

# Does sociality affect evolutionary speed?

Socias-Martínez Lluís<sup>\*1,2</sup>, Peckre Louise Rachel<sup>1</sup>

<sup>1</sup> Department of Sciences and Technology, Institut National Universitaire Jean-François Champollion, The University of Toulouse – Albi, France

<sup>2</sup> Institute of Forest Growth and Forest Computer Sciences, Technical University of Dresden – Dresden, Germany

\*Corresponding author

Correspondence: [lluissociasm@gmail.com](mailto:lluissociasm@gmail.com)

Lluís Socias-Martínez: <https://orcid.org/0000-0002-1739-0987>

Louise Rachel Peckre: <https://orcid.org/0000-0002-0065-8529>

## ABSTRACT

An overlooked source of variation in evolvability resides in the social lives of animals. In trying to foster research in this direction, we offer a critical review of previous work on the link between evolutionary speed and sociality. A first set of studies emerged that we grouped under the “selectionist perspective”. These studies conceive social interactions as knitting forces of an environment with specific selection pressures. Social pressures, in turn, promote evolutionary change in the characters they depend on. Studies in this perspective have investigated cladogenetic effects of sexual selection, while non-sexual contexts have been relatively ignored. We grouped a second set of studies grounded on population genetics under the “populationist perspective”. Such studies regard social interactions and the social units arising from them as a dividing force that splits a population into smaller parts, tweaking the number of reproducing individuals and unbalancing the contribution of both sexes. The consequences of these effects on the effective breeding population size are made responsible for changes in the speed of neutral evolution. Despite the manifold approaches used to measure sociality and evolutionary speed, there is support for both the selectionist and populationist perspectives on anagenesis. On the contrary, evidence for cladogenetic consequences is mixed. We suggest six areas for improvement to cope with the current situation: 1) Conceptually separating the potential for evolutionary change from its realization. 2) Considering that under social competition, a single axis of variation is unlikely to explain reproductive success. Acknowledging the existence of alternative social tactics could enrich the current framework. 3) Address both the selectionist and populationist perspectives simultaneously. Social selection strength and  $N_e$  consequences need to be assessed using 4) as many axes of social variation as possible and 5) in both sexes. 6) Considering the evolutionary covariances in communicative systems might improve the validity of tests for the current framework. In addition, we develop predictions for how variation in each social dimension and component might affect evolutionary speed. Continuing to refine the theory and evidence on social effects on evolutionary speed might come at a benefit not only for the current issue but also for the domains it integrates.

**Keywords:** Social system, Social selection, Sexual selection, Anagenesis, Cladogenesis, Evolvability

Animal species vary extensively in the ways social interactions take place, their duration, intensity, and valence. Scaling up from the variation in these interactions arise species differences in sociality. With increasing knowledge, social variation initially studied in a taxa-specific manner started to be regarded as a common concept: the social system (Di Fiore and Rendall 1994; Kappeler and van Schaik 2002; Rubenstein and Abbot 2017a; Kappeler 2019; Prox and Farine 2020). It is a beneficial conceptual framework that originated in primatology but is gaining ground in comparative research that differentiates between four dimensions: social organization, social structure, mating systems, and caring systems (Kappeler 2019). The organization captures the composition of social units regarding the number of adult males and females and their kinship. Structure defines the existence and flavor of equitability of outcome in conflicts and cooperation activities for access to resources. Mating systems capture how reproduction is distributed in social units regarding mating and genetic parentship. Lastly, the care system indicates how each sex takes the burden of care for offspring, including the presence or absence of helpers.

The suggested causes for the origins and maintenance of variation in different social dimensions are manifold (Dalerum 2007; Hughes et al. 2008; Shultz et al. 2011; Clutton-Brock and Lukas 2012; Opie et al. 2013; Kappeler and Pozzi 2019) but can be boiled down to at least two main prisms. The first corresponds to how ecology drives the distribution of resources and dangers, which in turn dictate the various payoffs for passively or actively cooperating and competing with conspecifics (Emlen and Oring 1977; Brockmann 1997; Rubenstein and Abbot 2017b). Such an ecological perspective usually incorporates sex-specific assumptions based on differential mating and parental investment. For example, if resources are clumped, the sex that competes more for feeding resources might be selected to gather and defend them (Wrangham 1980), while individuals from the sex that competes more for mates might, in turn, try to monopolize reproductive access to these social units (Emlen and Oring 1977). Such a perspective is the core of socioecological models, which posit that different environments should induce different social systems. The second corresponds to the role of the past, the phylogenetic history (reviewed in E. O. Wilson 1975; Rubenstein & Abbot 2017a). The phylogenetic history of a species makes it inherit characters such as aggressiveness towards conspecifics of the same or the other sex or, conversely, a need for social contact, which might constrain the plasticity of the social system in the face of changing ecological conditions in a sort of inertia (Di Fiore and Rendall 1994; Thierry 2008; Balasubramaniam et al. 2012; Kappeler and Pozzi 2019). Alternatively, preexisting characters might foster social innovation through exaptation, as shown by research on the precursors for social relationships between adults residing in characters related to offspring care (Griesser et al. 2017; Shell and Rehan 2018; Socias-Martínez and Kappeler 2019).

While researchers in animal sociality have sought causes for social systems emerging or being maintained, the consequences have remained understudied. Nevertheless, three main consequence types have been identified, including a species' ecological role, its capacity for transmission of information or disease, and its evolutionary speed. How animals distribute in space and time and how they cooperate and compete have consequences for their relationship with other species in their ecological community (Wilson 1992). For example, through their coordinated workforce, social species might be able to hunt bigger prey than if individuals acted alone. Similarly, their cooperative activities might allow them to buffer adults or offspring against biotic or abiotic challenging conditions (Socias-Martínez and Kappeler 2019). Thus, sociality might allow species to expand their niches (Sun et al. 2014; Cornwallis et al. 2017; Griesser et al. 2017) and become ecologically dominant (Wrangham 1980; Wilson 2013). The frequency and types of social interactions generate different opportunities for parasites (van Schaik and Kerth 2017), diseases (Altizer et al. 2003), and information (Evans et al. 2021) to disseminate through the population. Given the importance of ecological exploitation relationships for regulating population sizes and the multiple coevolutionary arms races and cascading effects, such consequences might also vastly impact a species' ecology. The last type of consequence, which will occupy us for the rest of the article, concerns the social environment being a powerful evolutionary force in and of itself.

Animal social interactions have been suggested to affect the way and the speed with which species evolve (West-Eberhard 1979, 1983; Rubenstein et al. 2019). More concretely, social systems have been suggested to affect, first, the directionality and speed of change in the genotype and phenotype of a given species (anagenesis hereafter) and, second, the rate of speciation events (cladogenesis hereafter, Fig. 1) (West-Eberhard 1979, 1983). Evolution is a continuous process; hence, understanding the different factors making it

occur faster or slower in different *époques* or lineages might be crucial for evolutionary theory (Gould and Eldredge 1977; Simpson 1984; Flegel 2010). Besides, studying the potential for change is needed to interpret present and past biodiversity patterns because evolvability (i.e., evolutionary speed potential) can determine selection above the species level (Vermeij 1973). If different social systems impact evolvability discordantly, they might result in animal lineages thriving, perishing, or diversifying depending on the social systems characterizing them (Wilson 1992).



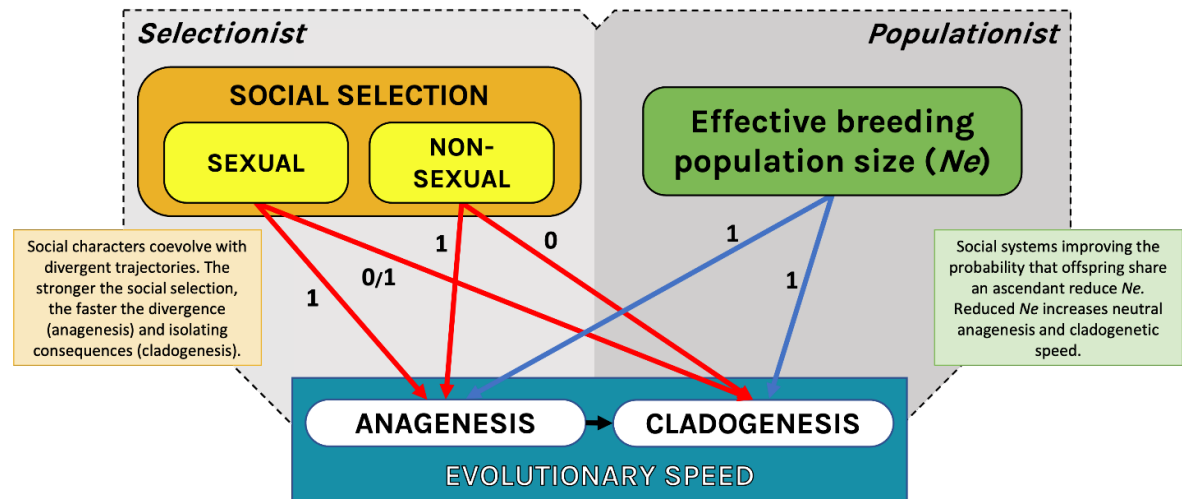
**Figure 1** – A given species can change anagenetically due to coevolutionary trajectories selecting for phenotypes that outcompete others in the social domain. For example, a coloration that might reflect condition and its associated preferences. If trajectories diverge in different parts of a metapopulation, as the bluer versus redder trajectories in this figure, over time, this can result in cladogenesis, the formation of different species.

While working on how sociality influences evolvability, we have noticed that it offers crucial avenues for new research beyond the fact that it has been understudied. The field seems unbalanced in the effort or attention paid to studying different types of social interactions. The effects of the strength of male sexual selection on speciation amount to the large majority of studies. Thus, most studies do not include non-sexual social selection nor drift, focus on one sex only, focus exclusively on one social dimension, and do not include the communicative role of social characters. Finally, most tests of the theory do not consider the gap between the potential for evolutionary change and its realization. For example, the role of empty ecological niches or their absence regarding speciation. In this paper, we start by reviewing the theoretical and empirical evidence linking sociality and evolutionary speed (Fig. 2). We then discuss the current situation and try to offer ways of moving forward.

## Linking social behavior and evolutionary speed

We have identified two complementary perspectives that drove past research on the link between evolutionary speed and social systems (Fig. 2). The first perspective, which we call the “selectionist”, has dealt with social interactions as a sort of niche that alters the type and directionality of selection (West-Eberhard 1979, 1983). Within the selectionist perspective, most hypotheses revolve around the struggle to access gametes for fertilization, i.e., sexual selection (Shuker and Kvarnemo 2021). A minority has tried to encompass selection arising from a broader set of socially competitive domains, i.e., social selection (West-Eberhard 1979, 1983). Although social selection includes sexual selection, and the latter might be affected by other components of the social struggle, like hierarchy, the distinction is helpful given that species might vary in these domains independently (e.g., Prox & Farine, 2020). The second perspective, which we call the “populationist”, has seen social interactions as determinants of the rate of neutral evolution through the effective breeding population size. Because in animal societies, the number of individuals accessing reproduction varies greatly, the extent of processes like drift and inbreeding were expected to differ, resulting

in different anagenetic and cladogenetic speeds among species with different social systems (Crozier 1979; Wilson et al. 1985). We will now review the theoretical and empirical evidence for each perspective.



**Figure 2** - Summary of the selectionist and populationist perspectives' predicted effects from sociality on evolutionary speed components. Links indicate the prediction of an effect, the color indicates the valence (red being positive, i.e., an increase leads to an increase, and blue being negative, i.e., an increase leads to a decrease). Numbers indicate the support (1) or absence of support (0) endorsed by the majority of the reviewed studies.

### Selectionist perspective

It was commonly believed that closely related species differed markedly in mating signals and preferences (Ritchie 2007; Boughman 2016). For this reason, research on evolutionary speed has focused on understanding how the struggle for fertilization could enhance or hinder speciation (Darwin 1871; Fisher 1930; Wilkinson and Birge 2010; Boughman 2016). When boiled down, this body of research suggests that characters that benefit mating quantity or quality in females and males coevolve and that the coevolutionary trajectory is likely to diverge in different parts of a putative population. Because such characters strongly modulate reproduction, as the divergence increases, emigrants should be counter-selected, thereby fragmenting the original population into isolated parts. Eventually, the isolated parts could become different species thanks to the sexual selective forces within them (Darwin 1871; Fisher 1930; West-Eberhard 1979, 1983; Panhuis et al. 2001; Wilkinson and Birge 2010; Boughman 2016; Mendelson and Safran 2021). Such rationale, therefore, predicts a path from sexual selection to anagenesis, followed by cladogenesis. The stronger the sexual selection, the faster the change and speciation.

While the link between sexual selection and speciation has gathered most research efforts to date (Panhuis et al. 2001; Wilkinson and Birge 2010; Boughman 2016; Mendelson and Safran 2021), isolated claims to broaden this focus exist. West-Eberhard (1979, 1983) suggested that the evolutionary forces linking sexual selection and speciation could arise in all socially competitive domains. Individuals compete in a social environment not only for accessing gametes but for any other crucial resources. Competition for food, shelter, or even the non-sexual favors of social partners can heavily determine the fitness of an individual (West-Eberhard 1979, 1983; Lyon and Montgomerie 2012; Tobias et al. 2012). Because social competition is also mediated by the expression and understanding of social signals, divergent evolutionary trajectories as those predicted for mating signals could occur. Thus, the stronger the social selection, the faster the anagenetic change in characters mediating social competition, and the faster the isolation and appearance of new species. Sexual selection is considered a specific form of social selection (Lyon and Montgomerie 2012). To avoid misguidance, we will refer to the selection in both sexual and non-sexual competition as social selection and to either as non-sexual social and sexual selection throughout the rest of the manuscript.

To meaningfully review and discuss the theory and the empirical studies, we think it is essential to understand which characters should be under social selection, why these are committed to set anagenesis, why cladogenesis ensues, and when to expect stronger or milder selection strengths driving the entire phenomena at higher speed. When there is competition, we might expect characters or their intensity to improve the chances of winning or the payoff of a victory. Now, because animals adapt their behavior to the

phenotypes of others, such characters conferring an advantage can be thought of as either direct or indirect. Direct characters confer an advantage in themselves, like being agile, big, or having a reproductive tract actively controlling fertilization or a seminal fluid invalidating other males' sperm (Arnqvist and Rowe 1995; Chapman et al. 1995; Rice 1996). Indirect characters, on the contrary, are flags that stand for the direct characters that make a difference in social competition or others that play a role in natural selection. For example, in the context of sexual selection, indirect characters are expressed as secondary sexual signals that do not help outcompete others or their gametes in themselves but through the responses of potential competitors or mates. Typical examples are the diversity of cuticle/skin/feather coloration and songs. Examples of non-sexual social characters can range from coloration patterns in the inside of nestlings' mouths in birds (Wiebe and Slagsvold 2009; Lyon and Montgomerie 2012) to signals of hierarchical position (Kavanagh et al. 2021; Alencar et al. 2023), kinship (Silk 2002), and even group or culture membership (Lemon 1975).

Unlike bare natural selection, which should push the phenotypes toward an optimum, the described social selection processes are predicted to be open-ended even under constant ecological conditions. In her enlightening paper, West-Eberhard (1983, p.163) suggests several causes why selection arising from social competition is expected to make divergence and speciation occur faster. First, (1) social signals and weapons have a "great importance [...] in determining access to resources critical to survival and reproduction" (West-Eberhard 1983). In addition, (2) there is a certain "generation-to-generation relentlessness of selection on these traits" (West-Eberhard 1983). While ecological pressures may vary over time and space, social pressures remain relatively constant over generations. In addition, there is no optimum solution because a covariance exists between the fitness of different individuals (Wolf et al. 1999; Lyon and Montgomerie 2012). The success of social characters will always be relative to those expressed by others. Whether it is size or strength in contests or the redness of a body part when being chosen, the result will depend on how big or red others are in the mind of a possible mate or competitor relative to a focal individual. One could substitute these examples for another character relevant to socially competitive domains, such as socio-cognitive skills or communicative complexity and effectivity (Dunbar and Shultz 2017; Freeberg et al. 2019). Constant selection confers (3) a "potential for unending evolutionary change in socially competitive traits" (West-Eberhard 1983). About this interdependence, West-Eberhard (1983) mentions (4) "the potential for mutually accelerating, genetically correlated evolution of preference and attractiveness in contests involving choice" (see also Fisher, 1930). Any novelty has (5) the potential of "accelerating the initial spread of traits" (West-Eberhard 1979) by proving decisive to stand out of the crowd and provide fitness gain. Thus, the combination of these different properties of social selection makes space for coevolutionary feedback loops driving the evolution of social characters (West-Eberhard 1979, 1983). Moreover, the lack of optima induces not only continuous change but also offers a potential for change in various directions (Fig. 1).

Social selection has been observed to operate towards optima and not only open-endedly (e.g., Brooks et al., 2005; Wheeler et al., 2012). This situation could result from selection in other domains constraining the fitness of social characters outside specific values. For example, imagine being socially integrated is a social character potential partners seek. If being socially integrated takes time, partners might be selected to choose individuals that integrate enough but not too much so that they neglect other important areas (e.g., food acquisition, parental care, or even agonistic interactions mediating access to other resources). Could social selection engender anagenesis and cladogenesis if it is not open-ended? We think the answer should be positive if there is enough intraspecific variation in social systems or the individuals that compose them and/or if environmental heterogeneity exists (see next section, "Amplification of social selection effects by environmental heterogeneity"). For example, social units might vary in critical aspects, such as how many individuals cohabitate (Schradin, 2013) or the types of relationships they can establish, so the optimum for many social characters should differ.

The cladogenetic effect of social selection results from different parts of a given population following divergent coevolutionary processes, thereby impeding gene flow and culminating eventually in reproductive isolation (Darwin 1871; Fisher 1930; West-Eberhard 1979, 1983; Panhuis et al. 2001; Wilkinson and Birge 2010; Boughman 2016; Mendelson and Safran 2021). The trajectories of different subpopulations will likely differ because depending on the subset of individuals that come to interact in each of them, the range of variation present and rare mutations occurring will vary. Moreover, the mutations affecting characters involved in social competition, on which the non-sexual social selection processes will act, might also differ as mutations are random. For example, in one subpopulation, a mutation might make individuals able to follow more accurately

the results of agonistic interactions in a group. In contrast, in another subpopulation, a mutation might instead affect the capacity for monitoring affiliative interactions. Theoretically, a vast array of possible bifurcating points leading to diverging trajectories in a given metapopulation is ahead of any species with social selection. The appearance of subpopulations bounded by mating preferences and signals has an additional speciating force: it decreases the effective breeding population size. As we will see in further detail (see section “populationist perspective”), smaller populations are more subject to drift, increasing the probability of neutral anagenesis and speciation.

The diverging trajectories among subpopulations could be maintained and even reinforced depending on the outcomes of interactions between migrants and locals. Firstly, if migrants can successfully breed but their genetic divergence leads to hybrid disadvantages, the sex that invests more in reproduction should be selected to breed with local variants (Dobzhansky 1940). Secondly, an emigrant might have socially competitive phenotypes not tuned to local variants. An example could be a mating song that doesn’t trigger a preference in a new population or a submissive signal that isn’t understood as such. In the former case, the singing individual will be less likely to find mates. At the same time, in the latter case, the immigrant is expected to see him- or herself in a higher rate of escalating agonistic interactions, both situations reducing fitness.

Finally, we have presented the rationale linking sociality with anagenetic and cladogenetic processes that should increase evolutionary speed relative to a non-social species. Further variation in the speed of anagenesis and cladogenesis arising from social selection should be proportional to the selection strength (Socias-Martínez 2023). Social variables affecting the potential for and the extent of asymmetries in access to reproduction and resources should be the key predictors of social selection strength and, thus, evolutionary speed. The stronger the asymmetries or the capacity for it (e.g., group size relates to the ability to monopolize access to mates), the faster a new successful mutation should spread each time it appears (i.e., anagenesis) (Socias-Martínez 2023). This relationship suggests that variation in social systems’ dimensions could engender different evolutionary speeds. We have detailed predictions for the relationship between specific social systems dimensions’ variation and selection strength in a further subsection of the discussion named “Predicting the effects of the different social systems’ dimensions on evolutionary speed.”

#### *Amplification of social selection effects by environmental heterogeneity*

It might be insightful to test the previous logic chains outside the sort of abstract uniform world they were made in. In this sense, ecological variation has been suggested to affect sexual selection processes (Boughman 2002, 2016; Mendelson and Safran 2021) and could also broadly apply to social selection.

First of all, given that non-sexual social competition depends on the competition for resources, if resource abundances/distributions change, the strength of competition is likely to change as well. Consequently, we could imagine that social systems would change in response to the changes in ecology, as socioecological models suggest (e.g., Emlen & Oring, 1977). Nevertheless, the phylogenetic inertia and temporal or spatial heterogeneity might constrain such social plasticity. In such cases, if the species can’t avoid the stress by changing their social system, those periods and areas where critical resources are scarcer could impose higher social selective strengths and ignite an evolutionary speed increase.

In addition, spatial ecological variation can constrain the fitness optima to the conditions of origin. If the environment after dispersal differs (e.g., parasites, predators, diet), migrants could find themselves poorly adapted. Given that the social lives of many species rely on the energetic and time-demanding fabrication of signals in several modalities, individuals might allocate different efforts towards sociality depending on their health and energetic conditions (Emery Thompson 2017). Thus, if the environment varies, the “good genes” and “magic traits” perspectives (Servedio et al. 2011) can also apply to social selection contexts. The condition of migrants might become negatively impacted, and the social signals depending on this condition could be reduced in the rate of production, the effectivity of transmission, or the attractivity. Such deficiency in health conditions will reduce fitness through lack of social integration or mating preference compared to locals, reducing gene flow (Boughman 2016).

The environment also constitutes the background, the matrix on which signals are displayed, thus determining those that will be more efficiently transmitted. Different environments will favor different signaling phenotypes (Lackey and Boughman 2013), reducing the efficiency of migrant communication if the environment is heterogeneous in aspects affecting signal transmission. Thus, under the same social selective strength, species inhabiting varied environments might result in a faster migrant incompatibility. Ecology might

drive not only the signaling properties but the receptive ones as well. If natural selection results in sensory systems adapted to the local environment, the whole communicative system involved in social selection should shift according to the environment in what is called sensory drive (Boughman 2002). Thus, environmental variation experienced by different subpopulations will bend the direction of anagenetic change of social selection towards different optima in different parts of the population range, inducing speciation (Boughman 2002, 2016; Mendelson and Safran 2021).

Overall, the combined effects of environmental heterogeneity and social selection could theoretically allow anagenesis to culminate in cladogenesis even in sympatry.

### Populationist perspective

The second major perspective on social effects on evolution has dealt with the social niche as a factor that alters the effective breeding population size ( $N_e$ ) (Fig. 2).  $N_e$  relates to how fast diversity would be eroded by chance (i.e., neutral evolution). To derive predictions about the speed of neutral evolution, population geneticists use idealized populations that follow Hardy-Weinberg assumptions (random mating, even sex ratio, no reproductive skew) (Kimura and Crow 1963; Waples 2022). To predict the neutral evolutionary speed for an observed population (unlikely to meet these hard assumptions), one establishes a correspondence with a Hardy-Weinberg population. Violating each of the assumptions leads to a smaller idealized population. Now, because size affects how fast chance operates in this idealized population, a smaller  $N_e$  means that diversity is eroded faster. When this happens, the population is, in a neutral sense, changing faster anagenetically in a neutral sense.

Researchers interested in social behavior noted that in many animal societies, like Hymenopteran colonies, only a tiny fraction of the adult population reproduces (i.e., the queens or dominants). Given the considerations about  $N_e$ , it was predicted that the fixation rate of nearly neutral mutations through drift should increase in such societies (Crozier 1979; Wilson et al. 1985). The comparable situation of cooperative breeding vertebrates (Brockmann 1997), but also of species with reproductive skew based on polygynous or polyandrous mating patterns, should also have higher rates of neutral change. Thus, social variation regarding access to reproduction should affect anagenetic speed, albeit neutrally. These neutral changes should affect the whole genome but be only observed for those parts that do not suffer from strong selection (Waples 2022). Since it has been proposed that small  $N_e$ s are associated with (Bush et al. 1977), or even necessary (Flegr 2010), for speciation to occur, societies that result in small  $N_e$  should also induce higher cladogenetic speed.

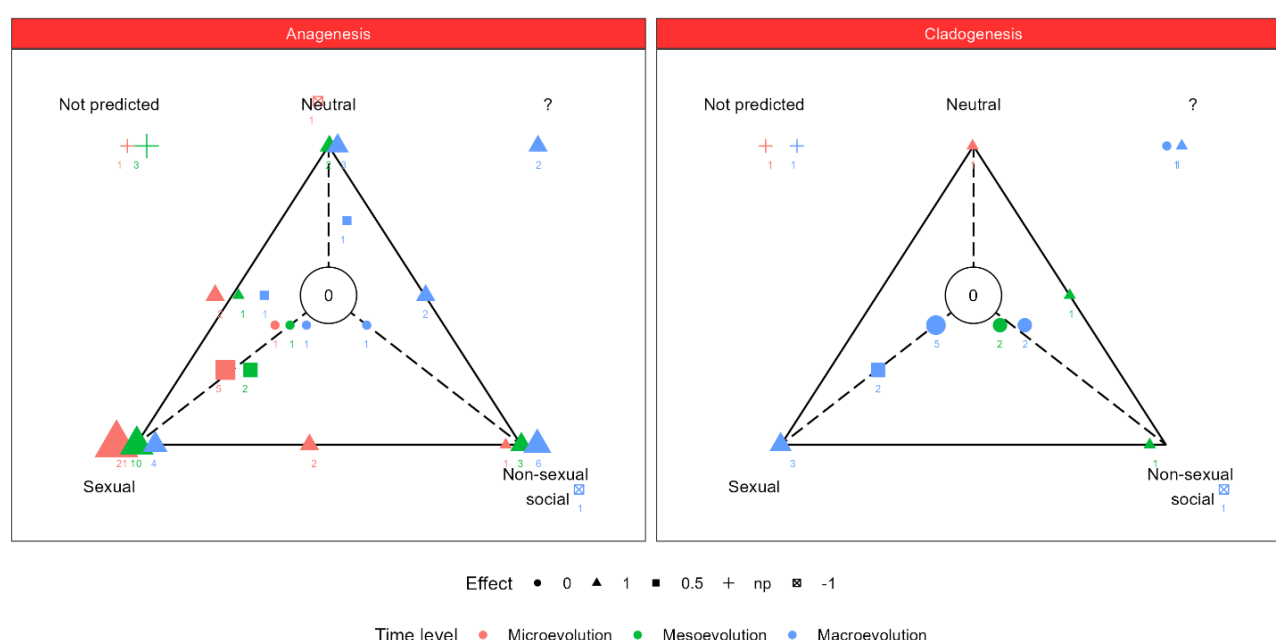
### Empirical and theoretical evidence

We have collected empirical evidence on the effects of social selection on evolution by using Google Scholar with the words “sexual selection”, “social selection”, “anagenesis”, “cladogenesis”, “speciation”, “divergent”, “contemporary”, “evolution”, “coevolution” and “runaway”. No connectors were used. When searching for examples of non-sexual social selection on anagenesis, we used the words “brain volume”, “intelligence”, and “group size”, as these were key evolutionary processes mediating social interactions known to us. If, while reading a study, further literature that treated the issue of sociality and evolution was cited, we also included it in our review (Table 1). All studies found, except for meta-analyses or reviews, are listed with details on the methodology and results in Table 1. We have organized the following sections according to whether studies show effects on anagenesis or cladogenesis. In addition, we have organized the studies according to whether they focus on microevolutionary (observed changes in the distribution of characters or genomes), mesoevolutionary (signatures of past microevolution in single species), or macroevolutionary time levels (signatures across species). Furthermore, within each of these time levels, we have sought, whenever possible, evidence from the laboratory, the field, and *in silico*.

Unless studies explicitly tested for the simultaneous effect of genes or characters to mediate social competition and signatures of neutral evolution, it is challenging to conclude whether results support or not the selectionist and populationist hypotheses. Most tests included in the reviewed studies focused on well-chosen characters or genomic regions with known social functions. Still, only a few also included elements allowing to test for neutral processes (28/98 in Table 1). We have tried to accommodate this variation by looking for each reviewed study, regardless of the authors’ focus, whether they tested for sexual, non-sexual social, and neutral selective processes. Studies were classified as supportive of sexual or social selection if the results show evidence for anagenesis arising from social competition, show evidence of signatures of divergence among subpopulations or subspecies, and if those changes were found to occur faster when



populations or species were subject to stronger social selection strengths (Table 1, values “1” or triangles in Fig. 3). If anagenesis was found to occur in neutral regions, or according to drift they were classified as supportive of the populationist perspective (Table 1, values “1” or triangles in Fig. 3). In the case of cladogenesis, studies were classified as supportive of sexual or social selection if clades with contrasting social systems or characters serving as proxies for the strength of social selection were found to have different numbers of species or different diversification rates in the direction predicted by the framework (Table 1, values “1” or triangles in Fig. 3). Whenever studies performed several tests with contrasting results, or clear trends were found in the direction predicted by the current framework without reaching statistical significance, we classified these as undecided (Table 1, values “0.5” or squares in Fig. 3). If tests found no evidence to reject the null hypothesis, found that there were no differences within populations at different time points, or differences between subpopulations, subspecies, species or clades, we classified them as non-supportive (Table 1, values “0” or dots in Fig. 3). If results went against the predicted effects, as for example when stronger social selection induced slower changes or speciation, we classified them as counter-evidence (Table 1, values “-1” or crossed squares in Fig. 3). If found effects arising from social selection or drift were not considered by the present framework they were classified as not predicted (Table 1, “np” or crosses in Fig. 3). If we were unsure what processes the tests addressed, we classified them as unknown (Table 1, “?” in Fig. 3).



**Figure 3** – Overview of the evidence reviewed regarding selectionist and populationist effects on anagenesis and cladogenesis: Each panel gathers an evolutionary speed component. Within each panel a triangle conforms the space for the reviewed evidence; the center indicates the results that do not support a given process (circle “0”), while each vertex indicates the three evaluated processes: neutral (populationist “Ne”, upper vertex), Sexual (selectionist, lower left), Non-sexual social (selectionist, lower right). Sides between two vertex indicate support for processes in adjacent vertices simultaneously. From each vertex and each mid-way between two vertex, a line from no support in the center to support in the edges can be traced and symbols representing results from tests in studies reviewed in table 1 are placed accordingly. Results that do not fit into such dichotomy are placed outside the triangle. Numbers indicate the quantity of studies in this category, the shape and position indicate support (“triangle”, edge), mixed support (“square”, midway edge-center), no support (“dot”, center), effect opposite to prediction (“crossed square”, outside triangle), unclassified selection (“?”, any shape, upper right) and not predicted in the framework (“Not predicted”, “crosses”, upper left). Colors indicate the time level of the evidence investigated, red indicating microevolution, green mesoevolution and blue macroevolution.

### Microevolution

Overall, microevolutionary studies support the effects of sexual and non-sexual social selection driving anagenesis (Table 1). Experimental evolution studies on sexual selection suggest that while complete behavioral pre-mating isolation does not appear in tens of generations, changing the competition level usually results in changes in traits related to competition and overall genomic changes. Microevolutionary field studies show a snapshot of cyclical change maintained by negative frequency-dependent selection (NFDS). At the same time, the modeling evidence reviewed clearly supports that social selection, if modeled under meaningful



ecological or spatial conditions, can induce divergent coevolution and that variation in multiple social system components can impact the strength of this process.

## **Anagenesis**

### Experimental evolution

Most studies using experimental evolution in the laboratory (11/12) support the role of sexual selection. Two of these studies also show some drift effects in the experimental populations. Only one experimental study clearly shows no evidence of sexual selection driving anagenesis. All studies concern invertebrate experimental populations allocated into different social unit sizes and/or mating systems. Most arrangements concern monogamous pairs versus other social systems, including polyandry or multi-male-multi-female units. The strength of sexual selection is supposed to increase in bigger units with more males. Studies then vary markedly depending on whether they measure changes in phenotypes, genotypes, or the evolution of reproductive isolation among populations that have evolved in a different social system. Phenotypes and genotypes show evidence for anagenesis. For example, in *D. pseudoobscura*, where females generally mate with one to three males in the wild, monogamy results in females developing a preference for longer male inter-pulse intervals in courtship songs, while increasing the number of males in social units results in a preference for shorter intervals (Snook et al. 2005; Debelle et al. 2014). On the contrary, when using outcomes of mating interactions or viability of offspring to measure reproductive isolation, the results are not statistically significant despite differences in the direction predicted by the theory (Bacigalupe et al. 2007).

One study tested the anagenetic effects of non-sexual social selection through the effects of parental care on artificial selection for body size in a species where care is facultative (Jarrett et al. 2017). The authors show that the presence of parental care affected the population's response to selection. Possible evidence could also concern a recent study showing plasticity in intelligence responding to the group size of residence in guppies (Triki et al. 2023).

### Field

Field studies monitoring anagenesis are rare (Svensson and Gosden 2007) (n=4) and have concentrated on observable polymorphic traits. These studies found cycling patterns driven by negative frequency-dependent selection driven by male-male competition in lizards (Sinervo and Lively 1996) or male harassment in damselflies (Svensson et al. 2005). We are unaware of any field study showing some anagenetic effects of non-sexual social selection in the field. In this sense, field studies do not show evidence for divergent anagenesis, although negative frequency-dependent selection can favor new variants that might differ among subpopulations (Svensson et al. 2005; Iserbyt et al. 2013; Le Rouzic et al. 2015). We are unaware of field studies monitoring directly the neutral evolution of populations arising from sociality.

### Modelling

We found 16 modeling tests of the anagenetic effects of sociality. Overall, the support of modeling studies on the anagenetic impact of sexual selection (n=12) has proceeded in a "U" shape that followed an increase in model complexity. Initial models investigated the most fundamental aspects and showed that the coevolution between female preferences and male traits could be reproduced. Further models that introduced costs to female and male traits tended to nuance that initial support and showed more restrictive conditions. Later models that included likely conditions in nature, such as spatial/ecological heterogeneity or demographic effects arising from mate searching, restored the initial support.

The study of anagenesis arising from social selection has lagged (n=4). Half of the models have focused on how social systems affect the evolution of neutral genomes, and the other two on how social variation affects evolution under selection. All find evidence for effects on anagenesis arising from social dimensions such as group size, dispersal regime, mating systems, and hierarchy strength. Hierarchy strength increases the rate of directional evolution but also decreases the speed of neutral changes. The group size, dispersal regimes, mating systems, and care systems affect the spread of a new successful variant by affecting the number of offspring dispersing and the level of contribution to the next generation. Furthermore, these same social system dimensions affect the level of heterozygosity and the alpha diversity of genomes by changing the number of social units and the number of adults that move across them and mix their genetic backgrounds through reproduction.

## **Mesoevolution**

We introduced into the mesoevolution section those tests that do not concern direct observations of anagenesis or cladogenesis but investigations of its signatures in the form of geographical or social variation in a single species (n=22). Overall, the evidence gathered in this section supports the presence of signatures of sexual and non-sexual social selection driving anagenesis (Table 1). There is a pattern regarding the taxa studied, with most support coming from insects and counter-evidence from birds for sexual selection and support from both clades regarding non-sexual social selection. The evidence from studies searching for cladogenetic signatures in a single species is mixed despite similarities in taxa and methodology.

### **Anagenesis**

Researchers either collected individuals and tested them in the lab for mating phenotypes and preferences or did so directly in the wild using playbacks and coys. Most studies on sexual selection (10/17) tended to find geographical variation in mating signals and/or preferences that translate to genetic variation, endorsing its role in anagenetic divergence. A single study found evidence for positive sexual and neutral selection (Hare et al. 2022). These studies supporting the rationale concern primarily insects. Those studies that fail to find mating signals/preferences and genetic structures covarying concern invertebrates and birds. Surprisingly, most non-positive evidence we could find comes from textbook examples of sexual selection and evolution, such as bird songs. Some bird species can learn new songs after dispersal unlinks genes and variation in mating phenotypes (n=3). Other non-supportive evidence comes from evidence for drift alone driving phenotype proportions in beetles (n=2; Green et al., 2014) and non-divergent preferences in a spider (n=1; Watts et al., 2019).

Regarding non-sexual social selection and anagenesis, we mainly found indirect evidence. One study found that the selective pressures of honey bee social lives induced an increase in recombination that is most pronounced in genes expressed in worker brains (Kent and Zayed 2013). Furthermore, a study found that social competition for territories shaped the evolution of territorial songs in two sympatric species of antbirds (Tobias and Seddon 2009). Thus, social competition among species could be a driver of anagenesis not contemplated in the mainstream theoretical rationale.

### **Cladogenesis**

Four studies have tried to see whether variation in social dimensions affects gene flow in species where two or more social forms coexist. The evidence from three ant species and one bee species appears mixed, with 50% supporting (Fontcuberta et al., 2022) and 50% not supporting (Ross & Keller, 1995; Soro et al., 2010) a covariance between sociality and gene flow despite remarkable similarities among the study systems and the underlying genetics of social morphs.

## **Macroevolution**

Macroevolutionary studies tend to support the anagenetic effects of social selection, sexual selection, and drift but tend to find mixed results regarding cladogenesis (Table 1). The studies presented here concern comparative multi-species datasets in extremely diverse taxa sets, including vertebrates and invertebrates. Generally, a comparison of the extent of change in a character (phenotypic or genotypic) or the number of species present/produced is made relative to a social selection measure. Studies vary on how they measure variation in sexual and non-sexual social selection, from social systems imputed to entire clades to more fine-tuned per-species proxies based on the number of individuals in social units, the presence or absence of cooperative care or the extent of sexual dimorphism. Social variation is used as a grouping or composite scale to test for differences/correlations in the character or diversification scores. Studies test the groups either directly, controlling for phylogeny (sister clades, phylogenetic regression) or modeling the character evolution/diversification using sophisticated phylogenetic models. To some extent, these three statistical approaches map the historical evolution of the subject with pioneering studies on the former and contemporary studies on the latter. The differences in taxa investigated, statistical procedures, and characters do not allow us to predict the support or lack of support for the effects of social selection on the speed of evolution. Still, we nevertheless discuss some prominent examples below.

## **Anagenesis**

Comparative studies on macroevolutionary anagenetic consequences of sexual and non-sexual social selection are relatively numerous (n=23). Despite the diversity in the methodologies, taxa, and questions, a trend appears towards endorsing a role of social variation generating anagenesis (see Fig. 3, blue forms not being clustered in space but with more studies towards the edges of the triangle). There is positive evidence for sexual (n=4), non-sexual social (n=6), drift (n=4), and both non-sexual social and drift simultaneously (n=2). Few studies find no effect from proxies for social variation when investigating sexual (n=1) and non-sexual social (n=1) selection. One study found opposite effects than the ones predicted for social variation. The results do not follow a pattern according to the proxies or the statistical methodology. Because most studies do not test for the neutral and the positive selection (non-sexual and sexual) simultaneously, it is impossible to conclude on the relative forces of each process.

## **Cladogenesis**

Studies investigating how sexual selection affects speciation are numerous and have covered a broad range of animal groups, from insects and spiders to most vertebrates (Kraaijeveld et al. 2011). Kraaijeveld et al. (2011) found a positive effect of sexual selection strength but of shallow magnitude. The proxy for sexual selection strength used significantly impacted the observed effect on diversification. While using dichromatism and mating system (i.e., number of males and females in social units in vertebrates and number of sexual partners by females in invertebrates) resulted in positive evidence, when using size dimorphism, generally no effect was found. The studies we reviewed (Sexual n=10, Social n=4) comprise significant variation in taxa and proxies for selection strength and diversification and show mixed results. Results of studies on sexual selection show at 50% no effect, at 20% partial support, and 30% support. The general methodology does not allow us to predict the support or lack thereof. For example, studies using the female number of mates as a proxy for sperm competition show both results (n=2). If we look more closely, the study that used only sister taxa and a broader sample size indicates a very strong positive effect of sperm competition on diversification, which could suggest that the quality of the analysis drives the result. Dimorphism shows two negative and one positive result, but this time, the two studies with more fine-tuned diversification measures instead of just crown size are on both sides. Using social system measures to target sexual selection tends to offer support (social organization and sex ratio in a polygyny scale, n=2), with increasing polygyny being associated with the number of species. Still, in one of the two studies, the reverse directionality is observed depending on body size and mutation rates. Finally, the study by Janicke et al. (2018) might suggest that going towards more direct measures of selection strength could help disentangling the trend. The authors found that taxa with more species tended to be those where males varied more than females in reproductive success and where males had steeper slopes relating mating and reproductive success.

Results that target social selection more broadly do not show any support. All studies tested the effects of cooperative breeding. These studies show either no effect on speciation (n=2; Carnivora: Muñoz-Durán, 2002 and Theriidid spiders: Agnarsson et al., 2006) or reduced diversity (n=1; passerine birds: Cockburn, 2003) with one of the former two finding increased extinction. The authors suggest these effects are due to cooperation generating reduced dispersal and allee effects. These effects of population viscosity and reliance on cooperation do not easily accommodate the rationale of social competition generating anagenesis and concern overlooked points that need integration in further frameworks. However, population viscosity has also been found to increase speciation (Bush et al. 1977; Marzluff and Dial 1991a).

## **Discussion**

From reviewing the literature, we noticed that thinking and measuring sociality and evolutionary speed need enlargement in several areas. The state of the art might benefit from moving towards more integrative approaches to compensate for previous limitations. In the following paragraphs, we discuss the following axes of improvement:

- 1) Confounding the potential for evolutionary speed and its realization should be avoided. Finding no relationship between measured social variation and evolutionary speed in tests for the present framework does not automatically invalidate it. Theoretical elaborations that include factors that constrain the unfolding of evolutionary speed potential are needed.

- 2) The theoretical framework might be excessively axed on individualist thinking, advocating a single winning phenotype in any given social competition. Acknowledging plurality might come to modify some of the predicted evolutionary dynamics.
- 3) The field could benefit from investigating simultaneously the selectionist and the populationist perspectives to allow assessments about their relative importance, but current studies rarely do so.
- 4) Sociality research, including the one regarding evolutionary speed, has proceeded in a taxa-specific manner, precluding comparative analysis. Studies focus on the most striking variation in each group of animals, resulting in taxa-specific definitions of social systems that conflate several social domains and components. Thus, possible analyses of the effects of different social system dimensions are invalidated.
- 5) Studies usually focus on measuring selection in one sex, ignoring the other. In the context of sexual selection, this usually translates to measuring male-male competition and female choice. In the context of non-sexual social selection, on the contrary, it tends to focus on female-female competition. Such a priori biases might preclude an assessment of the complex evolutionary processes at play.
- 6) The current state of the art needs to fully integrate theoretical developments linking the coevolution between sociality and communication. Significantly, more integrative approaches are needed. Doing so might allow for more tailored tests of the current framework.
- 7) We develop predictions for variation in each social system dimension and component to foster future research in this direction.

### **1) Separating the potential for evolutionary speed from its realization**

We find a general pattern for sexual, non-sexual social, and  $N_e$  effects driving anagenetic changes. Still, the translation to cladogenesis is not held by the studies reviewed nor by results from a previous meta-analysis (Kraaijeveld et al. 2011). It is essential to keep in mind that species live embedded in ecosystems and that extrinsic factors that can take the form of other species can affect how their potential for evolution unfolds. In this sense, while ecological theory contemplates inter-specific competition, no test on evolutionary speed accounts for the effects of diversification in other taxa or their ecological dominance. For example, while a hypothetical early mammal with a given social system could have had the same evolutionary potential 65 or 67 million years ago, it could only be realized 65 million years ago, after the K-Pg massive extinction happened. In addition, as E. O. Wilson (1992) points out regarding the controversy between Marzluff and Dial (1991a) and Bush et al. (1977), speciation includes turnover, and groups with high diversification rates might have reduced crown sizes. Thus, conclusions based on the absence of a speciation effect should be made carefully until the inclusion of the fossil record and the development of theory and methods to account for the impact of other lineages' fates are developed. Meanwhile, we advocate for new integrative models (e.g., Chevalier et al. 2022) to test the evolutionary potential of different social systems independently of their realization.

### **2) Going beyond the focus on a single winning phenotype**

We have proceeded for simplicity, as most of the theory in this domain, by thinking about characters and their trajectories singly. Such a procedure tends to project a view where, for each competition, a single phenotype should be selected (e.g., the strongest, the most colorful...). However, the complexity of species morphs and the multitude of phenotypes and variations in both sexes observed in nature calls for a note on diversity. The forces of selection and not only mutation construct a sort of community, not a unique best phenotype. Theoretical and empirical studies on alternative social tactics (Lewontin 1961; Maynard Smith 1988; Taborsky et al. 2008) show that this diversity can be maintained or even selected for under social competition. Therefore, the divergent coevolution of preference-signal might need an extra "s". The predictions for gene flow reduction between subpopulations under social competition will depend on how much overlap exists between the "communities" of social phenotypes in different subpopulations. The presence of "communities" could allow for higher overlap in the selected phenotypes between subpopulations, allowing migrants to breed successfully. However, such complexity and the necessary coevolution between the different phenotypes could reinforce the anagenetic speed described. Future studies are needed to tell apart or determine the conditions for these different outcomes.

### **3) Simultaneously addressing selectionist and populationist perspectives**

Most theoretical studies and empirical tests focus exclusively on either sexual, non-sexual social, or  $N_e$  effects of social competition. Based on secondary research (Ritchie 2007; Wilkinson and Birge 2010; Kraaijeveld

et al. 2011; Boughman 2016; Servedio and Boughman 2017; Mendelson and Safran 2021; Vries and Lehtonen 2023) and the present work, it appears that the vast majority of studies on social effects on evolution focus on sexual selection influencing speciation. Only a minority of tests investigate simultaneously selection and drift (28%, Table 1) and never the three processes together. Most studies focus on social mating systems and sexual dimorphism while ignoring the possible effects of selection in other competitive domains such as female hierarchies and cooperative care (Gluckman and Bryson 2011; Socias-Martínez 2023). Hence, there is a need to raise awareness on the importance of contemplating simultaneously sexual, non-sexual social, and  $N_e$  effects on evolution. As we have put forward, sexual selection and non-sexual social selection are expected to induce similar effects on evolutionary speed (West-Eberhard 1979, 1983; Lyon and Montgomerie 2012), and the reviewed evidence suggests that it is indeed the case (Fig. 3). In addition, the  $N_e$  effects should be correlated with the intensity of selection, but be observed across the genome where other sources of change are tamed down. Conclusions based on tests addressing these processes singly can be misled by unaccounted variation in the strength of the others.

#### 4) Stepping towards cross-taxa approaches is needed for a deeper understanding

The study of sociality has traditionally been carried out in a taxa-specific manner (Rubenstein & Abbot 2017a, but see E. O. Wilson 1975). For this reason, definitions and classifications explore the most striking variation in each study system (to the human observer) but tend to ignore the rest. For example, Hymenoptera tends to be classified according to the ways females form groups and divide reproduction (Michener 1969; wasps Hunt & Toth 2017; bees Wcislo & Fewell 2017). Vertebrate clades' classifications can be strikingly different. For example, primates are defined as social or solitary depending on whether they forage in groups or not (Shultz et al., 2011; Kappeler & Pozzi, 2019), while sociality in birds usually refers to the presence of cooperative care (Cockburn et al. 2017). Accordingly, tests for the effects of sociality on evolutionary speed tend to use the respective taxa-specific categories as social predictors. As a result, comparative research is impaired whenever the categories do not overlap between different taxa.

Deriving from this taxa-specificity, the limitations of reviewed studies are two-fold. Firstly, the taxa-specific categories tend to conflate co-occurring variation in several social systems dimensions (see Table 1, "Dimension" and "Component" columns). Such a situation prevents us from assessing the effects of each of these dimensions of social variation and perhaps existing synergies/compensations among their effects. Secondly, studies tend to focus on testing only the social variation considered key in their study clade or their respective background and ignore the rest. For example, Bromham & Leys (2005) compared the anagenetic speed of non-social versus social species, defined according to the absence or presence of non-reproductive workers. The lack of significant differences could result from variation in the other three social dimensions (e.g., mating system Schmitz & Moritz 1998, social structure Gluckman & Bryson 2011, and social organization Socias-Martínez 2023). Likewise, while Iglesias-Carrasco et al. (2019) used social organization to define the strength of male sexual selection in birds, the genetic mating systems often differ from the social ones (Brouwer and Griffith 2019). This could explain part of the enormous variation the authors found in the most abundant social organization, pair living. Thus, there is a need to include more basic measures that capture social variation, which can be applied across taxa. The framework conceiving four social systems' dimensions: social organization, social structure, mating systems and caring systems (Kappeler 2019), could be especially valuable in this regard. Such an approach might allow bypassing some biases based on taxa-specific classifications. Nevertheless, to do so effectively, there is a need to translate variation in social systems' dimensions into social selection strength and  $N_e$  (see our attempt in section 7).

We further suggest that comparative studies on sociality and evolutionary speed in the main taxa studied have yet to include at least two key variables. First, no empirical study has considered the variation in which sex disperses (Greenwood 1980; Mabry et al. 2013). If dispersal is done by the sex that has the potential to reproduce at faster rates, like in mammals, the spread of new variants should be more rapid. On the contrary, if dispersal is done by the sex with lower potential reproduction rates, like in birds (Parreira and Chikhi 2015; Socias-Martínez 2023), the spread of new variants should be slower. The unfolding of these differences is contingent on other variables, notably group size and the presence/absence of cooperative breeding (Socias-Martínez 2023), reinforcing our claim to include as many axes of social variation as possible in comparative analyses. Second, the type of sexual reproduction is also usually ignored. Most invertebrates used in studies on social evolution and its consequences are Hymenopteran species, whose haplodiploid sexual reproduction means that males contribute 100% of their haploid genome but only to daughters. Compared to other groups

with male-biased dispersal, such as mammals, their spread of new variants and anagenesis could be hindered because of this differential transmission of genes to the next generation (Socias-Martínez 2023).

## 5) A need to bypass one-sex approaches

Most studies examining sociality and evolutionary speed focus on sexual selection with a perspective of male signaling and female choosing (Kraaijeveld et al. 2011; Vries and Lehtonen 2023). This biased perspective has led to studies focusing on measuring traits where males are expected to signal, ignoring the female side of the story beyond choosiness. However, elaboration of characters mediating social competition is expected in both sexes (Tobias et al. 2012; Riebel et al. 2019; Vries and Lehtonen 2023). Even the main textbook example of male signal and female choice, birdsong, has proven to need revision in this concern (Odom et al. 2014; Riebel et al. 2019; Graham et al. 2021). Recent advances in our understanding of the condition dependence of sex roles (e.g., Kokko & Jennions 2008; Alonzo 2012), and the possibility of speciation being related to changes in the phenotypes of both sexes (Irwin and Price 1999; Gomes et al. 2016; Mason et al. 2017; Yang et al. 2019; Price-Waldman et al. 2020) call for using a new lens to look at these old problems. We suggest that studies should be planned as if there was no *a priori* reason for focusing on one sex regarding signaling or choosing.

On the non-sexual social selection side, Hymenopterans have been a critical taxon for understanding social evolution (Hamilton 1964). Given the notorious female-biased sociality in this taxon, researchers have focused on the female side of the story. These conceptual advances have then directed expectations for the evolution of vertebrate sociality (e.g., Kessler et al. 2016). While these situations are understandable, they also lead to non-explored areas of social variation that can affect evolutionary speed. For example, while classifying species according to female social variation is mandatory in Hymenoptera, studies only indirectly record the male side. For instance, in Schmitz & Moritz (1998), the possibility that several males impregnated queens is assumed to correlate with the most derived eusocial species having bigger nests. Nevertheless, there is virtually no knowledge about whether a given male can inseminate several queens and whether this results in different levels of male reproductive skew among different species (William Wcislo personal communication, Villalobos & Shelly 1991). Establishing the relative contributions of different males and females to the next generation would need challenging efforts. Still, the developments in AI technology and DNA sequencing might allow us to overcome this issue soon.

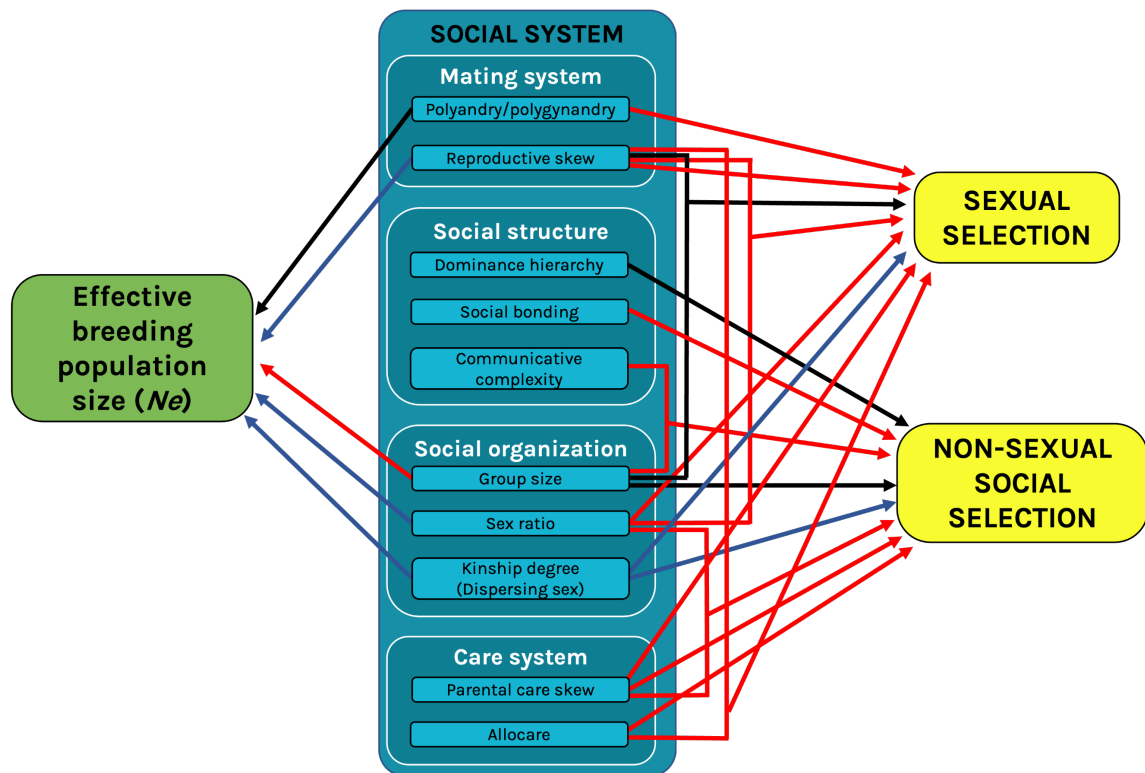
## 6) Characterising the communicative system should precede tests based on specific signals or modalities

The framework presented relies heavily on animal communication as it sustains social interactions. Therefore, the communicative system of animal species is a crucial chain link in the framework linking sociality and evolutionary speed. In this context, however, there is a need to contemplate the signaling phenotype (sometimes referred to as the “courtship phenotype” in the context of sexual selection) of a species or individual in its globality. In particular, most models and tests use specific modalities as proxies for selection strength or as measures of its anagenetic consequences (see Table 1). Such an approach ignores that communicative systems include signals conveyed through different modalities and that no *a priori* reason exists for selection to be concentrated in any specific modality (Peckre et al. 2019). As Seddon et al. (2013) put it, “*Bird species such as the nightingale Luscinia megarhynchos, for example, may be monomorphic in plumage yet experience strong sexual selection manifested in elaborate male acoustic signals. Indeed, it has long been hypothesized that investment in one signaling modality constrains investment in another [1], perhaps explaining why pairs of avian sister lineages with low levels of plumage divergence tend to have high levels of song divergence [52]*”. More generally, the existence of sets of signals might nuance the predictions based on theoretical models based on single traits. For example, the response to selection on one of a set of correlated signals depends on the strength and direction of selection acting on the other signals simultaneously. Rapid anagenesis and cladogenesis ensuing from social selection are expected when there is strong trait covariance facilitating response to selection (Agrawal and Stinchcombe 2009; Reichert and Höbel 2018). Such covariance has been observed in macro-evolutionary analyses (Webb et al. 2016; Ligon et al. 2018). Some studies find positive correlations in support of the idea that different signals may reinforce the same message (“Reinforcing signals hypothesis”, Gonzalez-Voyer et al., 2013; Webb et al., 2016). Conversely, other studies find negative correlations suggesting that trade-offs in the costs of expressing different signals are at play (“Transfer hypothesis”, Shutler & Weatherhead, 1990; Badyaev et al., 2002; Verzijden et al., 2010; Van Staaden & Smith, 2011; Elias et al., 2012; Martins et al., 2015; Clark et al., 2018). Yet others show that different traits may have evolved under independent evolutionary trajectories and serve separate functions, resulting in no correlations

between them (Ornelas et al. 2009; Mason et al. 2014; Gomes et al. 2017). Understanding which of the alternative hypotheses better explains the communicative systems of a species within and across modalities is a landmark for future research (Cooney et al. 2018; Peckre et al. 2019). Unless the covariance structure in a communicative system is known, measuring one specific signal might not represent the selective pressures happening at the system level.

## 7) Predicting the effects of variation in social systems' dimensions on evolutionary speed

We have reviewed the theoretical link between social selection,  $N_e$  and anagenesis, and cladogenesis. Yet, a missing step towards making this theoretical framework applicable across taxa is to connect the level of social selection strength and drift to social systems variation in different dimensions (Fig. 4). From this endeavor, we can predict that the faster evolving social system is as follows, regarding the selectionist perspective: big groups of unrelated individuals, unbalanced sex ratios, polygamy in mating but extreme reproductive skew in parenthood, steep hierarchies, unbalanced parental investment, and cooperative breeding. From the populationist perspective, bigger groups with extreme reproductive skew and limited dispersal by both sexes should evolve faster. We now detail how we came to such predictions by analyzing the effects of each social system dimension and component on evolutionary speed. We focus on anagenetic consequences to ease interpretation and assume that cladogenesis should be directly proportional.



**Figure 4** – Overview of the predicted links between the different social dimensions and sexual selection, non-sexual social selection and effective breeding population size. Red links indicate a positive predicted effect (i.e. increase leads to increase, decrease to decrease), blue links negative effects and black links coexisting positive and negative predicted effects.

### Social organization

Social organization, referring to the size and composition of a social unit, is likely to affect the intensity of competition. *A priori*, in the absence of reproductive skew, a change in group size should not affect the intensity of sexual selection. If reproductive skew is possible, a change in group size might affect the intensity of sexual selection. This change in the intensity of sexual selection arises because the probability of having an extreme phenotype in each social unit increases. Individuals with extreme phenotypes, having an advantage, become parents of a higher proportion of the offspring in a population. If we use the metaphor of a race, the more participants, the higher the probability of observing extremely fast or enduring individuals and the higher the reward for the winner. From this perspective, social organizations characterized by bigger group sizes (or



a higher number of overlapping home ranges for solitary animals) should generate increased sexual selection strength and, thereby, anagenetic speed (see results by Chevalier et al., 2022). Now, if groups are bigger and more individuals interact, sexual competition could become more similar to a bigger tournament if we go back to the sports competition metaphor. In a bigger tournament, more capacities (e.g., endurance, speed, strength, and agility) might have their test. From this perspective, the strength of sexual selection could decrease if everyone gets their cup of tea, and social organizations with more types of preferences could be associated with a slower evolutionary speed (Servedio and Bürger 2014). The result of these contradicting forces will likely depend on how costly it is to choose or express different phenotypes. If, as theorized, specific phenotypes signal an overall better fit to the environment, then the increased selection should be more prominent.

Regarding non-sexual social selection, *a priori*, if population size and resources are constant, no effects should prevail from increasing group size. Now, socioecological models have long predicted and tested that because groups move together, even if resources stay the same, bigger groups must navigate more extensive areas (Clutton-Brock and Harvey 1977). If relationships are egalitarian, bigger groups should lead to fewer resources per capita, increasing the selection strength on performance for translating resources into reproductive success in all individuals, but most strongly on the sex with higher parental investment. Now, if relationships can be uneven, the selection for performance should be stronger at the bottom of the hierarchy (Gluckman and Bryson 2011), while there should be overall a stronger selection for characters that allow climbing the hierarchy. For example, if in a brood, offspring compete for parental resources, increasing the size of the brood might lead to increased competition to receive enough parental care. New adaptations that foster parental attention, like throat colors, might spread quickly in such an environment. Still, their success depends on the coloration of other chicks, leaving the system in a possible perpetual anagenetic change. In addition, from an information theory perspective, more individuals interacting means more interaction and outcome types possible. This observation has led to hypotheses linking bigger group sizes with the evolution of more complex animal communicative systems and greater cognitive skills (Freeberg et al. 2012, 2019; Dunbar and Shultz 2017; Roberts and Roberts 2020). Overall, bigger groups are expected to induce faster anagenesis. Now, for those interactions that are cooperative, an increase in group size might allow non-linear access to resources (e.g., hunting much bigger prey), and group augmentation could induce an increase of per capita resources, thereby reducing the non-sexual social selection strength.

Regarding  $N_e$ , the effects of group size will depend on the rate of migration between groups (Chesser et al. 1993; Chikhi et al. 2010). If it is substantial, the  $N_e$  should stay consistent with estimates based on population size. Now, if dispersal is limited, social groups could act as mating pools of reduced size compared to the entire population, reducing the  $N_e$  (Wakeley 1999; Chikhi et al. 2010). In that case, smaller groups should be synonymous with smaller  $N_e$ , increasing the speed of neutral anagenesis.

The sex ratio is a crucial variable regarding the strength of sexual selection. If we assume no reproductive skew, the strength of sexual selection should be negatively related to the availability of mates. Hence, we have a simultaneous increase in sexual selection strength in one sex and a decrease in sexual selection strength in the other. One could wonder whether both effects cancel out, leaving evolutionary speed untouched. We think the anagenetic effects might be confined to the sex under stronger competition, but the cladogenetic effects affect both as a species. Now, if reproductive skew is possible, then the sex that can access more mates, the least numerous, should also face a strong selection. This is because those individuals from the least abundant sex have a higher potential for spreading an advantageous mutation if such mutation resides in an individual that monopolizes reproduction within groups (Socias-Martínez 2023). Thus, at the same time, the more abundant sex would face stronger sexual selection because per capita mates or gametes decrease while the less abundant would face stronger selection for accessing a bigger pie. Following such thoughts, one could predict that social systems with unbalanced sex ratios should induce faster anagenesis. Regarding non-sexual social selection, if sexes have different needs, then the effects should map that of sexual selection. If they have the same needs, then if group size doesn't change, no change arises from modifying the sex ratio.  $N_e$  generally decreases when the sex ratio deviates from 0.5, according to Equation 1 (Nomura 2002). Note that formulas used to calculate  $N_e$  translate to a random mating population. If there is reproductive skew and no extensive migration,  $N_e$  will be further decreased (Nomura 2002). These predictions assume that the sex ratios apply to the total population.

Dispersal regimes, i.e., which sex disperses out of the natal unit or farther from it, are likely to affect the strength of selection and the  $N_e$ . In light of inclusive fitness theory, competition within units can be tamed

down by shared inclusive fitness interests between individuals (Hamilton 1964). So, after calculating the sexual and non-sexual social selection strength based on other dimensions and components, relatedness could be used to reduce the strength predicted for the sex with natal philopatry. So, if both sexes disperse, the strength of selection should be highest, followed by when only one sex does so, and lowest when no sex disperses. Now, cladogenetic speed predictions might differ from the anagenetic ones here. Albeit less dispersal means less competition, it also implies that the direction of selection might be different in different social units because their genetic profiles differ. Because not only the strength of selection counts but also the directionality for a divergence to become effective (Rodríguez et al. 2013), those dispersal regimes that induce clusters of relatives should also engender islands of idiosyncratic selective pressures causing cladogenesis. Regarding the  $N_e$ , the extent of dispersal should make groups more or less equal to mating pools. In this sense, if both sexes disperse, neutral anagenesis should be the lowest; if one sex is philopatric, it should increase, and if both sexes remain in the natal unit, a drastic equality between group size and  $N_e$  should catalyze neutral evolutionary speed.

$$(1) \quad N_e = 4 \frac{N_m \times N_f}{N_m + N_f}$$

$N_e$  denotes the effective breeding population size,  $N_m$  denotes the number of males, and  $N_f$  is the number of females in the population.

### **Mating systems**

Mating systems characterize the connectivity in terms of mating and fertilization and are, therefore, unlinked from the sex ratio and group size of social units. These mating and fertilization connections will likely affect sexual selection and  $N_e$  foremost. First, increasing the number of mates per female has been linked to an increase in post-mating sexual selection strength through sperm competition and coevolutionary arms races (see previous section “Selectionist”)(Arnqvist and Rowe 1995). Thus, polyandry and polygyny mating systems should induce stronger sperm competition. Regarding pre-mating competition, those mating systems characterized by imbalances in access to sexual partners and fertilization should engender a strong selection strength to become a breeder. Thus, species with units prompting reproductive skew, like those with polygyny and polyandry, should have faster anagenesis on the characters that mediate accessing breeding positions. Thus, genetic mating systems such as polygyny and polyandry should induce stronger sexual selection and evolutionary speed. To some extent, then, the mating systems cause different pre-mating and post-mating sexual selection strengths, except for polyandry, which scores high in both. This points towards polyandry as an overlooked strength peak and the possibility of contradicting forces generating noise in comparative studies. According to equation 1, any imbalance in offspring conception between males and females should reduce the  $N_e$ , regardless of the mating skew. Thus, mating systems characterized by imbalances such as polygyny and polyandry should increase the neutral anagenetic speed.

The mating system and not only the dispersal regime can affect competition through kinship. The level of relatedness among residents depends not only on whether one sex is philopatric or not but also on reproductive skew (Schülke and Ostner 2008). For example, under female philopatry, increased polygyny should generate higher levels of kinship because of paternal relatedness on top of matriarchal kinship. Thus, mating systems such as polygyny or polyandry can reduce the strength of competition among the sex that remains philopatric.

### **Social structure**

Social structure describes the level of balance in social relationships, the distribution of benefits and costs of group living, and the access to resources and mates. In this sense, if social structure maps the mating system, like when the presence of a hierarchy and the position of one individual in it determines its access to reproduction, the predictions might be redundant to those for the mating system. Now, social structure determines access to non-sexual resources, sometimes independently of the reproductive side. Under such circumstances, the social structure will describe the strength of non-sexual social selection. For example, let us consider social hierarchies. When hierarchies are steeper, high-ranking individuals capitalize on access to resources while the lowest ranking capitalizes on the costs of group living. Now, depending on the character at stake and how hierarchies are maintained, predictions for anagenesis might differ. Those characters mediating climbing the social hierarchy will be positively selected, and the strength should be proportional to

the benefits of moving up. Thus, according to such perspectives, a more unbalanced social structure will likely engender faster evolutionary rates. Others have suggested that more egalitarian societies engender higher unpredictability and complexity. For such a way of thinking based on information theory, more egalitarian societies, i.e., with milder hierarchies or without any at all, should engender stronger selective forces to navigate a more chaotic environment, at least in terms of communication and socio-cognitive skills (Freeberg et al. 2012, 2019; Dunbar and Shultz 2017; Roberts and Roberts 2020). In a sense, the level of social complexity could change the optima of social characters (i.e., increasing the mean of socio-cognitive skills or communicative complexity), but whether this translates to faster anagenesis beyond attaining a different peak is uncertain. Yet another prediction can be made if one considers that some hierarchical structures are more or less fixed, as those of many female anthropoid primates, as shown by Gluckman & Bryson (2011). In such systems, those characters that improve reproductive output in the face of difficulties will likely be strongly selected in lower-ranking individuals. Thus, steeper hierarchies would generate stronger anagenesis for those characters that can compensate for being at the lower end of society (see Gluckman & Bryson, 2011). Regarding  $N_e$ , again, if the social structure maps the mating system, the same predictions apply.

Variations in the intensity of social bonds could affect the selection strength, but we are unsure about its effects on evolutionary speed. Social bonds relate to the stability and extent of exchanges of goods and services between individuals. Individuals in bonded societies navigate a network of alliances, implying, for example, that when competing with another individual, they also face his/her relationships. On the one side, this up-leveling of social complexity increases the range of new characters that can impact fitness through their effects on an enriched social environment. For example, such networks of alliances have been suggested to select for increased socio-cognitive skills and communicative complexity to understand better and coordinate social interactions (Freeberg et al. 2019; Roberts and Roberts 2020; Dunbar and Shultz 2021). Suppose one possesses characters that help establish meaningful alliances, like the capacity for reciprocity and other socio-cognitive and communicative skills. In that case, it is likely to have a more robust supportive network, enabling winning competition more often. In such a complex system, the possibilities for divergent anagenesis to appear in different subpopulations should increase, but, at the same time, this network of alliances might act as a limiting factor for new mutations. Beneficial mutations could have their potential for spread limited because they do not face isolated individuals but teams, which might have a broader range of resistance to invasion. Regarding  $N_e$ , there should be no effects beyond those related to reproductive skew.

### Care systems

Variation in care systems is crucial in determining the effects described in the previous paragraphs. We see two key aspects in this regard: the balance in parental investment and the presence or absence of communal/cooperative care. If there is equality in investment, then both sexes are equivalent, and the effects of uneven sex ratios are equivalent in any direction, going away from 0.5. Likewise, the effects of the mating system change from monogamy towards polyandry or polygyny should be similar. If the sexes invest differently in parental activities, the operational sex ratio (OSR) might differ from the adult sex ratio. The OSR regards the number of receptive males and females at any time  $t$ . If one sex has higher levels of investment, then the number of individuals available should be smaller than for the other sex. In this sense, the more abundant sex regarding the OSR is predicted to have stronger sexual selection. Thus, care systems characterized by unbalances in parental investment should have faster anagenesis. In addition, unbalances in parental investment create different needs between sexes regarding what can increase reproductive success. The sex investing less should be able to focus on mating more often (the mating sex for simplicity). In contrast, the other sex should focus on quality/diversity and the resources needed for parenting (parenting sex). For example, in a system with solely paternal care, the number of males will strongly determine the number of offspring produced in a unit. Under such a scenario, females should focus on finding available males to increase their success while males on good nests and whatever is needed to take care of offspring. Thus, if reproductive skew is possible, then sex differences in care open the way for increased sexual selection strength towards the sex that invests less per offspring. In contrast, the strength of non-sexual social selection should increase in the sex that invests most per offspring. All else equal, species with higher sex asymmetries in parental investment should have increased social selection strength and evolve faster. Some authors have shown that under sex asymmetries in care, investing in mating competition is only a viable strategy for the abundant sex if mortality is high (Kokko and Jennions 2008).

Positive interactions between adults to care for offspring (communal/cooperative care) in a social unit are likely to affect evolutionary speed in two ways. If there is no reproductive skew among the parenting sex and if taking care together induces non-additive gains, then increasing group size or moving the sex ratio towards parents reduces the level of competition. Thus, predictions for stronger social-selection strength among parents when these are more abundant (sex ratio imbalance or group size increase) should not hold if the gains in care offset the costs of competition for parenting resources. Moreover, there may be a selection for characters that improve the capacity to cooperate with others and detect cheaters as those predicted for increased social complexity under increased group size and complexity. If there is a reproductive skew among the parenting sex together with care by non-reproductives (alloecare), as in cooperative breeding or eusocial species, the strength of selection to become the breeder is further increased because this position represents a bigger reproductive success in the population. So, cooperative breeding coupled with polygamy, polyandry but also with monogamy (i.e., when only the breeding pair reproduces) should be associated with faster anagenesis and cladogenesis (Socias-Martínez 2023). Increased speed should be a function of the number of helpers. If these increase in number through a social organization characterized by bigger group sizes, the evolvability should do accordingly. Similarly, if being at the top of the hierarchy results in a higher proportion of the care in a social unit being provided to one's offspring, one could predict that the social selective strength to become dominant and the evolutionary speed increase as well. *We* should follow the reproductive skew patterns.

## Conclusion

There is plenty of work to be done to understand the evolutionary consequences of social selection. We have shown that there is a potential avenue by expanding previous research in all domains, including the combination of selectionist and populationist perspectives, measuring social variation in ways that can be applied across taxa, and assessing the communicative system of a species before targeting any specific trait. We have also offered explicit predictions for the consequences of variation in each social dimension and component, hoping this will encourage future integrative research. Although advocating for integrative approaches that need a lot of information potentially reduces the species studied, it can also stimulate new ideas and ways of studying wild species. We think that one unexpected key message of the present review is that contrary to the view that scientific research should narrow its targets, there is a need for designing data collection beyond the specific theory or hypothesis being tested. Thus doing, we might be able to collect datasets bypassing some of our own current theoretical biases.

**Table 1** – Reviewed studies investigating the effects of sociality on evolutionary speed: Column “Time level” indicates the time scale of the investigated effects with “Micro” indicating microevolution, “Meso” mesoevolution, and “Macro” macroevolution. The former includes observed processes of change over several generations, the middle signatures of such change in one species over spatial or cultural variation, and the latter signatures including several species. “Speed component” designs whether studies focus on anagenetic or cladogenetic effects. “Aspect” indicates which part of the presented framework connecting anagenetic and cladogenetic speed is being investigated. “Type study” shows the primary methodological approach used. “Dimension” designs information about the social system dimension used as a study variable. “Component” indicates the component within the social dimension. “Results” offer a description of the main findings in relation to our review. “Clade” gathers the taxa studied with minimal information on the number of species and/or families investigated. “Process” indicates which effect was investigated among sexual, non-sexual social selection and/or drift, “SxS” designs sexual, “So” non-sexual social, and “Dft” drift. “Effect” indicates the observed effect, “1” being positive, “0.5” both evidence and absence of evidence, “0” lack of evidence, “-1” contrary to the predictions, and “np” not predicted by the framework. “Perspective” indicates the theoretical focus of the authors when conducting the study. “Reference” cites the study in question.

Time level	Speed component	Aspect	Type study	Dimension	Component	Results	Clade	Process	Effect	Tested both	Perspectiv e	Reference
Micro	Anagenetic	Coevolution	Artificial selection	Care system	Presence/absence maternal care	Populations respond to selection for bigger size only in the presence of care and to smaller size only in the absence of care.	Burying beetle ( <i>Nicrophorus vespilloides</i> )	So	1	0	Selectionist	(Jarrett et al. 2017)
Micro	Anagenetic	Divergence	Artificial selection	-	-	Costs of fighter morph development and combats between developing individuals lead to lower diversity when selecting for this morph compared to the scrambler morph. Divergent SNPs are scattered across the genome.	Bulb mite ( <i>Rhizoglyphus robini</i> )	SxS.Dft	1	1	Selectionist	(Parrett et al. 2022)
Micro	Anagenetic	Divergence	Experimental evolution	Social organization ; Mating system	Group size	Increasing unit size out of monogamy did not result in differences in pre- or post-matin isolation indexes.	Bulb mite ( <i>Rhizoglyphus robini</i> )	SxS	0	0	Selectionist	(Plesnar-Bielak et al. 2013)
Micro	Anagenetic	Divergence	Experimental evolution	Social organization	Group size	Mating between individuals from different lines did not differ significantly from mating within lines, regardless of the unit sizes used to let populations evolve. Nevertheless, bigger unit sizes yielded more pronounced isolation.	Bruchid beetle ( <i>Callosobruchus maculatus</i> )	SxS	0.5	0	Selectionist	(Gay et al. 2009)
Micro	Anagenetic	Divergence	Experimental evolution	Social organization	Sex ratio	Housing flies under varying sex ratios did not result in statistically significant changes in the probability of mating within populations versus across populations.	Fruit fly ( <i>Drosophila melanogaster</i> )	SxS	0.5	0	Selectionist	(Wigby and Chapman 2006)

Micro	Anagenetic	Divergence	Experimental evolution	Social organization ; Mating system	Group size; Sex ratio	Increasing group size by adding males does not lead to statistically significant differences in pre-mating or post-mating isolation proxies, such as the number of mating pairs, mating speed, copulation duration, offspring viability and sterility. However, trends exist in the direction predicted by the framework.	Fruit fly ( <i>Drosophila pseudoobscura</i> )	SxS	0.5	0	Selectionist	(Bacigalupe et al. 2007)
Micro	Anagenetic	Arms race	Experimental evolution	-	-	Unbalancing coevolution towards male profit induces an advantage in remating and siring; females pay in terms of survival.	Fruit fly ( <i>Drosophila melanogaster</i> )	SxS	1	0	Selectionist	(Rice 1996)
Micro	Anagenetic	Arms race	Experimental evolution	Social organization	Sex ratio	Shifting the sex ratio towards males leads to the evolution of higher female resistance to male harm.	Fruit fly ( <i>Drosophila melanogaster</i> )	SxS	1	0	Selectionist	(Nandy et al. 2014)
Micro	Anagenetic	Arms race	Experimental evolution	Social organization ; Mating system	Sex ratio	Reducing competition among males under random monogamy led to a reduction in male genitalia, while female genitalia showed inertia.	Seed beetle ( <i>Callosobruchus maculatus</i> )	SxS	1	0	Selectionist	(Cayetano et al. 2011)
Micro	Anagenetic	Divergence	Experimental evolution	Social organization ; Mating system	Group size	Increasing the number of males per unit resulted in increased female preference for males from the same population, which led to drastic levels of pre-mating isolation.	Dung fly ( <i>Sepsis cynipsea</i> )	SxS	1	0	Selectionist	(Martin and Hosken 2003)
Micro	Anagenetic	Divergence	Experimental evolution	Social organization ; Mating system	Sex ratio	Females from male-biased sex ratio lines tend to mate more often with males from the same population.	Fruit fly ( <i>Drosophila melanogaster</i> )	SxS	1	0	Selectionist	(Syed et al. 2017)
Micro	Anagenetic	Divergence	Experimental evolution	Social organization ; Mating system	Group size; Sex ratio	Increasing or decreasing number of males per unit leads to changes in male courtship song inter-pulse interval and latency to sing.	Fruit fly ( <i>Drosophila pseudoobscura</i> )	SxS	1	0	Selectionist	(Snook et al. 2005)
Micro	Anagenetic	Divergence	Experimental evolution	Social organization ; Mating system	Group size; Sex ratio	Females from lines with different sexual selection strengths show coevolving preferences with male courtship song properties that diverge, as per Snook et al. (2005).	Fruit fly ( <i>Drosophila pseudoobscura</i> )	SxS	1	0	Selectionist	(DeBelle et al. 2014)

Micro	Anagenetic	Divergence	Experimental evolution	Social organization ; Mating system	Group size; Sex ratio	Genomes show signatures of divergence, most concentrated in chromosomes 3 and X. Lower diversity in one-F-multi-M lines.	Fruit fly ( <i>Drosophila pseudoobscura</i> )	SxS.Dft	1	1	Selectionist	(Wiberg et al. 2021)
Micro	Anagenetic	NFD cycling	Field observations	-	-	Negative frequency-dependent selection for three morphs of males kept the proportions of the different genes in constant change.	Side-blotched lizard ( <i>Uta stansburiana</i> )	SxS	1	1	Selectionist	(Sinervo and Lively 1996)
Micro	Anagenetic	NFD cycling	Field observations	-	-	Female morph frequencies were found to change over time. The most common female morph in each generation mated more often. Moreover, male harassment pressure is suspected to have negative fitness consequences.	Blue-tailed damselfly ( <i>Ischnura elegans</i> )	SxS	1	1	Selectionist	(Svensson et al. 2005)
Micro	Anagenetic	NFD cycling	Field observations	-	-	Female morphs have different advantages, but male mate searching impacts negatively when they become too abundant.	Blue-tailed damselfly ( <i>Ischnura elegans</i> )	SxS	1	1	Selectionist	(Le Rouzic et al. 2015)
Micro	Anagenetic	NFD cycling	Field observations	-	-	The rarer female morph each season produces bigger and heavier clutches.	Sedge sprite damselfly ( <i>Nehalennia irene</i> )	SxS	1	1	Selectionist	(Iserbyt et al. 2013)
Micro	Anagenetic	Coevolution	Modelling	Social structure	Hierarchy	More severe effects of hierarchy reduced the rate of change in the neutral genomes of agents.	-	Dft	-1	0	Populationist	(Hoelzer et al. 1998)
Micro	Anagenetic	Anagenesis	Modelling	Social structure	Female hierarchy strength	Stronger female hierarchies had faster evolution of adaptive genes selected for the low-ranking females.	-	So	np	0	Selectionist	(Gluckman and Bryson 2011)
Micro	Anagenetic	Coevolution	Modelling	-	-	Coevolution of male and female preferences is less likely when costs for preferences on females are introduced.	-	SxS	0.5	0	Selectionist	(Hall et al. 2000)



Micro	Anagenetic	Divergence	Modelling	-	-	Costs for female preferences only allow significant divergence if male signals reflect condition and adaptation to the local environment, but selection against choosiness leads to erosion of divergence. The signals reflecting male adaptation nevertheless reduce the possibility of sexual isolation in the face of secondary contact. Arbitrary male traits, on the contrary, can maintain divergence in the face of selection against hybrids.	-	SxS	0.5	0	Selectionist	(Yukilevich and Aoki 2022)
Micro	Anagenetic	Coevolution	Modelling	-	-	Under polygyny, there is no paternal care nor costs of female preferences; male traits and preferences for them can evolve even under the costs of expressing the male signal.	-	SxS	1	0	Selectionist	(Kirkpatrick 1982)
Micro	Anagenetic	Coevolution	Modelling	-	-	Fisher's runaway is continual and cycles up and down but might modify its trajectory, creating significant possibilities for divergence.	-	SxS	1	0	Selectionist	(Iwasa and Pomiankowski 1995)
Micro	Anagenetic	Coevolution	Modelling	-	-	Including mate sampling theory instead of assuming fixed costs of female preferences leads to coevolution of male traits and female preferences.	-	SxS	1	0	Selectionist	(Kokko et al. 2015)
Micro	Anagenetic	Coevolution	Modelling	Social organization	Group size	Increasing mating group sizes leads to faster and stronger anagenesis.	-	SxS	1	0	Selectionist	(Chevalier et al. 2022)
Micro	Anagenetic	Coevolution	Modelling	-	-	Including the effects of the social environment experienced as drivers of mating preferences results in extreme anagenetic coevolution even without genetic links between signals and preferences.	-	SxS	1	0	Selectionist	(Bailey and Moore 2012)
Micro	Anagenetic	Divergence	Modelling	-	-	Under no paternal care nor costs of female preferences, divergent coevolution between female preferences and male traits can be extremely fast.	-	SxS	1	0	Selectionist	(Lande 1981)
Micro	Anagenetic	Divergence	Modelling	-	-	Divergent runaway between female preferences and male traits can drive sexual isolation even in sympatry.	-	SxS	1	0	Selectionist	(Wu 1985)

Micro	Anagenetic	Divergence	Modelling	-	-	If the benefits of choosing a mate are large enough relative to costs, a stable equilibrium ensues. If not, there is a cyclic change, as per Iwasa and Pomiankowski 1995. In addition, if there are differences in ecology between populations, isolation evolves quickly through sexual selection.	-	SxS	1	0	Selectionist	(Pomiankowski and Iwasa 1998)
Micro	Anagenetic	Divergence	Modelling	-	-	If spatial or ecological heterogeneity affects the optimal male phenotype, female choosing costs do not preclude the runaway coevolutionary process.	-	SxS	1	0	Selectionist	(Day 2000)
Micro	Anagenetic	Divergence	Modelling	-	-	If there is ecological heterogeneity, and male ornaments reflect local adaptation, even in the face of gene flow, sexual isolation might ensue.	-	SxS	1	0	Selectionist	(Doorn et al. 2009)
Micro	Anagenetic	Gene replication and spread	Modelling	Social organization ; Mating system; Social structure; Care system	Group size; Sex ratio; Reproductive skew; Cooperative care	Social systems that maximise offspring production by immigrants and that reduce the number of breeding positions enhance gene replication and spread.	-	SxS.So	1	0	Selectionist	(Socias-Martínez 2023)
Micro	Anagenetic	Gene replication and spread	Modelling	Social organization ; Mating system; Social structure; Care system	Group size; Sex ratio; Dispersal regime; Reproductive skew; Cooperative care	Social systems that maximise the number of immigrants that reproduce increase the genetic diversity of offspring.	-	SxS.So	1	0	Selectionist	(Socias-Martínez 2023)
Micro	Cladogenetic	Divergence	Modelling	Social organization ; Mating system	Dispersal regime; Sex ratio; Mating patterns	Social systems induce an excess in genetic mixing per individual: heterozygosity compared to a random mating population. Dispersal by both sexes tends to reduce this effect while female philopatry increases it. Monogamous and polygamous units induced the highest heterozygosity, followed by extreme and moderate polygyny.	-	Dft	1	0	Populationist	(Parreira and Chikhi 2015)
Micro	Cladogenetic	Coevolution	Modelling	Social structure	Hierarchy	More severe effects of hierarchy induced longer living matriarchies because of beneficial effects to dominant females.	-	Dft	np	0	Populationist	(Hoelzer et al. 1998)
Meso	Anagenetic	Convergence	Field experiment	-	-	Territorial competition among antbirds leads to social selection for specific song variants among species.	Peruvian Warbling-Antbird ( <i>Hypocnemis peruviana</i> )	So	1	1	Selectionist	(Tobias and Seddon 2009)

Meso	Anagenetic	Convergence	Field experiment	-	-	Territorial competition among antbirds leads to social selection for specific song variants among species.	Yellow-breasted warbling antbird ( <i>Hypocnemis subflava</i> )	So	1	1	Selectionist	(Tobias and Seddon 2009)
Meso	Anagenetic	Divergence	Field experiment	-	-	Song characteristics and genetic distance are correlated, and playback experiments show males react mostly to local songs.	White-crowned sparrow ( <i>Zonotrichia leucophrys</i> )	SxS	0.5	0	Selectionist	(Lipshutz et al. 2017)
Meso	Anagenetic	Divergence	Field experiment	-	-	Females prefer male body shapes adaptive towards predatory pressure in the local environment.	Bahamas mosquitofish ( <i>Gambusia hubbsi</i> )	SxS	1	0	Selectionist	(Langerhans and Makowicz 2013)
Meso	Anagenetic	Divergence	Field experiment	-	-	Male calls differ among populations in dominant frequencies, and females tend to prefer calls from their own population in playback experiments.	Amazonian frog ( <i>Physalaemus petersi</i> )	SxS	1	1	Selectionist	(Boul et al. 2006)
Meso	Anagenetic	Divergence	Field experiment	-	-	Females and males approach more quickly songs and decoys from their own population. Increasing distance from origin increases latency.	European stonechats ( <i>Saxicola torquata rubicola</i> )	SxS	1	0	Selectionist	(Mortega et al. 2014)
Meso	Anagenetic	Divergence	Field experiment	-	-	Females more often solicited copulations to decoys with their local song dialect, while males do not respond differently to local and non-local displays.	Rufous-collared sparrows ( <i>Zonotrichia capensis</i> )	SxS	1	0	Selectionist	(Danner et al. 2011)
Meso	Anagenetic	Divergence	Field observations	-	-	While the frequencies of female rugged morphs differed across populations, genetic drift was only rejected as the cause in <i>H. impressopunctatus</i> .	Diving beetle ( <i>Dytiscus lapponicus</i> )	Dft	1	1	Selectionist	(Green et al. 2014)
Meso	Anagenetic	Divergence	Field observations	-	-	While the frequencies of female rugged morphs differed across populations, genetic drift was only rejected as the cause in <i>H. impressopunctatus</i> .	Diving beetle ( <i>Graphoderus zonatus</i> )	Dft	1	1	Selectionist	(Green et al. 2014)

Meso	Anagenetic	Divergence	Field observations	-	-	While the frequencies of female rugged morphs differed across populations, genetic drift was only rejected as the cause in <i>H. impressopunctatus</i> .	Diving beetle ( <i>Hygrotus impressopunctatus</i> )	SxS	1	1	Selectionist	(Green et al. 2014)
Meso	Anagenetic	Divergence	Field observations	-	-	Male songs from different populations differ in pulse rate, pulse duration, and carrier frequency, and females have unimodal preferences tailored towards local male songs.	Hawaiian cricket ( <i>Laupala cerasina</i> )	SxS	1	0	Selectionist	(Grace and Shaw 2011)
Meso	Anagenetic	Divergence	Field observations	-	-	Natural populations diverge most prominently through sexually mediated communication as the most diverging regions of the genome or phenotypes are linked to these functions.	Cichlid fish ( <i>Tropheus moorii</i> )	SxS	1	1	Selectionist	(Mattersdorfer et al. 2012)
Meso	Anagenetic	Divergence	Field observations	-	-	Signatures of positive selection are most prominent in regions of the genome related to sexual interactions and in sympatric populations.	Hawaiian Picture-winged Fruit flies ( <i>Drosophila</i> ; 3 species)	SxS	1	1	Selectionist	(Kang et al. 2016)
Meso	Anagenetic	Divergence	Field observations	-	-	Song dialects do not correspond to mating pools nor to neutrally evolving subpopulations.	White-crowned sparrow ( <i>Zonotrichia leucophrys</i> )	SxS	np	1	Selectionist	(Poesel et al. 2017)
Meso	Anagenetic	Divergence	Field observations	-	-	Acoustic characteristics of songs by males in leks differ geographically but do not correlate with genetics.	Wedge-tailed sabrewings ( <i>Campylopterus curvipennis</i> )	SxS	np	1	Selectionist	(González and Ornelas 2014)
Meso	Anagenetic	Divergence	Field observations	-	-	Two dialects in an urban environment do not conform to mating pools.	Orange-tufted sunbird ( <i>Nectarinia osea</i> )	SxS	np	1	Selectionist	(Leader et al. 2008)
Meso	Anagenetic	Divergence	Field observations	-	-	Female auditory spiracle size is subject to divergent sexual selection among populations.	Bushcricket ( <i>Kawanaphila nartee</i> )	SxS.Dft	1	1	Selectionist	(Hare et al. 2022)

Meso	Anagenetic	Coevolution	Genomic	-	-	Genes that suffer from the highest recombination rates are expressed in the brains of workers.	Honey bee ( <i>Apis mellifera</i> )	So	1	0	Selectionist	(Kent and Zayed 2013)
Meso	Anagenetic	Divergence	Laboratory experiment	-	-	Female preferences for male display traits are conserved across populations.	Wolf spider ( <i>Schizocosa crassipes</i> )	SxS	0	1	Selectionist	(Watts et al. 2019)
Meso	Anagenetic	Divergence	Laboratory experiment	-	-	Females from recently diverged subspecies have preferences tailored to males from their population for song but not for cuticular hydrocarbons.	Fruit fly ( <i>Drosophila athabasca</i> and <i>D. mahican</i> )	SxS	0.5	0	Selectionist	(Yukilevich et al. 2016)
Meso	Anagenetic	Divergence	Laboratory experiment	-	-	Females from African and non-African strains prefer the chemical compounds and behavior of their own strains.	Fruit fly ( <i>Drosophila melanogaster</i> )	SxS	1	0	Selectionist	(Jin et al. 2022)
Meso	Anagenetic	Divergence	Laboratory experiment	-	-	Females from different subspecies all prefer males with more pulses per burst but each subspecies has an optimum for inter-pulse interval.	Fruit fly ( <i>Drosophila athabasca</i> and <i>D. mahican</i> )	SxS	1	0	Selectionist	(Yukilevich et al. 2016)
Meso	Cladogenetic	Divergence	Field observations	Social organization	Group size	Gene flow among social morphs counteracts substantial negative selection on a single gene in ants that form new colonies in a group.	Fire ant ( <i>Solenopsis invicta</i> )	So	0	0	Selectionist	(Ross and Keller 1995)
Meso	Cladogenetic	Divergence	Field observations	Social organization ; caring system	Group size; cooperative breeding	Social morphs do not represent different lineages and thus gene flow is not precluded.	Sweat bee ( <i>Halictus rubicundus</i> )	So	0	0	Selectionist	(Soro et al. 2010)
Meso	Cladogenetic	Divergence	Field observations	Social organization	Group size	Gene flow among social morphs is restricted.	Wood ant ( <i>Formica truncorum</i> )	So	1	0	Selectionist	(Gyllenstrand et al. 2005)

Meso	Cladogenetic	Divergence	Field observations	Social organization ; caring system	Group size; cooperative breeding	Social morphs are genetically isolated, and group foundress morph has higher divergence due to reduced dispersal distances on foot.	Alpine silver ant ( <i>Formica selysi</i> )	So.Dft	1	1	Selectionist	(Fontcuberta et al. 2022)
Macro	Anagenetic	Neutral evolution	Genomic	Social organization ; Care system	Phylogeny	The presumably smaller <i>Ne</i> in honeybees with reproductive skew and cooperative care induced more changes in the mitochondrial genes CO-I and CO-II.	Honeybee ( <i>Apis mellifera</i> ); Fruit fly ( <i>Drosophila</i> )	Dft	1	0	Populationist	(Crozier et al. 1989)
Macro	Anagenetic	Divergence	Laboratory experiment	-	-	Certain song characteristics in males and female preferences for them appear to have diverged in the three species investigated.	Crickets ( <i>Grillus</i> )	SxS	1	0	Selectionist	(Hennig et al. 2016)
Macro	Anagenetic	Coevolution	Phylogenetic	Social organization ; Social structure; Care system	Group size; Cooperative care	Eusocial species have more transposable elements and microsatellite repeats resulting in increased genome sizes.	Snapping shrimps (33 species)	?	1	1	Both	(Chak et al. 2021)
Macro	Anagenetic	Neutral evolution	Phylogenetic	Social organization ; social structure	Phylogenetic groups	Those groups that live in spatially or socially structured populations have a genome that changed more rapidly in chromosome architecture and speciated more.	Vertebrates mammals, reptiles, Amphibians, Teleost fish	?	1	0	Populationist	(Bush et al. 1977)
Macro	Anagenetic	Neutral evolution	Phylogenetic	Care system	Cooperative breeding	There is no apparent link between sociality and anagenetic speed at the species level in nuclear and mitochondrial DNA. When aggregating species into families and tribes, the “deeper contrasts” reveal that eusocial clades have faster anagenesis.	Bees (13 pairs of species); wasps (1 pair); ants(5); termites(1); shrimps (3); mole rats (2)	Dft	0.5	0	Populationist	(Bromham and Leys 2005)
Macro	Anagenetic	Divergence	Phylogenetic	Social organization ; Care system	Group size; Cooperative breeding	Species that live in cooperative inbred families have a <i>Ne</i> 10 times lower than that of sister species living in outbred families with extensive dispersal, resulting in 5-8 times lower genetic diversity and 6-10 times lower heterozygosity in cooperative inbred families.	Stegodyphus spiders (7 species)	Dft	1	1	Populationist	(Settepani et al. 2017)
Macro	Anagenetic	Neutral evolution	Phylogenetic	Social organization ; social structure	Nest size	Bigger nests are associated with increased anagenesis in mitochondrial DNA and reduced anagenesis in nuclear DNA. The effects in the nuclear rDNA were interpreted because of higher levels of polyandry in species with bigger nests.	Apis (2 species); Vespidae(22 species)	Dft	1	0	Populationist	(Schmitz and Moritz 1998)

Macro	Anagenetic	Coevolution	Phylogenetic	Care system	Cooperative breeding	Species that transitioned to cooperative breeding tended to retain the ancestral rod-shaped melanosomes.	African starlings	So	-1	0	Selectionist	(Maia et al. 2013)
Macro	Anagenetic	Coevolution	Phylogenetic	Social organization ; Social structure; Care system	Phylogeny	Eusociality does not result in significant changes in DNA methylation patterns.	Insects (41 species)	So	0	0	Selectionist	(Bewick et al. 2017)
Macro	Anagenetic	Coevolution	Phylogenetic	Social organization	Group size	Bigger group sizes are associated with bigger brains.	Primates	So	1	0	Selectionist	(Dunbar and Shultz 2021)
Macro	Anagenetic	Coevolution	Phylogenetic	Social organization ; Mating system	Group size; Mating pattern	Transitioning to social systems with more individuals and promiscuity is associated with increments in brain volume.	Primates	So	1	1	Selectionist	(Grabowski et al. 2022)
Macro	Anagenetic	Coevolution	Phylogenetic	Social organization ; Care system	Phylogeny	Compared to parasitoid Hymenoptera, eusocial species tend to have unusually high recombination rates.	Hymenoptera (8 species)	So	1	0	Selectionist	(Wilfert et al. 2007)
Macro	Anagenetic	Coevolution	Phylogenetic	Social organization ; Social structure; Care system	Group size; Caste differentiation	Along a gradient of social complexity, show genetic evidence of different strengths of selection. Species show genomic signatures corresponding to their level of social complexity.	Hymenoptera (6 species)	So	1	0	Selectionist	(Dogantzis et al. 2018)
Macro	Anagenetic	Coevolution	Phylogenetic	Social organization ; Social structure; Care system	Group size; Caste differentiation	Gene families expand as a function of transitions into more advanced eusociality from solitaryness. Eusocial species show evidence of intense positive selection.	Bees (6 species)	So	1	0	Selectionist	(Shell et al. 2021)
Macro	Anagenetic	Coevolution	Phylogenetic	Care system	Obligate or facultative care	Obligate parental care allows species to grow in size.	Burying beetles (14 species)	So	1	0	Selectionist	(Jarrett et al. 2017)



Macro	Anagenetic	Coevolution	Phylogenetic	Social organization ; Social structure; Care system	Phylogeny	While eusociality imposes some genetic conservatism, it also unleashes a series of extremely fast changes in both coding and noncoding regions.	Ants (7 species); Honey bee; Solitary insects (8 species)	So.Dft	1	0	Selectionist	(Simola et al. 2013)
Macro	Anagenetic	Coevolution	Phylogenetic	Social organization ; Social structure; Care system	Phylogeny	Transitions from solitary to various forms of eusociality resulted in a mix of positive selection and enrichment of gene regulation capacities and relaxed and neutral evolutionary trajectories in genomes.	Bees (10 species)	So.Dft	1	1	Selectionist	(Kapheim et al. 2015)
Macro	Anagenetic	Divergence	Phylogenetic	-	-	Genera classified as having higher levels of intersexual competition do not evolve divergent genitalia more often.	Insects; Spiders; 361 genera	SxS	0	0	Selectionist	(Eberhard 2004)
Macro	Anagenetic	Divergence	Phylogenetic	Social organization ; Mating system	Group size; Sex ratio; Reproductive skew	Species diverged more rapidly regarding male nuptial coloration hue when promiscuous than monogamous or polygynous.	African Cichlid fishes (Cichlidae; 70? species)	SxS	1	0	Selectionist	(Seehausen et al. 1999)
Macro	Anagenetic	Divergence	Phylogenetic	-	Dichromatism	Species where males and females differ more in plumage coloration, are also those where male coloration diverged most and most rapidly from sister species.	Passerine birds (23 families; 84 recently diverged species)	SxS	1	0	Selectionist	(Seddon et al. 2013)
Macro	Anagenetic	Divergence	Phylogenetic	Mating system	Mating patterns	Species with polygynous harems diverged more rapidly than those with monogamous pairs regarding body mass, size dimorphism, baculum length and testes size.	Pinnipeds (14-25 species)	SxS	1	0	Selectionist	(Fitzpatrick et al. 2012)
Macro	Anagenetic	Divergence	Phylogenetic	Social organization	Group size; Sex ratio	Taxa with an increasing number of females and bigger groups of both sexes, had higher synonymous mutation rates in mitochondrial DNA and non-synonymous mutations in the nuclear DNA.	Birds (954 species)	SxS.Dft	0.5	1	Selectionist	(Iglesias-Carrasco et al. 2019)
Macro	Both	Divergence	Phylogenetic	-	-	Changes in coloration (in both sexes) were associated with higher speciation rates.	Tanagers (Thraupidae); 355 species	?	1	0	Selectionist	(Price-Waldman et al. 2020)

Macro	Both	Divergence	Phylogenetic	-	-	Color evolution rates in specific plumage patches in both sexes positively correlated with speciation rates.	Hummingbirds (Trochilidae); 237 species	SxS	1	0	Selectionist	(Beltrán et al. 2021)
Macro	Cladogenetic	Divergence	Phylogenetic	Social organization ; Mating system; Care system	10 different taxon-specific 1-dimensional scales relating group size, composition , timing of grouping, reproductive division of labor	Except for non-human primates, there was no significant correlation between diversity and group size.	Mammals (108 species); birds (29); bees (9); wasps (9)	?	0	0	Populationist	(Marzluff and Dial 1991b)
Macro	Cladogenetic	Divergence	Phylogenetic	Social organization ; social structure	Phylogenetic groups	Those groups that live in spatially or socially structured populations have a genome that changed more rapidly in chromosome architecture and speciated more.	Vertebrates mammals, reptiles, Amphibians, Teleost fish	?	1	0	Populationist	(Bush et al. 1977)
Macro	Cladogenetic	Divergence	Phylogenetic	Social organization ; Care system	Group size; Cooperative care	Genus with cooperative care tend to have fewer species than pair-breeding counterparts.	Oscine Passerine Birds (1684 species)	So	-1	1	Selectionist	(Cockburn 2003)
Macro	Cladogenetic	Divergence	Phylogenetic	Social organization ; Care system	Group size; Cooperative care	Clades living in social groups and characterised by reproductive skew do not have higher speciation rates.	Carnivora (74 species)	So	0	1	Selectionist	(Muñoz-Durán 2002)
Macro	Cladogenetic	Divergence	Phylogenetic	Social organization	Group size	Sister clades with social and non-social species do not differ in their number of species.	Theridiid spiders	So	0	0	Selectionist	(Agnarsson et al. 2006)
Macro	Cladogenetic	Divergence	Phylogenetic	Social organization ; Care system	Group size; Cooperative care	Clades living in social groups characterised by reproductive skew have higher extinction rates.	Carnivora (74 species)	So	np	1	Selectionist	(Muñoz-Durán 2002)

Macro	Cladogenetic	Divergence	Phylogenetic	-	-	The number of species having idiosyncratic genitalia does not differ among clades with high or low levels of intersexual competition.	Insects; Spiders; 361 genera	SxS	0	0	Selectionist	(Eberhard 2004)
Macro	Cladogenetic	Divergence	Phylogenetic	-	Dimorphism	More dimorphic genera do not contain more species.	Mammals (480 genera); Butterflies (105 genera); Spiders (148 genera)	SxS	0	0	Selectionist	(Gage et al. 2002)
Macro	Cladogenetic	Divergence	Phylogenetic	Mating system	Relative testes size	Genera with bigger testes do not contain more species.	Mammals (72 genera)	SxS	0	0	Selectionist	(Gage et al. 2002)
Macro	Cladogenetic	Divergence	Phylogenetic	Mating system	Female number of partners	Genera where females mate more do not contain more species.	Butterflies (54 genera)	SxS	0	0	Selectionist	(Gage et al. 2002)
Macro	Cladogenetic	Divergence	Phylogenetic	-	Dimorphism	Sexual dichromatism extent does not predict diversification rates.	Birds	SxS	0	0	Selectionist	(Huang and Rabosky 2014)
Macro	Cladogenetic	Divergence	Phylogenetic	Social organization	Group size; Sex ratio	Taxa with increasing number of females and bigger groups of both sexes had higher diversification rates except if they were large-bodied and had slow mutation rates.	Birds (954 species)	SxS	0.5	0	Selectionist	(Iglesias-Carrasco et al. 2019)
Macro	Cladogenetic	Divergence	Phylogenetic	Social organization	Group size; Sex ratio	Sexual size dimorphism increased towards males is associated with faster net diversification rates, but the number of females in units and the absence of paternal care are not.	Passerine birds (5812 species)	SxS	0.5	0	Selectionist	(Cally et al. 2021)
Macro	Cladogenetic	Divergence	Phylogenetic	Mating system	Female number of partners	Taxa where females mate multiple times have four times more species than sister taxa with single mating by females.	Insects (5 orders)	SxS	1	0	Selectionist	(Arnqvist et al. 2000)

Macro	Cladogenetic	Divergence	Phylogenetic	-	Dimorphism	Lineages with female-biased coloration have doubled net diversification rates.	African reed frogs (12 genera)	SxS	1	0	Selectionist	(Portik et al. 2019)
Macro	Cladogenetic	Divergence	Phylogenetic	Mating system	Bateman metrics	Clades with more species tend to be those where males vary more than females in reproductive success and where males have steeper slopes relating mating success and reproductive success.	Mammals; Birds; Reptiles; Amphibians; Fish; Echinoderms; Insects; Molluscs; Platyhelminthes; (42 families; 70 species)	SxS	1	0	Selectionist	(Janicke et al. 2018)

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874

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880

## Data, scripts, code, and supplementary information availability

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882

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