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Density-dependent network structuring within and across wild animal systems

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Theory predicts that high population density leads to more strongly connected spatial and social networks, but how local density drives individuals' positions within their networks is unclear. This gap reduces our ability to understand and predict density-dependent processes. Here we show that density drives greater network connectedness at the scale of individuals within wild animal populations. Across 36 datasets of spatial and social behaviour in >58,000 individual animals, spanning 30 species of fish, reptiles, birds, mammals and insects, 80% of systems exhibit strong positive relationships between local density and network centrality. However, >80% of relationships are nonlinear and 75% are shallower at higher values, indicating saturating trends that probably emerge as a result of demographic and behavioural processes that counteract density's effects. These are stronger and less saturating in spatial compared with social networks, as individuals become disproportionately spatially connected rather than socially connected at higher densities. Consequently, ecological processes that depend on spatial connections are probably more density dependent than those involving social interactions. These findings suggest fundamental scaling rules governing animal social dynamics, which could help to predict network structures in novel systems.

The number of individuals occupying a given space (that is, population density) is a central factor governing social systems. At higher densities, individuals are expected to more frequently share space, associate and interact, producing more-connected spatial and social networks and thereby influencing downstream processes such as mating, learning and competition. In particular, density-driven increases in network connectedness should provide more opportunities for parasites[1–5] or information[6] to spread between hosts[1–4,7]. Despite the fundamental nature of such density-dependent processes, evidence is relatively limited that individuals inhabiting higher-density areas have more spatial and social connections. Furthermore, density effects should differ for asynchronous space sharing (for example, home range overlap (HRO)) versus social associations (for example, den sharing or grouping) or interactions (for example, mating or fighting). Although several studies have compared animal populations at different densities to demonstrate variation in social association rates among populations (for example, refs. 7–9) or groups (for example, refs. 10–12), attempts to identify such density effects within continuous populations of individuals have been less common (but see refs. 7,13–16) and their findings have never been synthesized or compared for spatial and social behaviours. We therefore have an incomplete understanding of how density, as a fundamental ecological parameter, determines socio-spatial dynamics within and across systems. This inhibits our ability to identify and predict how changes in density (for example, through culling, natural mortality, dispersal or population booms) influence downstream processes that depend on shared space and social interactions.

The rate at which an individual interacts with conspecifics depends on its spatial and social behaviour within the context of the surrounding environment and population. Adding more individuals into the same space should cause them to more frequently spatially overlap and socially associate or interact (Fig. 1). Often, individuals are modelled as randomly moving and interacting molecules (using mass action or mean field theory). In this conceptualization, direct contact between

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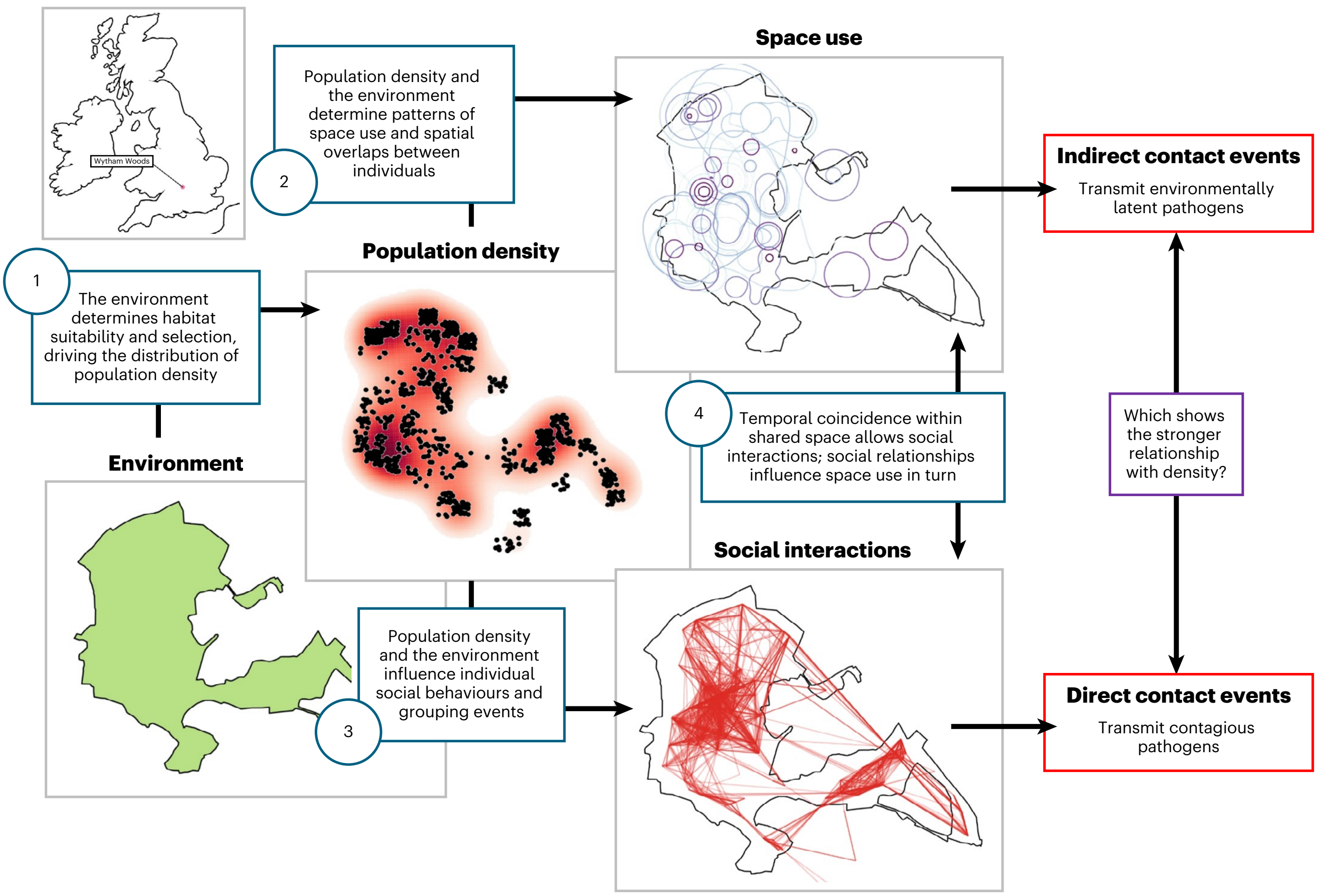

Fig. 1 | Outline of how population density drives the formation of spatial and social networks. The schematic details the rationale underlying this study, using Wytham Wood great tits as an example. In this case, the environment is represented by an outline of the woods. Under population density, the points represent the locations of individual birds, with some jittering added, and the red shading represents local population density. For space use, the different purple shades correspond to the home ranges of different individuals. Finally, for social interactions, the red lines depict connections among individuals, with each individual located at their centroid. Ultimately, one of our main aims is to ask whether spatial or social connections generally show a stronger relationship with density, partly functioning as a proxy for indirect and direct contact events with the potential to transmit pathogens. This framework moves between concepts of network and contact formation, traversing behavioural ecology, spatial and social network ecology and disease ecology.

two molecules is analogous to a social interaction or association; rates of such interactions are often assumed to increase with density (thus, they are density dependent; for example, ref. 17) and/or to be homogenous in space (for example, ref. 12). In reality, individuals are unlikely to behave and interact randomly in space, and instead will be influenced by spatially varying factors including local density[18] and competition for resources[7]. Changes in density may cause individuals to alter their foraging behaviour[19–21], dispersal[22,23], social preference or avoidance[15,24], mating behaviour[25] or preferred group size[9]. In some cases, density may have no effect on interaction rates, because individual animals alter their behaviour in a density-dependent manner to maintain a desired interaction rate[26]. These and related processes might produce strong nonlinearities in density–interaction relationships, which can complicate the predictions of density dependence models of pathogen transmission[2,4,5]. For example, individuals or groups may learn to avoid where competitors might go, resulting in greater spatial partitioning under higher densities[27]. Nevertheless, nonlinearities such as these are poorly understood and rarely considered.

Several wild animal studies have suggested that relationships between density and social association rates are often nonlinear and saturating[7,10–12,15]. Such relationships imply that association rates do not increase passively with density, but rather that behavioural or demographic processes probably change as the density increases, with the ultimate consequence of slowing association rates. However, these nonlinearities are difficult to examine between populations or species because they introduce a range of confounders and have few replicates along the density axis[2]. In contrast, lower densities may provide less ability to exert social preferences, but low-density populations may be more difficult to study due to (for example) low return on sampling investment; alternatively, failure to achieve sufficient interaction rates may result in Allee effects and ultimately drive populations towards decline[28,29].

Characterizing gradients of density across individuals within a population offers a workaround to these problems and facilitates an appreciation of the fact that interactions occur between individuals rather than at the population level. Examining between-individual variation is one reason that social network analysis, which allows characterization and analysis of individual-level social traits among other things, has become so popular in animal ecology in recent years[30–34]. Additionally, recent years have seen substantial growth in our understanding of socio-spatial behaviours, including harmonizing the concepts of spatial and social density[2,18,35]. Applying network analyses coupled with this socio-spatial understanding of density could provide an individual-level picture of density's effects on spatial and social connectedness, offering far higher resolution and statistical power and greater ability to detect within-system nonlinearities and between-system differences[2]. By providing new understanding of the correlates and emergent consequences of variation in density, this expansion could help to identify general rules underlying social structuring and network scaling in space.

Critically, different types of interactions or associations should show different relationships with density: for example, the need to compete for food at higher densities could drive a disproportionate increase in aggression[36], but this is unlikely to be true of mating interactions. In contrast, higher density and food scarcity should lead to lower exclusivity in resources and more overlapping home ranges, thus enhancing the effect of density on the spatial network[37]. This rationale is well understood in disease ecology, as differences in density–contact relationships are thought to drive differences in the density dependence of infection, where contact is defined as an interaction or association that could spread a pathogen (Fig. 1). Contacts then form the basis of spatial and social networks used to investigate pathogen transmission dynamics, which should likewise diverge with density just as contacts do. For example, density should drive greater transmission of respiratory pathogens but not sexually transmitted pathogens[1,38]. Establishing these density–contact relationships is integral to understanding disease dynamics and developing control measures[1,39], but we still have a poor understanding of how different interactions (and therefore contact events for different pathogens) are driven by density. This direct/indirect interaction dichotomy is most fundamental to disease ecology[35,40], but given building interest in the spatial–social interface and relationships between spatial and social networks in behavioural ecology[18], the framework is readily related to other fields (for example, direct versus indirect cues that can lead to social learning[41]). Previously established density–interaction relationships are diverse and include feral dog bites[13], ant antennations[42] and trophallaxis[26], ungulate group memberships[14,19], rodent co-trapping[10,43] and agamid association patterns[15,16], but no study has yet synthesized how the rates of multiple interaction or association types relate to density, within or across systems.

Identifying the general rules underlying density dependence requires quantifying density's relationship with proxies of interaction rates at fine scales across a diversity of systems, then identifying the factors determining their slope and shape. To this end, we collated a meta-dataset of over 58,000 individual animals across 36 wildlife systems globally (Fig. 2) to ask how within-population variation in density determines between-individual interaction rates based on connectedness in spatial and social networks. We fit multiple competing linear and nonlinear relationships to identify the slope and shape of density effects within each system and used meta-analyses to investigate general rules determining their slope and shape across systems. In particular, we focused on comparing space sharing with social interactions and associations as a cross-system case study. Ultimately, we present a de novo cross-system analysis of individuals' social and spatial behaviour that traverses fields of behavioural, population and disease ecology, which could help to inform general rules governing the structure of social systems and eventually shape management and conservation decisions in a wide range of systems.

Results and discussion

We compiled a comparative meta-dataset of over 14 million observations of 58,667 individual animals' spatial and social behaviour, across a wide range of ecological systems and taxonomic groups of animals. We then ran a standardized pipeline to align their spatial and social observations, identifying strong and predictable relationships between local density and network connectedness at the individual level.

We observed strong positive relationships between individuals' local population density and their connectedness in spatial and social networks across a wide range of wild animals. Of our 64 replicates, 51 (78%) were significantly positive when analysed using linear models (Fig. 3a). Meta-analyses identified a highly significant positive mean correlation between density and connectedness, both for social networks (estimated $r = 0.22$; 95% confidence interval (CI) = 0.17 to 0.27) and spatial networks ($r = 0.45$; CI = 0.36 and 0.53; Fig. 3b). Our study therefore provides fundamental evidence that high local population density broadly drives greater connectedness within ecological systems, at the individual level. Slopes were highly variable across systems for both spatial and social networks (Fig. 3a; Q-test of heterogeneity across systems: $Q_{37} = 5{,}627.33$ and $Q_{25} = 1{,}281.83$; both $P < 0.0001$), indicating that quantifying these slopes within and between multiple systems and comparing them is important for understanding animal socio-spatial structure. That is, relationships between density and individual connectedness differ substantially between populations and the biological mechanisms underlying these divergent trends are probably important. As well as adding resolution and allowing comparisons of density effects across systems, our methodology facilitated the fitting of nonlinear relationships (using generalized additive models (GAMs); see below). This approach has only rarely been applied before, and then at much coarser resolution (see refs. 10,11,13). As such, this study fills an important empirical gap by providing insights into the slope and shape of density–connectedness relationships for a diverse variety of animal groups and their social and spatial behaviours (Fig. 4). Nevertheless, despite this diversity, we were able to identify several further general trends in our data.

Remarkably, density's effect more than doubled in size for spatial compared with social networks (Fig. 3b; $r = 0.45$ versus 0.22). There was a difference of 0.26 (CI = 0.16 to 0.36; $P < 0.0001$) for this effect when we meta-analysed the two contact types together. This finding indicates that as density increases, wild animals are more likely to share space with each other, but that social connections increase at a much slower rate. Similarly, we discovered that saturating shapes were extremely common: as density increased, its effect on connectedness decreased, such that 48 out of 64 systems (75%) had a steeper slope at low density values than at high ones. This effect was strong for both social networks (effect on $r = -0.11$; CI = −0.19 to −0.03; $P = 0.01$) and for spatial networks, with substantial overlap between their estimates ($r = -0.22$; CI = −0.37 to −0.07; $P = 0.0042$). Due to the greater overall effect for space sharing, the latter half of density's spatial effect was still higher than the first half of its social effect (Fig. 3c). Together, these observations suggest that density-dependent processes act to limit the increase in social connectedness with density, but without limiting spatial overlaps to the same extent. Consequently, higher-density areas are characterized disproportionately by individuals asynchronously sharing space rather than socially associating, whereas in lower-density areas individuals are disproportionately more socially connected proportional to their shared space.

There are many possible social reasons for saturating nonlinearity in density-dependent network structuring. For example, individuals in higher-density areas may begin to avoid each other, seeking to avoid competition or aggression[36] or exposure to infectious disease[44]. Eastern water dragons (*Intellagama lesueurii*) show greater avoidance at higher densities[15], supporting avoidance-related mechanisms. Alternatively, in species with high social cognition or stable bonds, saturation could reflect lower social effort or inability to keep track of social affiliates at higher densities[45]. In general, individuals probably have a preferred social interaction rate or group size—a preference that they may increasingly exert at higher densities[9]. It remains to be seen how this preference varies among individuals, and whether individuals vary in their preferred social network position given a certain density. Given that individuals vary in their movement and spatial phenotypes[46–48] and social phenotypes[48–50] in ways that should manifest for density-dependent behaviours specifically[18], it seems likely that these slopes could vary between individuals as they do between populations. Future analyses might fit variable density–connectedness

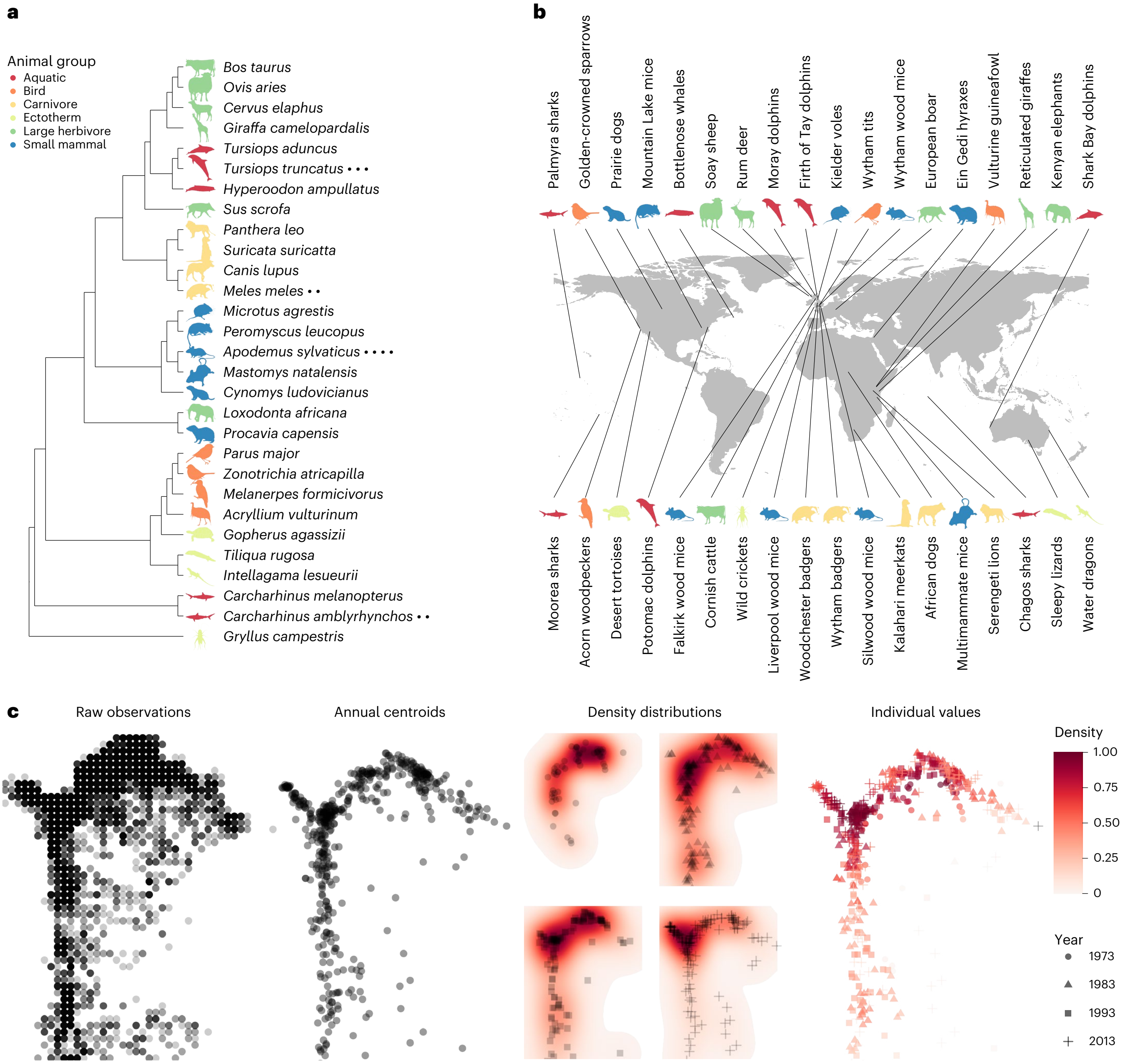

Fig. 2 | Phylogenetic and geographic distributions of the examined datasets of spatial and social behaviour and schematic. a,**b**, Phylogenetic (**a**) and geographic (**b**) distributions of our 36 examined datasets on spatial and social behaviour. The points next to the species' names in **a** denote where we had more than one population of that species. Note that the Potomac dolphins listed as *Tursiops truncatus* in **a** following Open Tree of Life nomenclature have since been reclassified as *Tursiops erebennus*. **c**, Schematic depicting the methodology for deriving local density values, using the Isle of Rum red deer data as an example. The *x* and *y* axes represent bivariate spatial coordinates. Shown are raw observations of individuals in space that we then averaged at the individual level to make centroids; we used the centroids to generate annual density distributions, which were then assigned to individuals in the form of local density measures. Animal silhouettes from phylopic.org; details on attribution appear in Supplementary Table 2.

slopes among individuals to identify socio-spatial syndromes across systems, as has been done previously in single systems, including caribou (*Rangifer tarandus*)[51] and American red squirrels (*Tamiasciurus hudsonicus*)[52]. Additionally, we could dissect the social network and its relationship with the spatial network to identify levels of attraction[53,54] or avoidance[55] and how they depend on density.

We considered that density-dependent changes in spatial behaviours might explain these trends. For example, density could create greater competition over resources and therefore reduce energy to roam (and contact others). Individuals may partition their niches[56] or reduce their territory or home range sizes[52,57,58], potentially driven by years of plentiful resources supporting higher densities alongside smaller home ranges sufficiently providing ones' resource needs, which could drive lower association rates. However, our findings do not seem to support explanations related to small home ranges because such explanations should produce an equivalent or stronger reduction in (relative) spatial connectedness. In contrast, we observed that density drives individuals to become spatially connected faster than they become socially connected, such that the underlying mechanisms probably involve behaviours and demographic processes

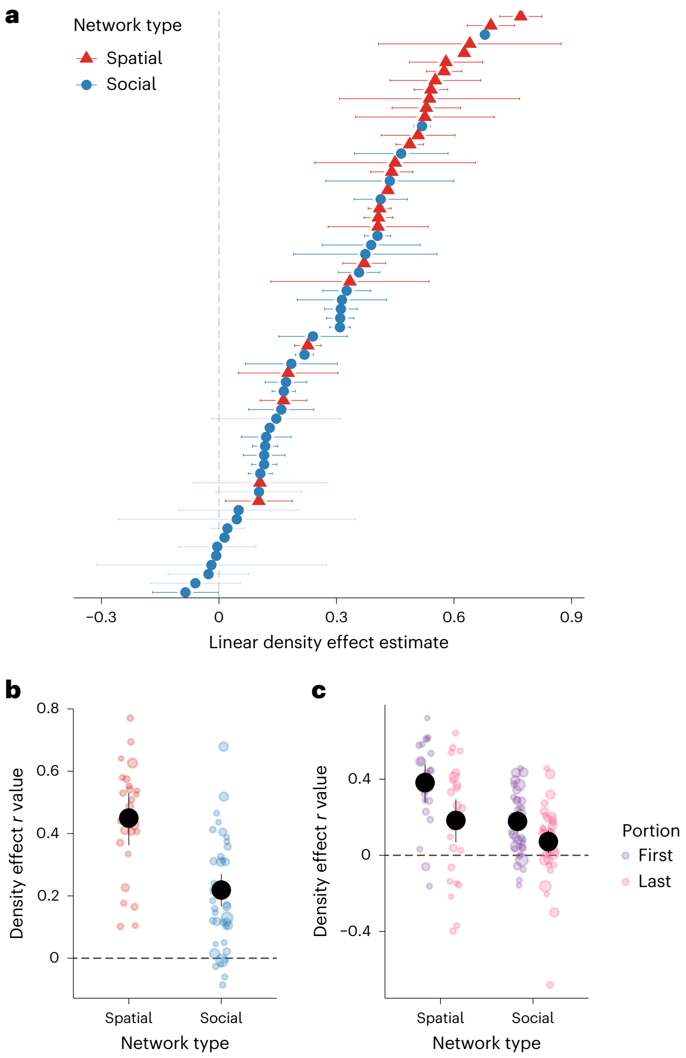

Fig. 3 | Drivers of variation in linear density effects on individual network connectedness. The results are based on a meta-analysis of $n = 36$ systems comprising $n = 64$ system–behaviour replicates. **a**, Our fitted linear model estimates of density effects on network strength. Each point represents the mean estimate from a given system and the error bars denote 95% CIs. Opaque error bars represent statistical significance (that is, they do not overlap with 0). The estimates are in units of standard deviation for both density and network strength. The colour of the point denotes whether the network being examined was defined using spatial or social connections. **b**, Centrality in spatial networks (that is, HRO; red points) had a significantly steeper relationship with density than that of social networks (blue points). **c**, We fitted linear models separately to two portions of the data within each study population (first and last represent values below and above the median). The slopes for the last (pink points) were generally less positive than those for first (purple points), implying a general saturation shape. In **b** and **c**, each coloured point represents a study replicate fitted to the strength estimate; points are sized according to sample size and jittered slightly on the x axis to reduce overplotting. The large black points represent the mean slope estimated from the meta-analysis and the error bars represent 95% CIs.

that specifically affect social collocation in space and time. Testing the precise underlying mechanism will probably require finer-scale behavioural observations, as described below. Regardless of the mechanism, these saturating density–connectedness relationships strongly support the idea that examining density effects at the individual level—rather than between populations—is highly informative. For many systems, mean field expectations of homogenous interactions under increasing density probably produce an inaccurate (that is, inflated) picture of density's effects. Importantly, our study included many examples of proximity-based social networks—most notably gambit-of-the-group measures[59]—but relatively few direct interactions, such as mating, grooming or fighting. It is interesting that these differences manifested even among two ostensibly spatially defined contact metrics (gambit of the group and HRO). This observation supports the assertion that social association metrics defined by spatiotemporal proximity are valuable for informing on social processes separately from more spatial behaviours sensu stricto, such as ranging behaviour[14]; we expect that more direct interactions could show even further differences in relationships with density. Incorporating a larger number of direct metric-based systems could help to address this question (Supplementary Discussion).

The fact that spatial networks show stronger and more linear density dependence than social networks could heavily influence the ecology of animal systems. For example, indirectly transmitted (that is, environmentally latent) parasites may exhibit greater density dependence than directly transmitted ones, given that individuals probably experience disproportionately more indirect contact at higher densities. This observation contrasts with orthodoxy that directly transmitted parasites are most likely to be density dependent[60], and supports the value of investigating nonlinear changes in socio-spatial behaviour and grouping patterns in response to density when considering density dependence. Saturating density–connectedness functions further have implications for disease modelling and control. Specifically, our findings lend behavioural support to the growing consensus that many diseases are density dependent at lower densities, but not at higher densities (that is, that the slope flattens with density)[17,61]. Rather than assuming constant behavioural mixing at higher densities, epidemiological models could benefit from incorporating density-dependent shifts in behaviours and demography that influence direct and indirect interaction frequencies, as was previously suggested empirically and by epidemiological theory[17]. These relationships could influence our targets for culling or vaccination coverage[62]. Given that animals at high density seem likely to have a relatively shallow relationship between density and contact rates, reducing the population's density (for example, by culling) might therefore be ineffective at reducing pathogen transmission initially, particularly when considering socially transmitted pathogens, where contact rates are particularly likely to have become saturated (Fig. 3c). Similar problems with culling have already been acknowledged in specific systems (for example, in canine rabies[39,63,64]), but our study implies that shallow nonlinear density–contact trends could be more general than was previously thought and could be driven by flexible density-dependent changes in behaviour and demography. Conversely, culling could be disproportionately effective at intermediate densities, such that identifying the inflection points of the curve might facilitate the design of optimal management strategies. Future studies should investigate whether the divergence in spatial and social connectedness with density drives a concurrent divergence in the prevalence of directly and indirectly transmitted parasites, as well as addressing several other biases in our selection of systems (for example, ref. 65; see Supplementary Discussion).

Beyond these general trends, we ran GAMs that revealed that 52 out of 64 density effects on network connectedness (81%) were significantly nonlinear (change in the Akaike information criterion (ΔAIC) > 2)); these relationships took a wide variety of shapes, representing a range of nonlinear functions that are difficult to generalize (Fig. 4). Notably, although many GAM smooths were eventually significantly negative (Fig. 4), the vast majority of linear models fitted to the second half of the data were positive (Fig. 3c); this result is probably an artefact of restricted model fitting, rather than true downturns in connectedness with density. Nonlinearity did not cluster according to connection type definitions or according to animal group. These observations were largely corroborated by our meta-analytical models, which found no factors influencing the slope and shape of density effects overall

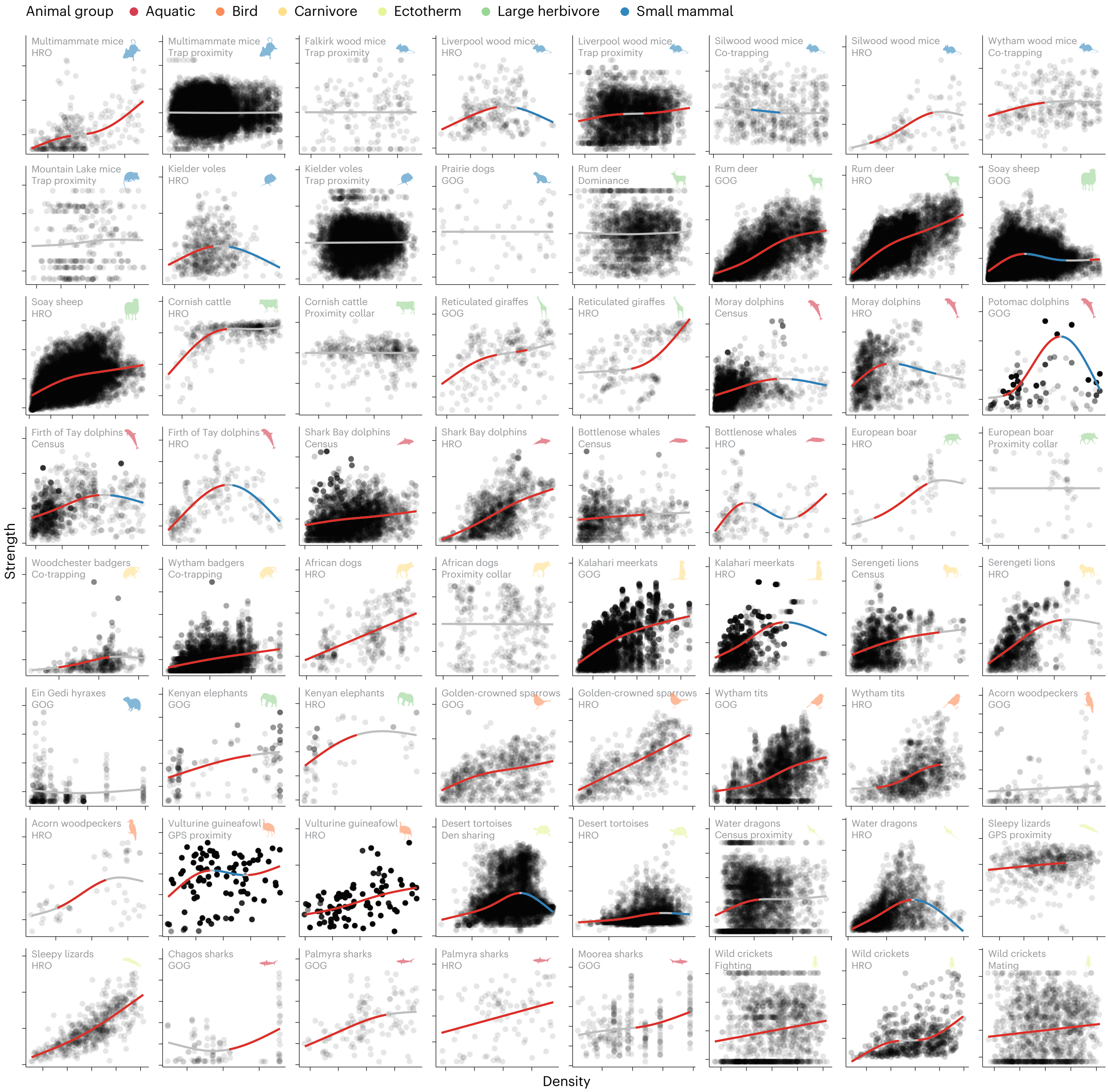

Fig. 4 | Relationships between density and network connectedness. Graphs of the relationships between density and network connectedness across $n = 64$ animal systems comprising $n = 151{,}835$ individual animals, showing substantial variation. The x and y axes represent density (in individuals per area) and network connectedness (strength centrality), respectively. The values have been standardized to have a mean of 0 and a standard deviation of 1 within each system. The axis ticks are in units of 1 standard deviation, so are self-referential within each panel, and hence we have left the axis tick values unlabelled to improve clarity. Each point represents an individual–year–behaviour replicate. The lines portray model fits from our GAMs. Red, grey and blue represent a positive statistically significant relationship, no statistical significance or a negative statistically significant relationship, respectively. The points are semi-transparent to enhance visibility. The panels are arranged phylogenetically following the tree displayed in Fig. 2a. GOG, gambit of the group. Animal silhouettes from phylopic.org; details on attribution appear in Supplementary Table 2.

($P > 0.05$; Supplementary Table 3), including no clear phylogenetic signal (ΔAIC = 2.71). This observation speaks to the complexity of these relationships within and across systems while accentuating that simple functional relationships are often likely to be complicated by contravening ecological factors such as habitat selection[66,67], group formation[7], parasite avoidance[68] and demographic structuring[69]. Although we were unable to identify specific between-system predictors of the nonlinearity of density–connectedness relationships, the finding that most such relationships are strongly nonlinear is an important consideration for future work.

Density is a universal factor underlying the dynamics of animal populations and its linear and nonlinear effects on spatial and social network structure are likely to impact myriad processes in behaviour, ecology and evolution. Similar to other studies that have reported general scaling patterns in network analysis[70] and food web ecology[71], the patterns we report strongly suggest that animal systems generally become more connected spatially than socially under increasing density. These trends might extrapolate to human networks, given that other scaling patterns in animal networks do[70]. As these patterns seemingly manifest regardless of animal group and interaction type, they may reflect a generalizable rule governing the socio-spatial structure of ecological systems. Further refinement and implementation of these models could facilitate the prediction of network structure in new systems.

Finally, this study is relatively unique in that it comprises an expansive meta-analysis of behavioural data from individual animals across a diverse selection of systems. As datasets accumulate, comparative analyses are increasing in frequency in social network ecology[72], but they often revolve around analysing whole networks rather than individuals[73] and (to our knowledge) are never performed in conjunction with analyses of spatial behaviour. These analyses therefore hold exceptional promise for disentangling spatial and social behaviour across diverse systems. For example, given that our dataset includes many repeatedly sampled known individuals, future analyses could investigate individual-level repeatability or multi-behaviour behavioural syndromes across a variety of different taxa and environments[18,74]. Additionally, capitalizing on the wide range of methodological approaches to behavioural data collection (for example, censuses, trapping and telemetry), the methodological constraints of socio-spatial analyses could be tested in this wide meta-dataset as they have been in other recent comparative analyses of wild ungulates[75]. As well as being diverse, our meta-dataset contained several replicate examples of (for example) marine mammals and trapped rodents, which could be used for finer-scale and more targeted comparative analyses within these smaller taxonomic groupings. For now, it is highly encouraging that we uncovered general trends across these disparate animal systems, and further explorations of these socio-spatial patterns may help to inform a wide range of exciting and longstanding questions at the spatial–social interface[18].

Methods

Data standardization and behavioural pipeline

Data were manipulated and analysed using R version 4.2.3 (ref. 76) and all R code is available at https://github.com/gfalbery/DensityMetaAnalysis. Our 36 datasets each involved at least one continuous uninterrupted spatial distribution of observations in a single population; some datasets comprised multiple such populations, all systems had at least one social network measure, and two had two different types of social interaction. These datasets covered 30 different animal species, including sharks, carnivores, cetaceans, ungulates, rodents, elephants, birds, reptiles and one orthopteran insect (Fig. 2). In one case (the Firth of Tay and Moray dolphins), we used two distinct replicates despite the data relating to overlapping groups of individuals, because of their distinct spatial distributions, which made it difficult to fit a coherent density distribution.

To standardize the timescale across studies, all systems were analysed as annual replicates (that is, social and spatial networks were summarized within each year). Our analyses used 64 system–behaviour replicates (listed in Supplementary Table 1) and totalled 151,835 unique system–individual–year–behaviour data points.

All spatial coordinates were converted to the scale of kilometres or metres to allow comparison across systems. To provide an approximation of local density, following previous methodology[14,77], we took each individual's average location across the year (their centroid) and created a spatial density kernel using the adehabitatr package[78], which provided a probabilistic distribution of population density across each study system based on the local frequencies of observed individuals. Each individual was assigned an annual estimate of local density based on their centroid's location within this spatial density distribution. We made these density distributions as comparable as possible between systems by incorporating the density raster using metre squares; however, there were large differences in density across populations that were difficult to resolve and put on the same scale (for example, interactions per individual per km^2 unit of density). Consequently, we scaled and centred density to have a mean of zero and a standard deviation of one within each population, which allowed us to focus on differences in relative slope and shape across systems.

To validate the local density measures estimated using the kernel density approach, we also estimated local density for individuals across all populations based on the locations of individual annual centroids within a designated area. To do so, we first estimated the area of the minimum bounding box within which all individuals were censused during the study period based on their annual centroids. For each individual's mean location, we then estimated a circular boundary of radius = 1/20 multiplied by the the area of the minimum bounding box. We then calculated the number of individuals present within this boundary as an individual's local density measure. We estimated the Pearson correlation coefficients between the local density measures derived using the kernel density estimation approach and the proportional area-based approach (Supplementary Fig. 1).

To provide a measure of asynchronous space sharing, we constructed HRO networks based on the proportional overlap of two individuals' minimum convex polygon (that is, the bounding polygon around all observations of each individual in a given year). These HRO networks were restricted to only individuals with five or more observations in a given year to allow us to create convex polygons effectively; ten out of 36 (28%) systems did not have sufficient sampling for this analysis. We also repeated our analyses with a series of higher sampling requirements for observation numbers to ensure that our findings were robust to this assumption. The minimum convex polygon approach is relatively low resolution and assumes uniform space use across an individual's home range; however, this approach is less data intensive and less sensitive to assumptions than density kernel-based approaches that would estimate variation in space use across the home range, allowing us to apply the models across more systems, more generalizably and more conservatively.

To provide a measure of social connectedness, we built social networks using the following approaches, as defined by the original studies: direct observations of dyadic interactions (for example, fighting or mating); gambit-of-the-group measures (that is, assessing which animals are members of the same group)[59]; co-trapping (that is, analysing which animals are trapped together or in adjacent traps within a given number of trapping sessions); or using proximity sensors to determine the incidence of direct contact (defined by a certain distance-based detection threshold). Notably, some analyses use indirect interactions (that is, spatial overlap) to approximate direct interactions. This requires spatiotemporal coincidence, which we caution against, particularly when modelling pathogen transmission[35,79]. Although the two often correlate, here we do not use HRO to approximate direct interaction rates, but rather as a measure of indirect interactions (for example, as an indication of the transmission of environmental parasites).

For each social network, we scaled connection strength relative to the number of observations of each individual in a dyad (that is, the simple ratio index[80]). Our response variable therefore took the form of summed strength centrality, scaled to between 0 and 1 for each dyad, for each social and spatial network. We focused on comparing density effects on social interactions and associations with density's effects on space sharing.

Density–connectedness models

We developed a workflow to allow us to derive and compare density's effects on connectedness—and their drivers—in a standardized way across our animal systems. We fitted models with three main forms: linear models fitted to the entire dataset; nonlinear generalized additive models fitted to the entire dataset; and linear saturation models fitted separately to low- and high-density subsets of each dataset.

Linear models. For each system–behaviour replicate, we first fitted a linear model using the lm function in R, fitting scaled density as an explanatory variable to estimate linear density effect slopes. The linear fits and residuals are displayed in Supplementary Figs. 2 and 3, respectively.

GAMs. We fitted GAMs in the mgcv package[81] to identify whether each density effect was better described by a linear or nonlinear relationship and to identify the shapes of these nonlinear relationships. For each model, we fitted a default thin plate spline with $k = 4$ knots. This knot number was selected to reduce overfitting in our models, which formed several fits to the data that were difficult to reconcile with functional formats. To assess whether nonlinear models fit better than linear models, we used AIC, with a contrast of 2ΔAIC designated to distinguish between models.

Saturation models. To quantify whether density effects were generally saturating (that is, that density had steeper relationships with individuals' connectedness at lower density values), we split the data into two portions: all values below the median density value; and all values above the median. We then re-ran linear models examining the relationship between density and strength in each portion. We attempted to investigate nonlinear patterns (especially saturating effects) across all of our systems using a range of other methods (for example, comparing specific functional relationships with nonlinear least squares), but found that they were generally incapable of fitting well to the data in a standardized way across the many datasets (that is, there was non-convergence of nonlinear least squares using semi-automated starting estimates across systems). As such, this approach represented a tradeoff between tractable, generalizable model fitting, interpretability and accurate representation of the relationship's shape. All else being equal, we posit that investigating the relative slopes of two otherwise identical portions of the data is a conservative and informative method of identifying saturation, which was our main hypothesis for the expected shape of density effects.

Heteroskedasticity and log–log models. To ensure that our estimates were robust to non-normality and to provide another source of information concerning possible saturation effects, we also conducted tests of heteroskedasticity on our linear models and accompanied them with simulations and fitted log–log linear models. First, we carried out a simple simulation study to test how (1) the skew in residuals, (2) a saturating relationship and (3) heteroskedasticity impact whether we may under- or overestimate the slope of an assumed linear relationship between density and strength (Supplementary Methods section 'Heteroskedasticity simulations'). These demonstrated that our models were resilient to skew and saturating effects, but that heteroskedasticity in residuals could drive overestimated linear effects in our models.

To examine this possibility further, we derived the Breusch–Pagan statistic for each linear model as a measure of heteroskedasticity and then plotted it against the meta-analysis covariates and fixed effects. There was no evidence that the density effect was being skewed to be greater for spatial behaviours due to heteroskedasticity, nor were the second portions of the data more heteroskedastic, which would be expected if this was driving the saturating effect (Supplementary Fig. 4). Finally, we fitted log–log linear models with the same formulations as our main linear models defined above, but with both density and strength $\log(x + 1)$ transformed, rather than scaled to have a mean of 0 and a standard deviation of 1 (Supplementary Fig. 5). Our results showed broadly identical findings of greater estimates for spatial behaviours, and the fact that the slopes were largely under 1 is indicative of a saturating effect. As such, these tests strongly support the resilience of our findings to uneven data distributions.

Meta-analysis

To characterize the typical relative slope of density effects across systems and identify the factors influencing their variation, we fitted hierarchical meta-analytical models using the metafor package in R. The response variable was the standardized slope of the linear density effect; because both individual network strength and density were scaled to have a mean of 0 and a standard deviation of 1 in the linear regression, this was equivalent to the correlation coefficient (r)[82]. We converted all correlation coefficients into Fisher's Z (Z_r) and computed the associated sampling variance.

For our hierarchical meta-analysis models, we used an initial model that nested observations within a system-level random effect to account for within- and between-system heterogeneity[83], as 26 of 36 systems had more than one density effect. We used another random effect for species to account for repeat observations per animal species.

We then added a separate random effect for animal phylogeny[84]. This effect used a phylogenetic correlation matrix of our 30 animal species derived from the Open Tree of Life via the rotl package[85], with the ape package used to resolve multichotomies and provide branch lengths[86].

We then fitted intercept-only models using the rma.mv() function with restricted maximum likelihood, weighted by inverse sampling variance, and used variance components to quantify I^2, the contribution of true heterogeneity to the total variance in effect size. We used Cochran's Q to test whether such heterogeneity was greater than that expected by sampling error alone.

We next fitted models with the same random effects structure that included explanatory variables. To detect whether some animals were more likely to experience density effects, we fitted animal group as a factor with six categories, representing a combination of species' taxonomy and general ecology: aquatic (fish and dolphins); birds; large herbivores (elephants and ungulates); small mammals (rodents and hyraxes); carnivores; and ectotherms (insects and reptiles). We also fitted several explanatory variables indicative of greater statistical power that might increase the strength of density effects (that is, geographic area (km^2; $\log_{10}$ transformed); number of years of study; and number of individuals), all of which we fitted as continuous covariates. Broadly, the animal group model was highly uninformative and competed with the other effects, and we expected that the phylogeny would be more informative, so we report the results of the model without the animal group effect fitted.

We ran several different versions of these meta-analyses. First, we fitted meta-analytical models to the overall linear models of spatial and social interaction types separately, and then together, to investigate differences between the spatial and social networks in terms of their mean density slope. Next, we fitted duplicated versions of these models, but with the saturation models. These models were identical, but each system replicate had two linear estimates: one taken from the first 50% of the data (up to the median); and one taken from the latter 50%. By fitting a binary fixed effect of data portion to the meta-analytical models, this model would tell us whether the slopes were generally higher in the first portion of the data than the last (and therefore showed generally saturating shapes). We were unable to fit meta-analytical models to our GAMs, as methods for the meta-analysis of nonlinear estimates are not yet well defined.

Reporting summary

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

Data availability

The data required to run the meta-analysis models are available from Zenodo at https://doi.org/10.5281/zenodo.15847435 (ref. 87) and

GitHub at https://github.com/gfalbery/DensityMetaAnalysis. The 36 behavioural datasets for each study system can be requested from the data collectors; requests via the corresponding author will be relayed to them.

Code availability

All of the code is available from Zenodo at https://doi.org/10.5281/zenodo.15847435 (ref. 87) and GitHub at https://github.com/gfalbery/DensityMetaAnalysis.

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Author contributions

G.F.A. conceived of and led the study, collated and analysed the datasets and wrote the paper, supervised by S. Bansal. A.R.S. helped to clean the data. D.J.B. helped with meta-analysis of the data. S.R. conducted an independent assessment of the density metric. J.A.F., D.D.M., M.S., E.V.W. and Q.W. advised throughout. All of the other authors donated data. All authors commented on drafts of the paper.

Competing interests

The authors declare no competing interests.

Additional information

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Reporting Summary

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Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
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☐	☒	A description of all covariates tested
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☐	☒	For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☐	☒	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☐	☒	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	NA
Data analysis	Data were manipulated and analysed using R version 4.2.3.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
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The data required to run the meta-analysis models are available on Zenodo at https://doi.org/10.5281/zenodo.15847435 on GitHub at github.com/gfalbery/DensityMetaAnalysis. Datasets are available from contributing coauthors upon request.

Research involving human participants, their data, or biological material

Policy information about studies with human participants or human data. See also policy information about sex, gender (identity/presentation), and sexual orientation and race, ethnicity and racism.

Reporting on sex and gender	NA
Reporting on race, ethnicity, or other socially relevant groupings	NA
Population characteristics	NA
Recruitment	NA
Ethics oversight	NA

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We aggregated 36 animal study systems donated by a series of collaborators. In each system, we built density distributions and social and spatial networks, with which we derived individual-level measures of density and connection strength. For each system we built linear and non-linear models examining the relationships between density and connectedness, which we then meta-analysed.
Research sample	The samples described as much data as researchers were willing and able to share. We contacted any researchers we knew had access to spatial and social behavioural datasets, with regular updating when we encountered a new publication with available apparently suitable data. Nobody we contacted did not agree to participate.
Sampling strategy	NA
Data collection	NA
Timing and spatial scale	The study systems were globally distributed and variably over the course of the last four decades, as detailed in the figures in the main text.
Data exclusions	We eliminated individuals that did not have at least 5 observations from the home range overlap analyses, and removed study systems with insufficient replication.
Reproducibility	NA
Randomization	NA
Blinding	NA

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

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Materials & experimental systems

n/a | Involved in the study
☒ ☐ Antibodies
☒ ☐ Eukaryotic cell lines
☒ ☐ Palaeontology and archaeology
☒ ☐ Animals and other organisms
☒ ☐ Clinical data
☒ ☐ Dual use research of concern
☒ ☐ Plants

Methods

n/a | Involved in the study
☒ ☐ ChIP-seq
☒ ☐ Flow cytometry
☒ ☐ MRI-based neuroimaging

Plants

Seed stocks	None
Novel plant genotypes	None
Authentication	None