these values include sites the maximum distance apart for Australia, Finland, and France. N sites = 2365 (Africa), 5875 (Asia), 1917 (Australia), 1324 (Europe), 4479 (North America), 4165 (South America), 369 (Oceania, including New Zealand), 774 (Canada), 21 (Finland), 65 (France), 3400 (India), 54 (Japan), 19 (New Zealand), 167 (United Kingdom), 2270 (continental USA).
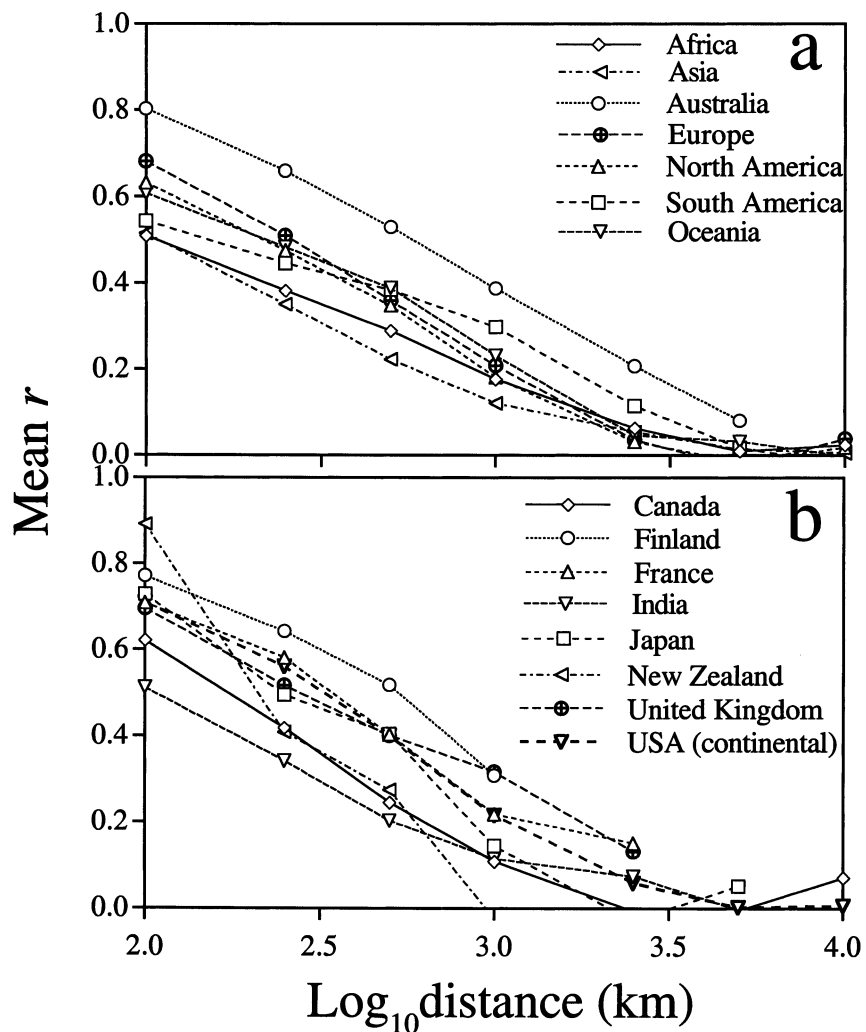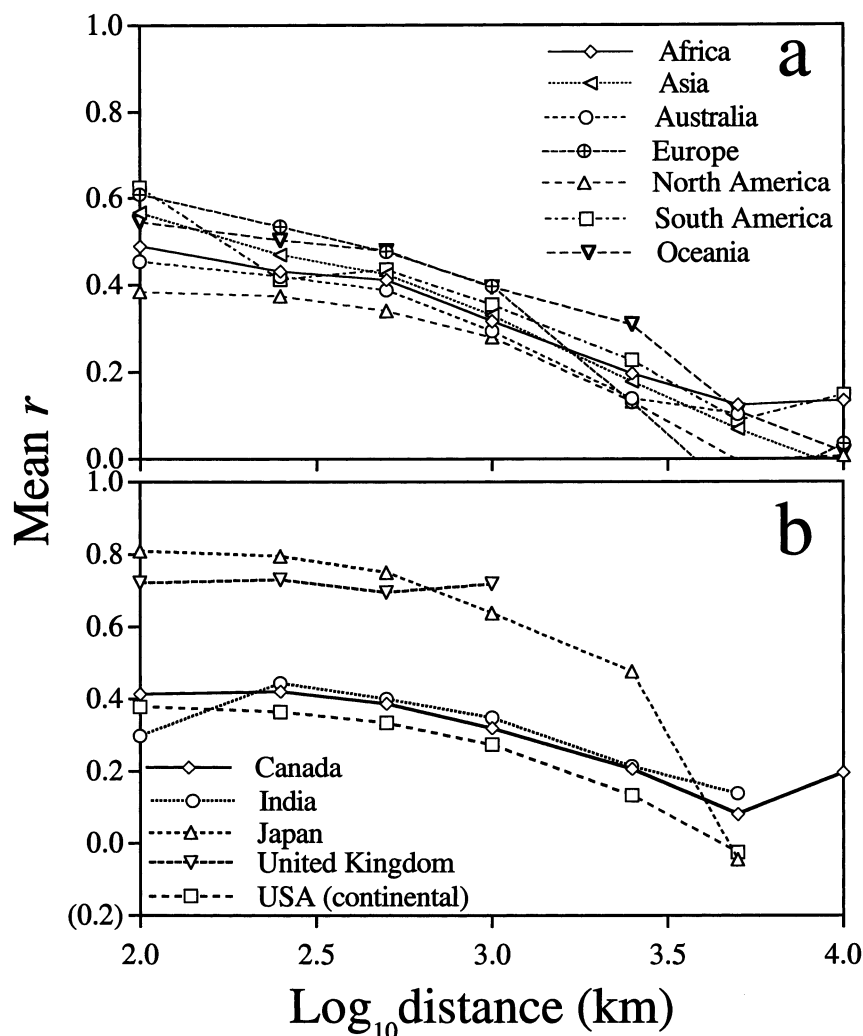
Fig. 2. Mean spatial autocorrelation in mean annual temperature (January–December) in the same regions as in Fig. 1. For the continents and large geographic areas in panel a), all values are statistically significant ($p \leq 0.01$) up to 2500 km (North America, Europe, Oceania), 5000 km (South America, Asia, Australia), and > 5000 km (Africa; this was the largest distance category considered). For the countries in b), values were significant up to 1000 km (United Kingdom; this was the largest distance category for this country), 2500 km (continental USA, Japan), and across all distance categories (Canada, India). N sites = 303 (Africa), 1020 (Asia), 420 (Australia), 823 (Europe), 2390 (North America), 159 (South America), 77 (Oceania, including New Zealand), 595 (Canada), 40 (India), 153 (Japan), and 1658 (continental USA).

$p = 0.18$) after controlling for distance category; however, in this case, there was a barely significant difference between hemispheres ($F_{2,103} = 3.6$, $p = 0.03$), with the Western Hemisphere exhibiting lower synchrony than either half of the Eastern Hemisphere. For both precipitation and mean temperature, the interactions between hemisphere and distance category were not significant.

Discussion

These results demonstrate that spatial synchrony in annual rainfall and mean temperature is both considerable and detectable over large geographic distances virtually anywhere in the world. Although this does not demonstrates causality, it suggests that these basic environmental factors are potentially capable, via the Moran effect, of having a synchronizing effect on a

wide range of ecological phenomena. Environmental synchrony is very high among closely related sites (on the order of at least $0.5 > r > 0.9$), and declines with distance but is still detectable and statistically significant up to sites 5000 km apart or, in some cases, even more. Temperature appears to be less strongly synchronized between sites relatively close together (< 250 km) than rainfall, but is slightly more synchronous between sites farther apart. No significant latitudinal differences were evident in spatial synchrony of either rainfall or temperature.

These patterns are similar to, and involve a degree of synchrony matching or exceeding, many of the ecological phenomena that have been examined thus far for spatial autocorrelation. For example, Koenig (2001) examined winter population sizes of 323 species of North American birds and found that virtually all were less synchronous than either mean spring/summer temperatures or annual precipitation up to distances of

Fig. 3. Mean ($\pm$ 1.96 SD) difference in synchrony between annual precipitation and mean annual temperature, both measured over calendar years, for the seven continents/large geographic areas analyzed (see top panels of Fig. 1 or 2). Synchrony is greater in annual rainfall compared to annual mean temperature between sites close together (<250 km apart) but vice-versa for sites far apart (>500 km).
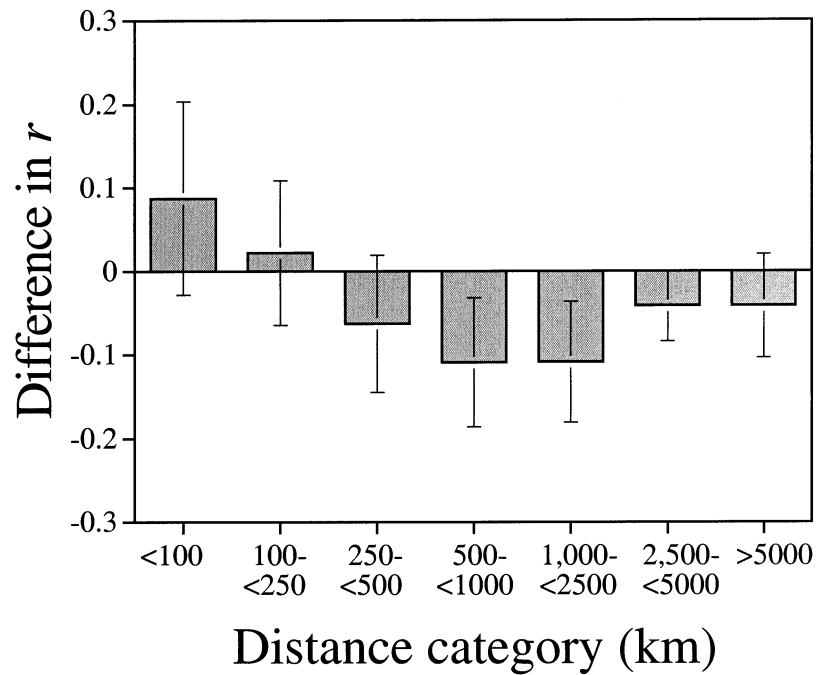
2500 km. A comparison between synchrony in winter population sizes of pine grosbeaks *Pinicola enucleator*, the most spatially synchronized of all 323 North American species tested by Koenig (2001), and the two environmental variables considered here is presented in Fig. 4. The absolute degree of synchrony in the grosbeaks is slightly greater than that of annual precipitation and less than that exhibited by mean annual temperatures, but in both cases closely matches their decline with distance. Given that the remaining 322 species are less synchronous than this species, synchrony in the population fluctuations of many North American wintering birds could, at least potentially, be strongly affected by the Moran effect. Similarly, spatial autocorrelation in seed crops of boreal trees is comparable in magnitude to those of annual rainfall (Koenig and Knops 1998b). However, in this case the patterns differ in other key aspects including temporal autocorrelation, variability, and distribution, indicating that factors other than the Moran effect contribute to mast-fruiting (Koenig and Knops 2000).

As one additional example, Grenfell et al. (1998) reported high synchrony in population sizes (r = 0.69) in feral sheep populations on two islands 3.5 km apart in the St. Kilda archipelago. Given that no dispersal is possible between the islands and that predation is not an issue, the Moran effect must provide the primary driving force behind this synchrony. However, because of nonlinear population growth, Grenfell et al. (1998) estimated that the actual correlation in the environmental factor driving synchrony had to be as large as r = 0.9.

Missing from this and subsequent reexamination of these results (Blasius and Stone 2000, Grenfell et al. 2000) is any consideration of the actual level of environmental synchrony between the two islands. Unfortunately, meteorological measurements are apparently not available. However, considering all of the United Kingdom (U.K.), mean synchrony (r) in annual mean temperature between sites <100 km apart is 0.74 (n = 56 pairwise comparisons) and synchrony in annual rainfall between sites <100 km apart is 0.68 (n = 1169 comparisons), both very close to the level of synchrony observed in the sheep. Considering only U.K. sites
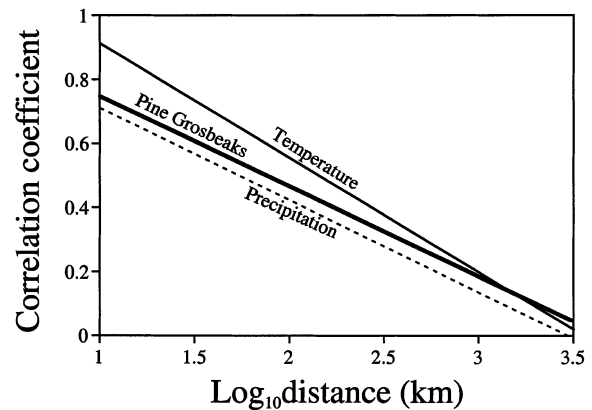

Fig. 4. A comparison of synchrony in pine grosbeak winter population size, annual precipitation, and mean annual temperature in North America (north of Mexico). All lines based on $>10^6$ pairwise correlations; only the regressions are plotted. Pine grosbeak values based on log-transformed and standardized Christmas Bird Counts (Koenig 2001).

> 55°N latitude (the latitude of St. Kilda is 57°10′N), mean synchrony in annual mean temperature between sites < 100 km apart is 0.94 (n = 13 pairwise comparisons), while synchrony in annual rainfall between four pairs of sites < 10 km apart is 0.86. Given that the mean distance between these latter four sites is 7.8 km, over twice the distance between the islands studied, while the average distance between sites < 100 km apart ranges between 65 and 68 km, the actual degree of environmental synchrony between the islands is probably higher than these values. Thus, environmental synchrony between the islands is almost certainly sufficient to explain the observed degree of population synchrony, even given the nonlinearities inherent in the population dynamics of the sheep.

An additional consideration provides a caveat to the prediction of Moran's theorem that synchrony in the population should match that of the density-independent factor driving the system. Simulations of the St. Kilda sheep system by Blasius and Stone (2000) indicate that because of small sample sizes, in this case 18 yr of matched data from the two islands, the level of synchrony observed in the sheep can be plausibly generated by relatively small environmental correlations as low as r = 0.3. Given that relatively short time series are a problem in almost all datasets involving animal populations, this suggests that the large-scale environmental synchrony documented here can potentially be important in driving synchrony even in animal populations exhibiting higher levels of synchrony than observed in the environmental factors themselves.

These results demonstrate that patterns of spatial autocorrelation in environmental factors should be carefully considered before concluding that synchrony in any particular system is driven by some factor beyond environmental correlation. Not only is the Moran effect almost always likely to be important (Ripa 2000), the "base level" of synchrony it sets is often likely to be sufficiently high to potentially drive much, if not all, of the synchrony observed in natural populations over large geographic areas. Thus, despite the demonstrable importance of dispersal in synchronizing some populations (Ranta et al. 1995, Ims and Andreassen 2000) and its potential importance in many others, much of the observed synchrony between animal populations, as well as in other kinds of ecological phenomena (Koenig 1999), may be attributable to the Moran effect.

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