

## REVIEW

# An evolutionary framework outlining the integration of individual social and spatial ecology

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**Abstract**

1. Behaviour is the interface between an organism and its environment, and behavioural plasticity is important for organisms to cope with environmental change. Social behaviour is particularly important because sociality is a dynamic process, where environmental variation influences group dynamics and social plasticity can mediate resource acquisition. Heterogeneity in the ecological environment can therefore influence the social environment. The combination of the ecological and social environments may be interpreted collectively as the "socioecological environment," which could explain variation in fitness.
2. Our objective was to outline a framework through which individual social and spatial phenotypes can be integrated and interpreted as phenotypes that covary as a function of changes in the socioecological environment. We propose the socioecological environment is composed of individual behavioural traits, including sociality and habitat selection, both of which are repeatable, potentially heritable and may reflect animal personality traits. We also highlight how ecological and social niche theory can be applied to the socioecological environment framework, where individuals occupy different socioecological niches. Individual sociality and habitat selection are also density-dependent, and theory predicts that density-dependent traits should affect reproduction, survival, and therefore fitness and population dynamics.
3. We then illustrate the proximate links between sociality, habitat selection and fitness as well as the ultimate, and possibly adaptive, consequences associated with changes in population density. The ecological, evolutionary and applied implications of our proposed socioecological environment framework are broad and changes in density could influence individual fitness and population dynamics. For instance, human-induced environmental changes can influence population density, which can affect the distribution of social and spatial phenotypes within a population. In summary, we outline a conceptual framework that incorporates individual social and spatial behavioural traits with fitness and we highlight a range of ecological and evolutionary processes that are likely associated with the socioecological environment.

**KEYWORDS**

adaptive landscape, animal personality, ecological niche, indirect genetic effects, isodar analysis, quantitative genetics, resource selection function, social network analysis, social niche specialization, socioecological environment

## 1 | INTRODUCTION

Sociality is common among animals and is a continuum on which species and individuals exist (Alexander, 1974). Sociality broadly refers to interactions among conspecifics in which individuals can display social plasticity, while populations or species can adapt socially; both of which are critical for dealing with environmental change (Hofmann et al., 2014). Individual sociality and the social structures in which individuals exist are highly variable and decisions about sociality are optimized to maximize individual fitness (Farine, Montiglio, & Spiegel, 2015; Silk, 2007). Although links between sociality and fitness are becoming increasingly established (Silk, 2007), this relationship may vary spatiotemporally (Naud et al., 2016). For instance, predation risk and resource availability vary depending on an individual's social position, a relationship which can change through time and space (Hirsch, 2007). As biophysical environmental conditions change spatiotemporally, it becomes important to understand individual variation in resource selection and sociality, and how these traits combine to influence fitness.

Environmental heterogeneity affects social and spatial behaviours, such as social centrality and habitat selection (see definitions below), where spatial and temporal heterogeneity in resources can generate social conflict leading to alternative decisions on resource selection (Sueur et al., 2011). Individual differences in social centrality, defined as “the extent to which an individual is connected to other individuals” (Brent, 2015), and social conflict can affect the relationship between sociality and fitness. Specifically, fission–fusion dynamics are one form of social conflict leading to temporary spatial segregation, which can be adaptive (e.g. Haydon et al., 2008) or maladaptive (e.g. Sigaud et al., 2017). Individuals are expected to benefit from fission–fusion by reduced competition during foraging, a process which could occur through social familiarity. For example, spotted hyaenas (*Crocuta crocuta*) adjusted grouping behaviour through fission–fusion in response to changes in feeding competition (Smith, Kolowski, Graham, Dawes, & Holekamp, 2008), while in great tits (*Parus major*), fledging success was greater for females with socially familiar neighbours (Grabowska-Zhang, Wilkin, & Sheldon, 2011). These examples highlight how fission–fusion dynamics are a product of ecological variation, and also the catalyst for producing a social environment that can affect fitness. The social environment reflects interactions among conspecifics that occur during a specific time frame (Saltz, Geiger, Anderson, Johnson, & Marren, 2016), and fission–fusion may represent a possible link between social and ecological environments.

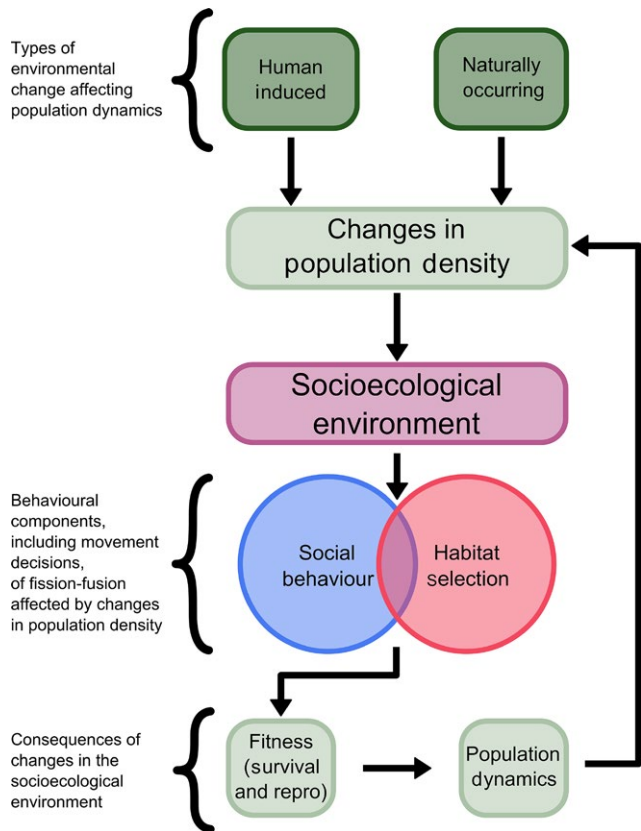
A promising route linking fission–fusion and fitness exists through understanding how individuals interact with their environment through habitat selection (Morris, 2011) and through social attraction (Fletcher, 2009). We adopt the definition of habitat used by Morris (2003), where habitat is: “a spatially bounded area, with a subset of physical and biotic conditions, within which the density of interacting individuals, and at least one of the parameters of population growth, is different than in adjacent subsets.” While this definition of habitat is idealistic, it is important to note that natural systems are often difficult to delineate as stringently. Habitat selection determines the spatiotemporal distribution of individuals

with consequences for individual behaviour, population dynamics and intraspecific interactions (Morris, 2011; van Beest et al., 2014). Theoretically, individuals select habitat that maximizes fitness (McLoughlin, Morris, Fortin, Vander Wal, & Contasti, 2010), illustrating the adaptive value of habitat selection. Heterogeneity in the spatiotemporal distribution of resources reveals strategies of resource selection, where individuals can range from resource specialists to generalists, a process that indicates that resources are selected along a gradient (Fortin, Morris, & McLoughlin, 2008). Resource gradients reflect heterogeneous environments, which favour fission–fusion dynamics (Sueur et al., 2011). Therefore, variation in habitat selection as a function of spatiotemporal variation in resources could affect social interactions among individuals (Fortin et al., 2009; Haydon et al., 2008), individual fitness and, in turn, population dynamics.

Environmental heterogeneity promotes population-level variation in individual behaviour because different phenotypes have different adaptive values through space and time. Although individual social and spatial behaviour are important, social and ecological environments are particularly likely to covary. The social environment can therefore be perceived as a reflection of the ecological environment and the combined “socioecological” environment represents a novel intersection between individual sociality and habitat selection, which could explain variation in fitness. Intraspecific variation in habitat selection and sociality are therefore inherently linked through the socioecological environment (Figure 1). Adaptive (co) variation in the relationship between habitat selection and sociality could also be subject to selection as individuals maximize fitness. Individual social and ecological environments are highly dynamic, e.g. through fission–fusion, and individuals likely differ in their responses to environmental (social and ecological) heterogeneity. Individual variation is therefore the crux of the socioecological environment and reflects the phenotypes upon which natural selection acts.

To fully elucidate the relationships between sociality, habitat selection and fitness, we have four objectives:

1. We interpret components of the socioecological environment as animal personality or behavioural syndromes. We then propose that traits associated with the socioecological environment are density-dependent and can affect population dynamics (Figure 1).
2. We apply niche theory to the socioecological environment and discuss possible implications of individual fitness in the context of ecological and social niche theory. We also address individual niche specialization and suggest that social and ecological niches likely covary and are repeatable across time or contexts and could therefore reflect an axis of animal personality in the context of the socioecological environment.
3. We propose two conceptual models informed by behavioural ecology and habitat selection theory. These models are thought experiments that include: (1) an illustration of an adaptive landscape used to quantify density-dependent changes in the socioecological environment (Box 1); and (2) a hypothetical fission–fusion society



**FIGURE 1** A simple conceptual framework to illustrate eco-evolutionary dynamics linking components of the socioecological environment and density. Here we illustrate how environmental changes, including naturally occurring and human induced, could affect population density, which drives changes in the socioecological environment through individual social behaviour and habitat selection. This subsequently could affect fitness (i.e. survival and reproduction) and population dynamics

where density-dependent habitat selection and sociality covary to affect fitness (Box 2).

4. We conclude by summarizing our synthesis of the socioecological environment and generalize our conceptual framework by discussing possible ecological, evolutionary and applied implications. We also propose four testable hypotheses, with associated predictions, which could be tested under the framework we develop here (Table 1). We avoid developing our narrative with a specific system in mind so the framework can serve as a general tool for researchers to generate predictions, test hypotheses and apply it broadly to specific systems (but see Table S1 for examples).

## 2 | IMPLICATIONS OF DENSITY-DEPENDENT BEHAVIOURS ON POPULATION ECOLOGY

In the context of the socioecological environment, the link between individual behavioural traits and population ecology may exist through

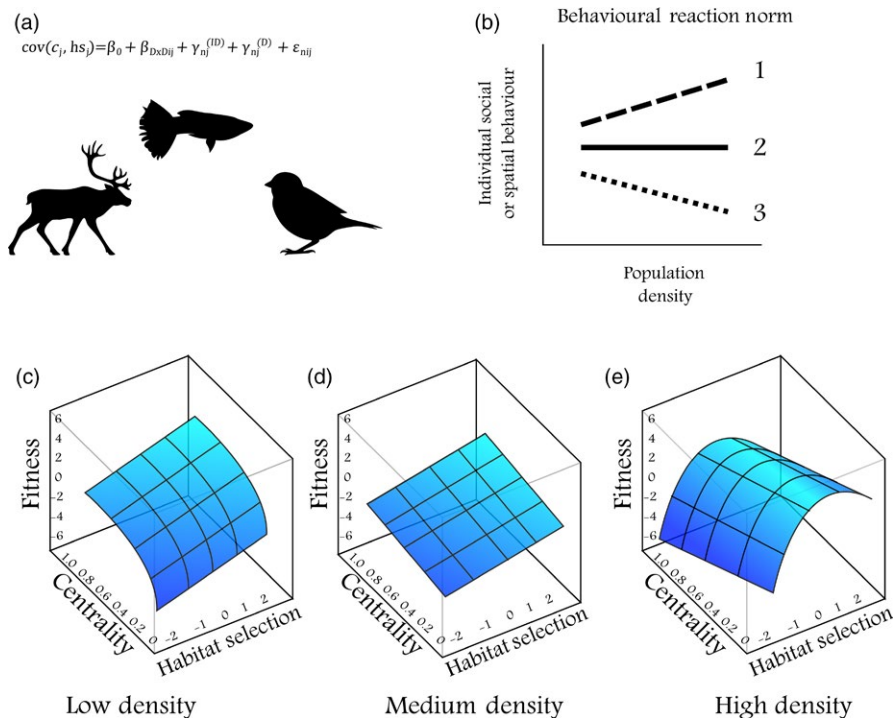
an eco-evolutionary feedback between the distribution of behavioural phenotypes and population dynamics (Figure 1; Ezard, Côté, & Pelletier, 2009). This feedback is possible when environmental conditions affect population density, therefore altering the adaptive value of the trait, which in turn influences the population-level distribution of individual-based phenotypes (Figure 1). The feedback is completed if the phenotype(s) affect population ecology parameters, such as survival and reproduction, which inherently affect population density (Figure 1).

Density dependence is important for the socioecological environment because changes in density are linked to changing fitness proxies. Our understanding of density dependence can help predict how behavioural mechanisms associated with habitat selection influence parameters of population growth (Morris, 2011). Density dependence transcends scales, where the ecological perspective is similar between local and population densities, but the mechanism differs. Density-dependent habitat selection is predicated on the assumption of limited availability of resources per individual at the population scale, but access to resources at the local scale. Habitat selection is density-dependent and has received significant theoretical and empirical attention (Fortin et al., 2008; Morris, 2003; van Beest et al., 2014). An increase in local density via social aggregation can decrease the per capita risk of predation, but predator success may increase as a function of density (Pettorelli, Coulson, Durant, & Gaillard, 2011). However, conspecific competition for resources also changes with overall population density (Hansen, Stenseth, Henttonen, & Tost, 1999) and social behaviours, such as interaction duration or rate, are often density-dependent (Brashares, Werner, & Sinclair, 2010; Vander Wal, Yip, & McLoughlin, 2012).

Individual components of the socioecological environment, including social behaviour and habitat selection, could be interpreted as animal personality, i.e. consistent individual differences in behaviour (Sih, Bell, Johnson, & Ziemba, 2004). The integration of sociality, habitat selection and animal personality, represents an important advance in behavioural ecological theory (for examples integrating sociality and personality, see Krause, James, & Croft, 2010; Wilson, Krause, Dingemanse, & Krause, 2013). The socioecological environment is not itself a measurable trait, but rather it is the combination of social and ecological factors that drive (co)variation between individual social and spatial phenotypes. If these traits are repeatable and correlated, they could be interpreted individually as animal personality. Repeatability ( $r$ ) is a critical aspect of animal personality and is quantified as:

$$r = \frac{V_{\text{among}}}{V_{\text{among}} + V_{\text{within}}} \quad (1)$$

where  $V_{\text{among}}$  is among-individual variation and  $V_{\text{within}}$  is within-individual variation (Bell, Hankison, & Laskowski, 2009). Individually repeatable traits associated with the socioecological environment, such as social centrality (Aplin et al., 2015; Vander Wal, Festa-Bianchet, Réale, Coltman, & Pelletier, 2015) and habitat selection (Leclerc et al., 2016), could be interpreted as a socioecological behavioural syndrome, i.e. a suite of personality traits that are correlated across time and



**BOX 1** (a) Possible applications of multivariate “Animal Model” to quantify the socioecological environment. Covariance between individual values for social centrality ( $c_j$ ) and habitat selection resource selection functions ( $hs_j$ ) are modelled using in a bivariate Animal Model framework (for details and tutorials on appropriate implementation see Housley & Wilson, 2017). Model slope ( $\beta_0$ ) and density ( $\beta_{D \times D_{ij}}$ ) are included as fixed effects, while individual ID ( $\gamma_{n_j}^{(ID)}$ ) and density ( $\gamma_{n_j}^{(D)}$ ) are fit as random intercepts and slopes, enabling the model to be interpreted as a behavioural reaction norm (BRN: Dingemanse et al., 2010). This model could also include simple fixed effects, such as sex or year, while more complex extensions could include matrices of relatedness (i.e. pedigree) or a dyadic network (i.e.  $V_S$ ). While the incorporation of pedigrees within the Animal Model is common, the use of dyadic social network matrices, instead of a pedigree, is a potential tool which could account for variance in one or more response variables as a function of social network position. We note the inclusion of density as a fixed and random effect in our hypothetical “Animal Model” framework fulfils two purposes: (1) inclusion as a fixed effect is to describe the *mean* change of the dependent variable(s) and (2) inclusion as a random effect is to describe *individual* deviation from the fixed effect mean, i.e. plasticity (Dingemanse, Barber, Wright, & Brommer, 2012).

(b) Variation in personality and plasticity can be captured by applying BRNs, which model individual differences (BRN intercept) in the plasticity (BRN slope) of a social or spatial phenotype across an environmental gradient, such as population density. Our hypothetical BRN shows three possible scenarios. Variation in the intercepts of lines 1, 2 and 3 indicate individual differences in social or spatial behaviour in response to changes in population density, while the slopes of lines 1 and 3 represent two ways an individual (or population) could display plasticity, i.e. an Individual–Environment interaction, in response to changes in population density. If social or spatial traits are heritable, lines 1 and 3 represent a Genotype–Environment interaction (Nussey et al., 2007). Line 2 represents a scenario with no behavioural plasticity.

(c, d and e) Hypothetical adaptive landscapes at three densities: low, medium and high. Each landscape models the relationship between centrality ( $c$ ) and habitat selection ( $hs$ ) and estimates their covariance to produce an optimal fitness based on two predictions derived from (1) the social centrality hypothesis and (2) density-dependent habitat selection theory. (1) We predict that the benefit of being central will be higher at low density when competition for resources is lowest, whereas as population density increases so too do the costs of competition with conspecifics. (2) Density-dependent habitat selection predicts that at low density individuals will improve their fitness by being selective, i.e. resource specialists, whereas at higher density individuals should become resource generalists (Fortin et al., 2008).

Adaptive landscapes illustrate the covariance of traits which accord the highest fitness in light blue, while lowered fitness is denoted by darker blue segments. Values for habitat selection reflect an individual's selection (positive numbers) or avoidance (negative numbers) of specific habitats and values for centrality range from highly central (close to 1) to peripheral (close to 0). For each adaptive landscape, individual values of centrality and habitat selection at fitness optimum could be extracted and plotted across densities using the BRN approach to determine individual differences (intercept) and plasticity (slope).

(Continues)

**BOX 1** (Continued)

- (c) Adaptive landscape at low density yields highest fitness for individuals with high centrality that strongly selects a given habitat, while fitness is lowest for individuals with low centrality that avoids that habitat.
- (d) Adaptive landscape at medium density yields highest fitness for individuals that select a focal habitat, e.g. Habitat A from Box 2, and tend to be less social relative to low density, while fitness is lowest for individuals with higher centrality that avoid that habitat.
- (e) Adaptive landscape at high density yields highest fitness for habitat generalists that have low centrality, while fitness is lowest for central individuals that select and avoid that habitat.

contexts (Sih, Cote, Evans, Fogarty, & Pruitt, 2012). Traits which comprise behavioural syndromes are also repeatable and these correlations are likely driven by underlying genetic covariation. The relationship between social and spatial behavioural traits and fitness is important because consistent correlations among behaviours across changes in population density could represent a potential adaptive landscape, where fitness varies as a function of the correlation between social and spatial traits (for detailed illustration see Box 1). Although animal personality is focused broadly within evolutionary and behavioural ecology, and personality can be quantified relatively easily, it is through theoretical and practical approaches that we aim to ground our integration of personality within the socioecological environment.

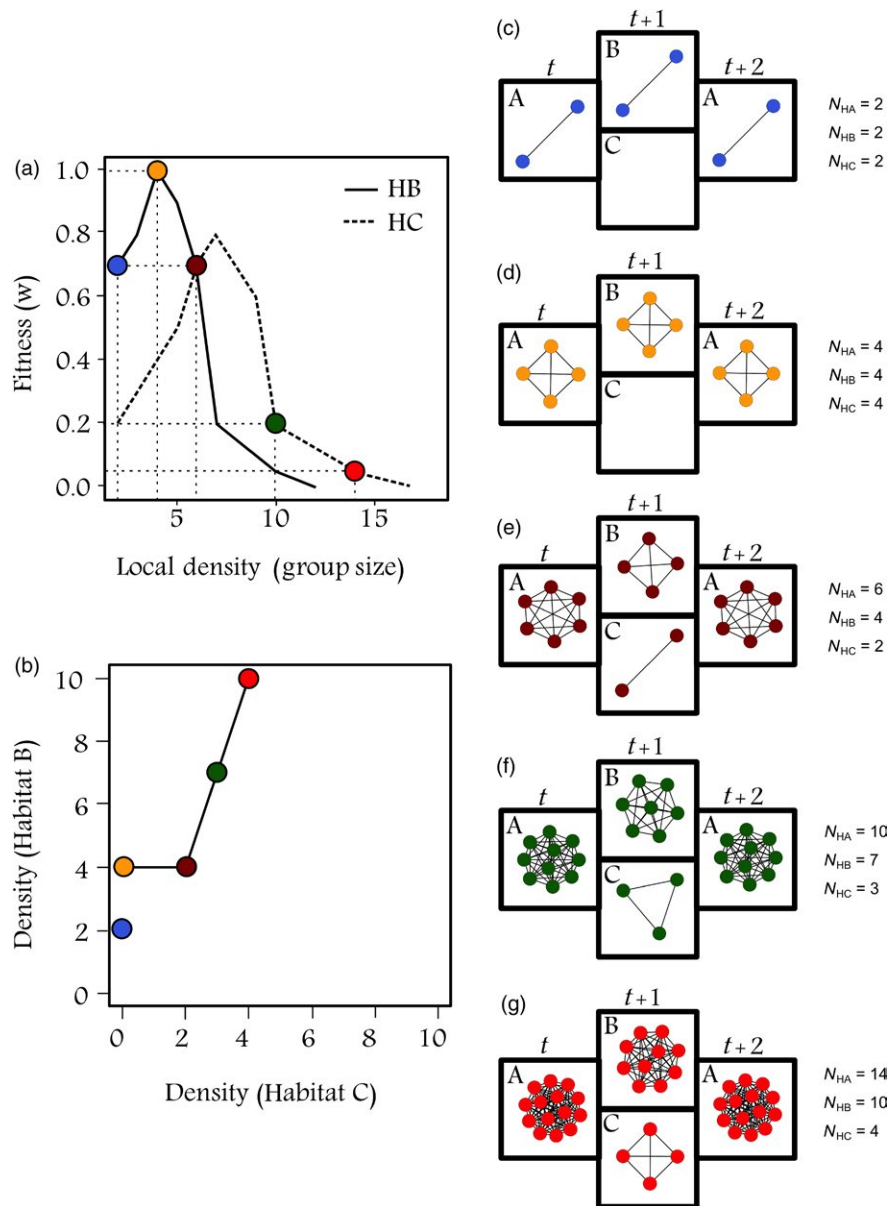
The animal personality concept purports that individual behaviours are consistent across time and context and are likely the result of adaptive evolution (Wolf & Weissing, 2010). However, plasticity is an important aspect of behavioural variation because it allows individuals within a population to respond appropriately to environmental variation and optimize fitness (DeWitt, Sih, & Wilson, 1998). Behaviour is not infinitely plastic and individuals are often limited in their responses through constraints in sensory processing, cognitive ability and morphology (Mathot & Dingemanse, 2015). While personality traits were historically interpreted as consistent, and thus relatively fixed, an exciting aspect of personality research incorporates behavioural plasticity associated with personality traits (Brommer, 2013). Specifically, personality incorporates aspects of plasticity and individuals should respond appropriately, but consistently relative to conspecifics, to changing environments (e.g. using behavioural reaction norms: Mathot, Wright, Kempenaers, & Dingemanse, 2012). Moreover, repeatability of behavioural plasticity, for instance year-to-year repeatability, is adaptive when costs associated with plasticity decrease with an individual's experience to environmental variation (Wolf, van Doorn, & Weissing, 2008). Indeed, while behavioural plasticity can be adaptive, personality explains a large proportion of variation in behavioural plasticity (Dingemanse, Kazem, Réale, & Wright, 2010; Nussey, Wilson, & Brommer, 2007) and the integration of animal personality and quantitative genetics has confirmed the importance of genetic and environmental effects in personality-related differences in plasticity (Dochtermann, Schwab, & Sih, 2015; Mathot & Dingemanse, 2015).

The application of quantitative genetics in the context of the socioecological environment could elucidate underlying genetic mechanisms which drive variation in social and spatial phenotypes. Selection can have direct and indirect genetic effects (DGEs and IGEs,

respectively), where DGEs are the effect of an individual's own genotype on their phenotype and IGEs are the effect of a conspecifics genotype on the focal individual's phenotype (Bijma & Wade, 2008; Ellen et al., 2016). IGEs may be important for the evolution of social behaviour because social plasticity could arise as a function of phenotypes expressed by conspecifics (Dingemanse & Araya-Ajoy, 2015), a process which could be particularly important for our understanding of the socioecological environment. If habitat selection is linked to social cues from conspecifics (Fletcher, 2007), IGEs could also be important for understanding how individuals rely on conspecifics for information about habitat quality. In the context of the socioecological environment, IGEs can be proximately manifested as inter-individual interactions, such as aggression (Wilson, Gelin, Perron, & Réale, 2009), or emergent properties of a social group, such as group phenotypic composition (Farine et al., 2015), and these processes can ultimately explain variance in individual behaviours as well as the population-level distribution of a given behaviour.

Changing population density has potential as a selective pressure which can alter the socioecological environment. At high population density one might expect an increase in competition for resources, which could affect social aggregation and spatial distribution of individuals (Box 2). Changes in population density, or other environmental variables, can influence the relationship between social or spatial behaviours and fitness, and represent a gradient across which fitness is maximized (Sih, 2013). A given social or spatial behaviour is adapted to the environment in which the genotype controlling the phenotype reproduces at least once, and to be adaptive, these behavioural phenotypes must vary at the population-level across an environmental gradient (i.e. with minima, maxima and a mean). In the case of the socioecological environment, individuals range along a social continuum from highly social to relatively asocial (Wey, Blumstein, Shen, & Jordán, 2008) and a habitat selection continuum from specialist to generalist (Fortin et al., 2008). If environmental conditions associated with a behavioural phenotype change, there could be a mismatch between the original distribution of phenotypes, which matched the historical environment, and the current environment (Hendry et al., 2011). The distinction of individually based traits with a given population-level distribution is important because a hypothetical repeatable and heritable behavioural phenotype may be well-suited to the historical environment, but is maladaptive in the current environment. While individual plasticity is typically sufficient to cope with most environmental perturbations, behavioural adaptation occurs when a subset of individuals reproduce and another subset of individuals fail to reproduce.





**BOX 2** Classic habitat selection theory is centred around the ideal free distribution (IFD) model where animals select habitat to maximize fitness (Fretwell & Lucas, 1969). IFD theory posits, among other things, that habitat selection is density-dependent such that variation in density in different habitat patches leads to a fitness equilibrium (Bradbury, Vehrencamp, & Clifton, 2015). Fitness in a habitat patch depends on density where, ideally, the available resources on a habitat patch can sustain a specific number of individuals. Extensions of IFD have yielded important contributions to habitat selection theory. Specifically, Morris (1987) developed “isodar analysis” to model density-dependent habitat selection. Isodar analysis assumes that, in a finite world, fitness in a habitat declines after a critical threshold as a function of density (Morris, 2011); unlike IFD, isodar theory does not have an assumption of proportionality, hence the nonlinear relationship between fitness and density in (a). IFD theory has received extensive attention at the population-level (Morris, 1987, 2003, 2011), despite the expectation that *individuals* are predicted to distribute themselves across habitats that accord the highest fitness. Indeed, IFD predicts that *mean* fitness in each habitat will be equal, implying that individual variation should still exist among individuals within each habitat.

(a) Distribution of fitness ( $w$ ) values as a function of *overall* local density, which is analogous to group size, in two habitats (HB, solid line and HC, dashed line). Animals move from Habitat A (HA), a neutral starting point for our conceptual game, to HB and HC to equilibrate fitness (see below). Carrying capacity ( $K_i$ ), i.e. the group size at which  $w = 0$ , for habitat B ( $K_{HB}$ ) = 12, while  $K_{HC}$  = 5 (points at which solid [HB] and dashed [HC] habitat isoclines intersect and  $w = 0$ ). Note, values of  $K$  were arbitrarily selected for this example. Each habitat has an optimal

(Continues)

**BOX 2** (Continued)

group size where mean fitness is maximized and the distributions of fitness represent a functional response to changes in local density for each habitat (Krause & Ruxton, 2002; Sibly, 1983). Coloured points represent one of five scenarios outlined in (c–g) where a fission–fusion population with different starting densities moves through space. At low density ( $n < 4$ ), fitness in HB > fitness in HC, so individuals remain in a single group and enter HB as a single group (c and d), a process which occurs up to a certain density threshold. Consistent with density-dependent habitat selection, this threshold is surpassed when isoclines for each habitat intersect, in this case  $n = 6$  (e). At this point, individuals begin to filter, i.e. fission, into HC where fitness is *equal* for individuals in HB and HC (f and g), which can be visualized as an isodar (i.e. line of equal fitness) in (b). As dictated by density-dependent habitat selection, population density represents the *sum* of the values from the x-axis where fitness is equal in both habitats, so, for example, if local density is 10 individuals (green point), the first seven individuals will filter into HB and the next three individuals will filter into HC (f). This generates a scenario where fitness is equal and can be visualized by following the horizontal dashed lines in (a), e.g.  $w = 0.2$  from (a) between habitats and the link between the isodar in (a) and the fission–fusion diagram in (f) is the *sum* of population densities in each habitat (7 and 3 respectively) where fitness is equal. *Note:* without the IFD assumption that habitats increase proportionally, the relationship between habitat and density is nonlinear relationship in both habitats.

(b) The functional response observed in (a) can be mapped using the logistic population growth function:

$$\frac{1}{N_i} \frac{dN_i}{dt} = r_i \left( 1 - \frac{N_i}{K_i} \right) \quad (4)$$

where  $N_i$  is the density of individuals in habitat  $i$ ,  $r_i$  is the rate of population growth. Following Equation 4, a habitat isodar, i.e. the pair of local densities from HB and HC where fitness is equal, can be generated. In the two-habitat scenario described above, strategies are identified by the proportion ( $p$ ) of individuals in HB ( $0 \leq p \leq 1$ ), or alternatively ( $q$ ) the proportion of individuals in HC ( $q = 1 - p$ ). Following Morris (2011), mean fitness for any strategy is:

$$p \cdot r_1 \left( 1 - \frac{N_1}{K_1} \right) + q \cdot r_2 \left( 1 - \frac{N_2}{K_2} \right) \quad (5)$$

Equation 5 is the adaptive landscape of how fitness varies as a function of density-dependent habitat selection. The positive trend line through coloured points represents an isodar, which can be interpreted as the density in a pair of habitats where fitness is equal. Density-dependent habitat selection theory posits that individuals in a population will occupy a given habitat up to a certain density before filtering, or in this case fissioning, into a new habitat. *Note:* colours for each point represent scenarios outlined in (c–g).

(c–g) Schematic representation of fission–fusion dynamics for the same population of a hypothetical gregarious organism at different local densities in Habitat A across an initial time ( $t$ , left-hand boxes), second time step ( $t + 1$ , centre boxes) and a final time step ( $t + 2$ , right-hand boxes). Time  $t$  reflects an ideal habitat patch, while time  $t + 2$  is a return to this patch via the patchy landscape displayed in time  $t + 1$ . These hypothetical scenarios were parameterized based on: (1) density-dependent habitat selection theory, which suggests that individuals occupy a given habitat up to a certain density at which point animals distribute themselves according to IFD (i.e. from HA to HB and HC); and (2) optimal group size theory, suggesting an optimal group size that maximizes fitness. Costs of sociality are predicted to increase more rapidly than the benefits, so the relationship between fitness and group size should be bell-shaped (a).

Coloured nodes in each network represent individuals and each series of fission–fusion events begins at a given local density (2, 4, 6, 10 and 14, for each panel). We held individual centrality values equal across all networks, and individuals were never solitary because the hypothetical organism in our model is gregarious and, in our example, being solitary incurs a fitness value of zero. In each scenario, three habitats (HA, light green boxes on left and right side of each diagram; HB, purple box on top; HC, light blue box on bottom) are represented. At time  $t$ , one of two events occur: (1) the group transitions from HA to HB as a fused unit (c and d); or (2) the group fissions from HA to HB and HC (e, f, and g). Groups remain fused in (c and d) because fitness is higher if individuals stay together, while the groups fission in (e, f and g) to ensure mean fitness is equal between habitats.

Maladaptive phenotypes result in reduced reproduction and survival, which subsequently change population density and can result in a shift in the adaptive capacity of a given phenotypic trait. Behavioural plasticity is important because, in the context of the socioecological environment, maladaptive behavioural responses can affect how animals forage or disseminate social information about novel food patches. For instance, bison (*Bison bison*) are hunted at higher rates

on agricultural patches, but bison that foraged on agricultural patches for the first time were more likely to access these patches with bison that had previously foraged on these patches (Sigaud et al., 2017). Although using agricultural patches may provide proximal benefits, i.e. higher quality or quantity of forage, ultimately, this behaviour is maladaptive because it reduces survival. As population density changes, behavioural plasticity could improve an animal's ability to

**TABLE 1** Summary of four hypotheses with associated predictions and empirical examples. These hypotheses could be tested in the context of the socioecological environment framework outlined in our conceptual synthesis

Hypotheses	Associated predictions	Example	References
Social Phenology Hypothesis	P1: Social interactions or aggregations will change across seasons in response to environmental variation.	In desert night lizards ( <i>Xantusia vigilis</i> ), social aggregation promotes social thermoregulation during winter, when ambient temperature is low, which confers an increase in reproductive success and survival among adult lizards.	Rabosky, Corl, Liwanag, Surget-Groba, and Sinervo (2012)
	P2: Social or socioecological decisions of an animal in one season will carry-over and enhance fitness in a subsequent season.	In great tits ( <i>Parus major</i> ), social foraging associations in winter carried over to spring territory establishment, where close associates in winter had adjacent territories in spring.	Firth and Sheldon (2016)
Social Assortment Hypothesis	P1: Individuals will actively assort through sexual segregation, where individuals tend to have stronger social associations with members of the same sex or age classes.	For ungulates, resource acquisition appears to drive sexual segregation because males and females vary in their activity levels, and thus energy-forage requirements. Females are expected to require higher quality forage, while males rely on lower quality, but higher quantity, forage.	Ruckstuhl (2007)
	P2: Individuals will behaviourally assort according to variation in their personality traits. Behavioural assortment can be positive or negative.	In guppies ( <i>Poecilia reticulata</i> ) and three-spined stickleback ( <i>Gasterosteus aculeatus</i> ), individuals assorted based on the shy-bold personality axis, where shy fish had stronger, but fewer, social connections compared to bold fish, which had many weak social connections.	Pike, Madhumita, Lindström, and Royle (2008); Croft et al. (2009)
Conspecific Attraction Hypothesis	P1: Individuals will use social information to make habitat searching and settlement decisions.	Least flycatchers ( <i>Empidonax minimus</i> ) used conspecific cues during habitat settlement regardless of patch size, suggesting flycatchers use social information to make decisions during habitat selection.	Fletcher (2009)
Resource Dispersion Hypothesis	P1: Territory size will be determined by dispersion of habitat patches with a given resource.	Dingo ( <i>Canus lupus dingo</i> ) territories were smaller when resources (food supplementation sites) were spatially aggregated on the landscape.	Newsome, Ballard, Dickman, Fleming, and van de Ven (2013)

use social or spatial cues to access resources. This type of behavioural response could shape future evolution and facilitate a phenotypic transition from one adaptive peak to another (Sih, Ferrari, & Harris, 2011). Moreover, while natural fluctuations in density are common, anthropogenic factors can expedite changes in density (negatively or positively) and alter the distribution of density-dependent phenotypic traits in the population.

As individually quantifiable components of the socioecological environment, sociality and habitat selection are linked through possible (co)variation in response to changes in population density. Density is a selective agent for habitat selection and some social behaviours and could be incorporated into a feedback loop (Figure 1). Few studies have empirically quantified the relationship between sociality, habitat selection and population density. In an experimental manipulation, flycatchers (*Empidonax minimus*) and American redstarts (*Setophaga ruticilla*) used social cues about habitat settlement, a process which was strongest at moderate densities (Fletcher, 2007). At low densities, individual birds received little benefit from social cues, while at high densities, competition was costly and individuals did not display social cues (Fletcher, 2007). Meanwhile, vigilance behaviour and territorial vocalizations, i.e. aspects of social behaviour, were higher for red squirrels (*Tamiasciurus hudsonicus*) at food-supplemented sites where

squirrel density was consistently high (Dantzer, Boutin, Humphries, & McAdam, 2012). While these examples represent valuable contributions linking sociality, habitat selection and density, density-dependent changes in the trait distribution of adaptive social and spatial phenotypes could affect reproduction, survival and ultimately fitness.

### 3 | THE APPLICATION OF NICHE THEORY

#### 3.1 | Ecological niche

The socioecological environment can also be integrated with other ecological concepts. An ecological niche is a species distribution that is constrained based on the “biophysical and environmental conditions across geographical space” (Soberón, 2007; Trainor & Schmitz, 2014). Ecological niches are quantified using species distribution models (SDMs), by denoting the area occupied by a species, compared to the available area, as a function of a set of environmental variables which constrain or facilitate species persistence (Trainor & Schmitz, 2014). Within a species distribution and ecological niche, fitness varies because resources and competitors are heterogeneous, resulting in a series of optimal biophysical and ecological conditions where fitness is optimized (Trainor & Schmitz, 2014). Fitness



can be visualized using contours that represent biophysical space (i.e. niches) with equal fitness levels as contours (Soberón, 2007). Inherently, a model with fitness contours also assumes intraspecific variation (or “internal structure,” sensu Trainor & Schmitz, 2014), indicating that individuals possess a range of phenotypic characteristics (e.g. behavioural, physiological or life-history traits) which allows them to optimize fitness based on spatiotemporal variation in resources within their biophysical environment. This process is equivalent to the adaptive landscape concept (Box 1), where individuals occupy social and ecological environments that maximize fitness.

Differences in habitat selection among individuals within a population has been interpreted as an “individual niche” (Bolnick et al., 2003), where an ecological environment is partitioned among individuals and occupied differentially. Ecologically, the niche concept could help explain intraspecific variation in behavioural processes, such as diet specialization (Araújo, Bolnick, & Layman, 2011), while evolutionary, these behavioural processes could explain variation in fitness. The fundamental assumptions underlying niche theory can be transferred to the classic habitat selection literature (Morris, 2003). Fine-grained habitat selection is often quantified with resource selection analyses (e.g. step selection functions: Fortin et al., 2005; ecological niche factor analysis: Basille, Calenge, Marboutin, Andersen, & Gaillard, 2008; resource selection functions [RSFs]: McLoughlin et al., 2010; integrated step selection functions: Avgar, Potts, Lewis, & Boyce, 2016). RSFs are likely the most commonly used method and are defined by characteristics measured on resource units such that selection of a unit is modelled as being proportional to the probability of a unit being occupied by an individual (Manly, McDonald, Thomas, McDonald, & Erickson, 2002; McLoughlin et al., 2010). Similar to SDMs, RSFs represent spatiotemporal selection of resources by an individual, or population, relative to randomly distributed available habitat and can reflect habitat selection for an individual or population-level subset of the SDM. The sum of all individual RSFs are equal to the SDM and emerging theoretical and empirical evidence suggests individual behavioural consistency in resource selection (Leclerc et al., 2016; Matthiopoulos et al., 2015).

Individuals make resource selection decisions to maximize fitness. For example, in female red deer (*Cervus elaphus*), lifetime reproductive success (LRS) was higher for grassland specialists at low densities, whereas habitat generalists had higher LRS at high densities (McLoughlin, Boyce, Coulson, & Clutton-Brock, 2006). An individual's RSF, i.e. ecological niche, can be considered along a gradient, ranging from resource specialists to generalists, a process which is density-dependent (Fortin et al., 2008). Moreover, habitat selection can influence fitness (e.g. adult reproductive success: McLoughlin et al., 2006; survival: DeCesare et al., 2014) suggesting that, if repeatable and heritable, variation in habitat selection is evolutionarily adaptive (Wolf & Weissing, 2010). For example, brown bears (*Ursus arctos*) selected for bogs and timber-harvest cut blocks, and this behaviour was strongly repeatable over time, providing empirical evidence for consistent individual differences in habitat selection (Leclerc et al., 2016). Animal personality theory could therefore contribute to the habitat selection

and individual niche concepts and is one possible mechanism explaining individual variation in habitat and resource selection.

### 3.2 | Social niche

Niche theory can also be readily applied to social specialization, where the social environment is analogous to the ecological environment and individuals occupy specific social niches (Montiglio, Ferrari, & Réale, 2013). This integration is highly relevant to the socioecological environment. While consensus to adequately define a “social niche” is lacking, we rely on the definition proposed by Saltz et al. (2016), where “the social niche is the set of social environments in which the focal individual has non-zero inclusive fitness.” Importantly, this definition incorporates fitness which, based on ecological niche theory, should be optimized as a function of the social environment and individual behaviour to generate social niches (Saltz et al., 2016). The inclusion of fitness also provides an important analogue to Morris's (2003) definition of habitat, where fitness is affected by variation in a phenotypic trait (social or spatial) across environments that differ in at least one parameter of population growth (e.g. survival or reproduction). This parallel is important in the context of the socioecological environment because we expect social and spatial phenotypes to differentially affect fitness as a function of density (Box 1), an expectation which extends to individual-based social and ecological niche theory. Moreover, the analogy between ecological and social niches also relies on fitness, and by co-opting ecological niche theory, an individual's social niche could be mapped using fitness contours, e.g. an adaptive landscape (Box 1), to denote variation in fitness across social and ecological environments.

Similar to an individual ecological niche (Bolnick et al., 2003), social niche specialization also assumes consistent individual differences in behaviour. Individual differences in social niches should arise when different social environments favour different behavioural phenotypes (Saltz et al., 2016). Individual differences in social associations can emerge from the population-wide social niche, and between-individual variation in social niche specialization could be adaptive. Social niche specialization could arise through several possible behavioural mechanisms. Stable and predictable behavioural differences among group members along with repeated interactions among individuals could reinforce social specialization and result in the development of social niches (Montiglio et al., 2013). For example, spider colonies that interacted frequently had similar consistency in social behaviours, indicating colony similarity could maintain the social niche (Laskowski & Pruitt, 2014). In addition, social niche specialization could arise through social assortment (see Table 1), where individuals are predicted to assort according to specific phenotypic similarities or dissimilarities. In the context of social niche specializations, individuals may consistently assort according to particular combinations of their own social phenotype and the social phenotypes of conspecifics (Laskowski, Montiglio, & Pruitt, 2016).

In contrast to ecological niches, consensus on standardized methods for quantifying social niches is lacking; however, social network analyses represent a promising tool for quantifying individual social

niches (Saltz et al., 2016). Quantifying aspects of social niches requires social interaction and fitness data to be collected across a range of social environments. Arguably, the simplest way to quantify social niches is to quantify the number of social partners of a focal individual, i.e. degree (see glossary). Determining the identity and social phenotype of a focal individual's social partners adds a layer of complexity to social niche specialization, while determining the repeatability of dyadic social interactions across social environments provides information about an individual's social fidelity (Modlmeier et al., 2014). While individual social niches can be quantified using network analyses, individually based traits could also be integrated within the broader socioecological and statistical framework that incorporates aspects of animal personality, RSFs and quantitative genetics.

Niche theory provides an opportunity to integrate IGEs into the socioecological environment framework. Genetic variance is partitioned into direct genetic effects (DGEs), which is synonymous with  $V_I$  (genetic variance explained by the phenotype of a focal individual), and IGEs, which is synonymous with  $V_S$  (genetic variance explained by the phenotypes of conspecifics).  $V_I$  reflects social specialization of a focal individual and  $V_S$  reflects social specialization of conspecifics (Dingemanse & Araya-Ajoy, 2015). Incorporating IGEs into niche theory could help explain variation in individual social and ecological niche specialization. In the context of the socioecological environment, social phenotypes of conspecifics could affect both social and spatial phenotypes of focal individuals. Individuals range along specialist-generalist social or ecological niche continua (Saltz et al., 2016). The breadth of a social or ecological niche is the total niche width (TNW) of all individuals within the population (Bolnick et al., 2003):

$$\text{TNW} = \text{BIC} + \text{WIC} \quad (2)$$

where BIC and WIC are the between- and within-individual components of the niche respectively. TNW measures the size of the average individual's niche (Araújo et al., 2011). To fully integrate niche theory within the conceptual framework of the socioecological environment, we propose a modification to Equation 2. Based on Equation 1, repeatability is calculated from  $V_{\text{within}}$  and  $V_{\text{among}}$ , and Equation 2 could be modified to calculate ecological or social niche repeatability, as  $\text{TNW}_r$ :

$$\text{TNW}_r = \frac{\text{BIC}}{\text{BIC} + \text{WIC}} \quad (3)$$

where BIC is equivalent to  $V_{\text{among}}$  and WIC is equivalent to  $V_{\text{within}}$ . Thus,  $\text{TNW}_r$  is analogous to  $r$  and we suggest that by calculating  $\text{TNW}_r$ , the niche concept could be effectively translated to the individual niche, where ecological or social niche repeatability could be calculated across time or contexts. Mathematically, Equation 3 is a simple form of variance partitioning where individual niche variance is attributed to among (BIC) and within (WIC) individual components of a niche. This extension also empirically links the socioecological environment and niche theory. For instance, similar to quantifying repeatability of habitat selection (for methodological details, see Leclerc et al., 2016), individual niches may be repeatable and reflect personality traits, while correlations among social and ecological niches could be one component of a socioecological behavioural syndrome.

Niche theory is a foundational ecological concept, and while it has largely been applied at the population and species levels, empirical and theoretical advances (Bolnick et al., 2003; Pruitt et al., 2017) have expanded niche theory to individuals. For instance, individual behaviour and niche theory have recently been integrated as "behavioural hypervolumes," which is defined as the multi-dimensional behavioural trait space of an individual or population (see glossary; Pruitt, Bolnick, Sih, Dirienzo, & Pinter-wollman, 2016; Pruitt et al., 2017). Ecological and social niche covariance is expected within a behavioural hypervolume context because certain ecological and social niches may facilitate the realization of niche space for the opposite trait. However, if social or ecological environments change, the evolutionary trajectory of an individual's social or ecological niche could be displaced. In red squirrels and eastern chipmunks (*Tamias striatus*), fluctuation in the abundance of food via seed masting can result in fluctuating selection of personality traits where certain individuals have higher fitness when food resources are abundant vs. scarce (Boon, Réale, & Boutin, 2007; Montiglio, Garant, Bergeron, Messier, & Réale, 2014). In the context of the socioecological environment, group size of bison was greater in meadow habitats compared to forested habitats (Fortin et al., 2009), but if meadow niches are altered, covariance between social and ecological phenotypes may be disrupted and the distribution of these traits may shift (Box 1). This shift could therefore alter the range of social niches within the population. We propose that variation in social and spatial phenotypes could, at least partially, be explained by incorporating niche theory, animal personality, and quantitative genetics within the broader framework of the socioecological environment.

## 4 | DISCUSSION

We propose a framework through which the socioecological environment, measured as individual social and spatial phenotypes that affect fitness, can be quantified across population densities (Figure 1). In our synthetic review, we suggest parallels between ecological and social niche theory and what we term the socioecological environment, while we also argue the socioecological environment is composed of individual-level traits that can be interpreted as animal personality, but collectively may represent a behavioural syndrome. Our conceptual models reflect (1) the socioecological environment as a series of adaptive landscapes which change as a function of density (Box 1) and (2) the importance of density-dependent habitat selection and optimal group size theory for fission-fusion dynamics in the context of the socioecological environment (Box 2).

Individual sociality and habitat selection are often density-dependent, and changes in density could alter the distribution of these traits in ways that could affect fitness and population dynamics (Figure 1). The shift from one adaptive landscape to another reflects adaptation in social and spatial phenotypes, a process which could be facilitated by behavioural plasticity. While plasticity is important, individual components of the socioecological environment may reflect repeatable, and possibly heritable, personality traits. Correlations

between social and spatial personality traits may also reflect a socioecological behavioural syndrome.

#### 4.1 | Ecological, evolutionary and applied implications

Variation in the socioecological environment is ultimately driven by changes to the biophysical environment (Figure 1). While changes in environmental conditions, such as population density, can change the distribution of phenotypes within a population, a range of mechanisms exist which could affect the relationship between social or spatial phenotypes and fitness. For instance, animal social and spatial cognitive processes (see glossary) could be important mechanisms underlying adaptive behaviours (Seyfarth & Cheney, 2015). Specifically, an individual's ability to access and exploit resources is inherently associated with a range of cognitive strategies, including inherited genetic triggers, memory of past experiences or direct social cues (Fagan et al., 2013; Spiegel & Crofoot, 2016). Factors associated with cognition can therefore influence the proximate relationship between an organism and their socioecological environment. Cognition is an important aspect of the socioecological eco-evolutionary feedback loop linking individual phenotypes to down-stream fitness outcomes (Figure 1).

Social and spatial cognition are inherently linked, and in the context of the socioecological environment, fission–fusion dynamics are highly relevant. Fission–fusion dynamics are cognitively complex because individuals are required to process cues from both social and spatial environments (Aureli et al., 2008). Individuals form long-lasting social associations with conspecifics who they may not encounter for extended periods of time, and to maintain social cohesion over time individuals must remember former group members. In bison, fission–fusion operates on a short time-scale (21 hr: Merkle, Sigaud, & Fortin, 2015), while for some birds, fission–fusion occurs on a seasonal, or yearly, time-scale (Silk, Croft, Tregenza, & Bearhop, 2014). Fission–fusion is also a spatial process, where movement decisions associated with the timing of fission or fusion are driven by environmental variation. Species with fission–fusion societies represent potential model systems to test the “social phenology hypothesis” (Table 1), where, for example, seasonal variation in resources (e.g. foraging resources) may drive changes in covariance of social and spatial phenotypes, and thus fission–fusion dynamics. Whether an animal's decision to fission or fusion occurs on short- or long-term time-scales, animals process complex information acquired from, among other things, ecological and social cues (Box 2; Seyfarth & Cheney, 2015; Spiegel & Crofoot, 2016).

In an applied context, the conceptual framework of the socioecological environment (Figure 1) is fundamental to social animals, but is particularly apt for understanding human-induced rapid environmental change (HIREC). The ability to respond to naturally occurring environmental change is typically within the trait distribution observed in a population; however, HIREC can expedite the mismatch between old phenotypes and new environments (Sih et al., 2011; Vander Wal, Garant, Festa-Bianchet, & Pelletier, 2013).

Integrating the socioecological environment within HIREC is important because HIREC is predicated on the density-dependent adaptive value of traits that are often affected by human disturbance: habitat selection and social structure. Habitat loss and fragmentation are important aspects of HIREC (Sih et al., 2011), and fragmentation can influence resource selection decisions and social dynamics. Habitat fragmentation can also alter density through changing diversity, availability or access to resources (e.g. foraging or breeding sites; Tuomainen & Candolin, 2011), processes which could also affect the social environment. For example, in brushtail possums (*Trichosurus cunninghami*), occupancy rates of tree hollows was low in undisturbed areas where trees were abundant, but in fragmented habitats where tree hollow availability decreased, occupancy rates increased, resulting in larger group sizes (Banks et al., 2013). For least flycatchers, variation in selection of habitat patches was modulated by conspecific attraction and social cues (Fletcher, 2009), suggesting the social environment can influence, or be influenced by, habitat selection (see details on conspecific attraction and resource dispersion hypotheses in Table 1). These examples highlight how ecological and social environments mirror one another, and how changes in one can affect the other, for example, removal of natural corridors could reduce encounter rates among conspecifics. While other aspects of HIREC influence the socioecological environment, habitat fragmentation is a clear example illustrating how social and ecological environments can be decoupled. HIREC-associated habitat fragmentation is one mechanism which directly alters the ecological axis of the socioecological environment, and indirectly alters the social axis.

HIREC can be catastrophic for some species. Specifically, if population density decreases below a critical threshold, extinction may be expedited, a phenomenon known as the Allee effect (Berec, Angulo, & Courchamp, 2007). Allee effects occur when individual fitness or population growth rates decrease below a given threshold (Berec et al., 2007). Species with complex social structures or those where social aggregation or information transfer improve fitness may be particularly vulnerable to Allee effects. For instance, in Vancouver Island marmots (*Marmota vancouverensis*) declining density and increased distance between neighbouring social groups contributed to fewer social interactions and lower feeding rates because individual marmots increased vigilance, a behaviour which would have historically been shared among colony members (Brashares et al., 2010). Incorporating Allee effects within the socioecological environment could yield critical insight into how social and spatial phenotypes respond to changes in population density.

In the context of framing socioecological environment within a broader conservation paradigm, HIREC reflects the habitat selection axis, while Allee effects reflect the social axis. Ultimately, HIREC and Allee effects are linked by density dependence; HIREC changes density, while Allee effects represent a response to changes in density. Understanding how *individuals* respond to HIREC, Allee effects and changes in density, in the context of the socioecological environment, could be a critical, yet under-appreciated aspect of how we apply conservation and management strategies.

## 5 | SUMMARY

We propose the social and ecological environments can be perceived as reflections of one another, linked by their density dependence and interpreted as the socioecological environment. Our conceptual framework outlines ecological and evolutionary analogies of social and spatial phenotypes and the likelihood of a socioecological behavioural syndrome. Components of the socioecological environment are density-dependent, and while we expect they are sufficiently plastic to respond to changes in density, they are also likely repeatable, thus meeting the criteria for individual animal personality traits. We also infer possible evolutionary outcomes associated with the socioecological environment by incorporating quantitative genetics. We suggest the heritability of components of social and spatial phenotypes are influenced by the phenotypes of conspecifics, particularly for fission–fusion societies, suggesting the importance of accounting for IGEs when estimating heritability. The socioecological environment concept shares many similarities with social and ecological niche theory, with an emphasis on the importance of fitness. Density-dependent social and spatial phenotypes, including niches, can therefore influence births and deaths, which over a given time frame can cumulatively affect individual fitness and its sum: dynamic population growth. Therefore, covariation in density-dependent individually consistent social and spatial behaviours and their adaptive value may explain variation in population dynamics. If social and spatial phenotypes are heritable and (co)vary across a population density gradient, their adaptive value is density-dependent, and if their distribution affects population dynamics, it may constitute an eco-evolutionary feedback or correlation (Pelletier, Garant, & Hendry, 2009; Smallegange & Coulson, 2013). Early evidence suggests that social and spatial phenotypes satisfy these conditions. Individual traits which respond to variation in the socioecological environment likely represent a density-dependent driver of fitness, population and evolutionary dynamics.

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## AUTHORS' CONTRIBUTIONS

Both authors contributed equally to all aspects of this manuscript.

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