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Opinion

Conformity and differentiation are two sides of the same coin

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Variation between individuals is a key component of selection and hence evolutionary change. Social interactions are important drivers of variation, potentially making behaviour more similar (i.e., conform) or divergent (i.e., differentiate) between individuals. While documented across a wide range of animals, behaviours and contexts, conformity and differentiation are typically considered separately. Here, we argue that rather than independent concepts, they can be integrated onto a single scale that considers how social interactions drive changes in interindividual variance within groups: conformity reduces variance within groups while differentiation increases it. We discuss the advantages of placing conformity and differentiation at different ends of a single scale, allowing for a deeper understanding of the relationship between social interactions and interindividual variation.

Highlights

Socially driven behavioural conformity is key in social learning, cultural transmission and collective behaviour, whereas socially driven behavioural differentiation occurs in leadership, dominance hierarchies, and division of labour.

While traditionally studied as separate phenomena, we propose that behavioural conformity and differentiation are two sides of the same coin, each being defined by their impact on interindividual (and group) behavioural variation.

Analysing interindividual behavioural variation is already widespread across the behavioural sciences and so considering conformity and differentiation together requires only a shift in perspective, not a shift in methods.

Quantifying conformity and differentiation on the same scale enables stronger tests of alternative hypotheses about the feedbacks occurring between individual behaviour and social processes.

Social interactions and variation within groups

Research on the effects of social interactions on individual behavioural variation has a long history [1]. Of primary interest is how individuals alter their behaviour to be similar to that of others (**conformity**; see Glossary), or in contrast, adopt different behaviour from their social group members (**differentiation**). Additional attention to both conformity and differentiation has come with recent intense interest in two areas of animal behaviour: consistent differences between individuals in behaviour (**personality variation**) and how groups form, are maintained and how they make decisions (**collective behaviour**). Major goals in these fields are to understand the influence of individual behavioural variation on groups, how social groups can shape individual behavioural variation, and then the ecological and evolutionary causes and consequences of these feedback processes [2–4]. Both conformity and differentiation have been documented across a wide range of social species, but the two processes have generally been treated as independent and unrelated phenomena (conformity [1,4] and differentiation [5,6]). However, recent studies are beginning to integrate these processes [7–10] and here we formally propose that conformity and differentiation can be placed on the same scale by treating both as processes that affect interindividual variation within groups (Figure 1). This allows conformity and differentiation to be quantified using the same statistical approach, facilitating comparisons across species, behaviours and contexts, and hence predictions for when we would expect one, the other, or neither.

Conformity and differentiation are widespread and important

A wide range of taxa have evolved social grouping strategies which suggests that the benefits of grouping, such as dilution of predation risk, must outweigh the potential costs, such as increased competition for food [11]. Within groups, individuals can further modify their behaviour as a result of social interactions to gain further benefits or mitigate costs. To appreciate the value of integrating conformity and differentiation, it is worth briefly considering the diverse range of behaviours of intense interest to biologists that can be classed as conformity or differentiation, as well as their wider implications.

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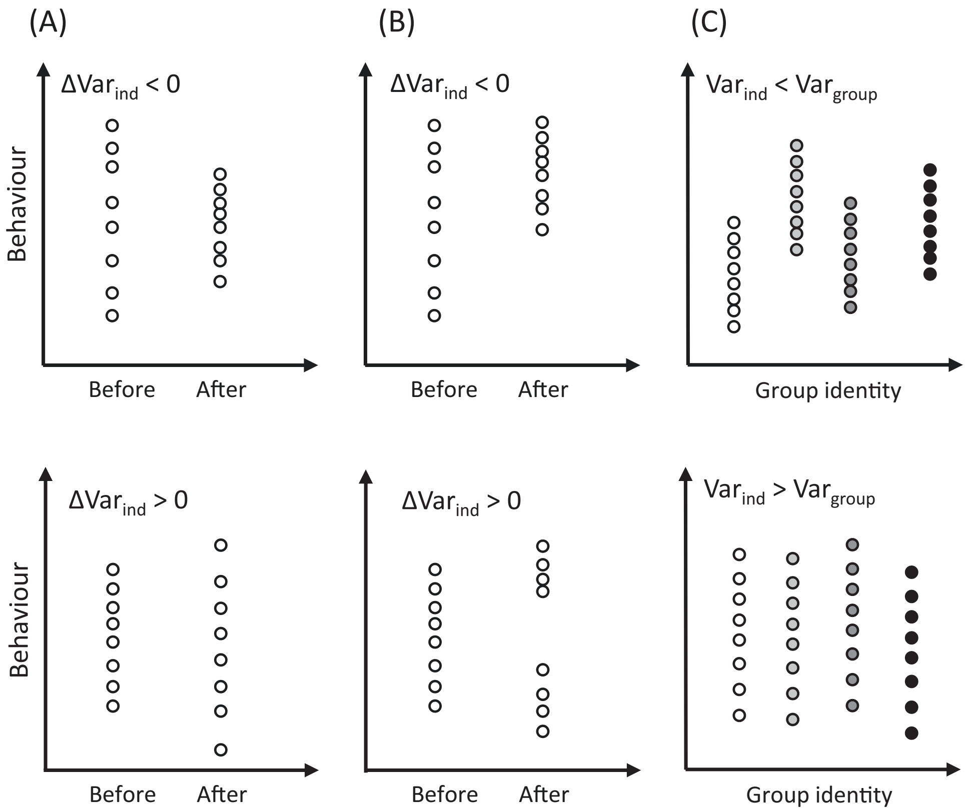

Figure 1. Patterns of socially driven conformity or differentiation in data. Each circle represents an individual's average behaviour. The top row represents patterns of conformity; the bottom row represents patterns of differentiation. In column (A), interindividual behavioural variation either decreases (conform) or increases (diverge) in a group of individuals measured before and after a social experience. In column (B), this variation either conforms on one extreme or diverges to both extremes. In column (C), several different groups are observed, and conformity and divergence is determined by comparing patterns of interindividual and intergroup variation; when individuals in groups conform in their behaviour, intergroup variance is expected to be large compared to interindividual variance whereas the opposite is true when individuals in groups show greater differentiation.

Copying the behaviour of others is a key mechanism driving conformity, and forms the bedrock underlying most collective behaviours. For groups on the move, maintaining group cohesion while determining when, how and where to travel requires behavioural conformity. For example, conforming swimming speeds is necessary to maintain group cohesion during schooling [12]. For a group to reach consensus about when and where to travel requires information transfer within groups, which can be driven by copying changes in movement direction [13,14]. The degree of conformity can vary with the number or proportion of other individuals in the group already expressing that behaviour, which is exemplified most clearly by **quorum** responses in **eusocial** insects [15]. Rapidly copying the behaviour of near neighbours can facilitate effective avoidance of predation risk [16,17]. Collective decision making often allows larger groups to make more accurate decisions, driven by copying the decisions of better informed individuals, or through a reciprocal exchange of information and conformity to a single group decision [18].

Social learning is another intensively researched form of conformity [19–21]. Information from others is remembered (for example, viewing where another individual found food) and used

Glossary

Closed-entry groups: groups where membership of the group is restricted by those already in the group.
Conformity: an increase in the similarity of individuals' behaviour within groups as a result of social interactions.
Collective behaviour: an aspect of social behaviour where interactions between individuals leads to the formation, maintenance and dissolution of groups, group-level properties such as group shape and speed, how information transfers between individuals within a group, and how groups are able to make decisions as a group.
Differentiation: a divergence of individuals' behaviour within groups as a result of social interactions.
Dominance hierarchy: a ranking system of individuals within groups that gives preferential access to limited resources, including mating opportunities, to those higher in the hierarchy.
Eusocial: a form of group living characterised by some individuals specialising in reproduction while others (often sterile) specialise in helping through brood care, foraging, and other nonreproductive activities; the specialisation can occur to the extent that individuals can be distinguished into castes and cannot change roles. Generations of adults within the group are also overlapping.
Free-entry groups: groups where membership of the group is unrestricted.
Obligately social: animals which show high levels of stress when isolated from suitable group mates.
Personality variation: differences between individuals in behaviour that are consistent over time and/or contexts that cannot be explained by traits such as sex and age.
Producers and scroungers: a distinction between strategies of individuals investing to achieve a reward (e.g. producers would spend time searching for food) and the alternative where the resource from producers is exploited by others that gain a reward without the investment (e.g. scroungers would steal food).
Quorum: a mechanism of decision-making within groups where once the number or proportion of individuals expressing a preference or behaviour reaches a threshold, the rate that this is copied increases rapidly, resulting in

later to copy this behaviour. As a consequence of conformity from social learning, a wide range of behaviours can be culturally transmitted from diet choice and foraging innovations [22,23] to long distance migration routes [24] and habitat settlement [25]. While conformity can often have positive effects on individuals, it also has the potential to result in suboptimal behaviour [26] with implications for how well animals can adapt to environmental change [27,28]. If individuals use the presence or actions of conspecifics as indicators of habitat quality, this can facilitate settlement in areas with suitable but underexploited habitats [25] or could result in ecological traps [29] if habitat quality has degraded.

While typically associated with behavioural differentiation, in rarer cases conformity can occur where antagonistic interactions between individuals within a group drives the similarity in individuals' behaviour. For example, the conformity in movement direction that characterises huge marching bands of locusts and crickets emerges from cannibalism between individuals [30]. In some eusocial wasps and bees, conformity within worker castes not to breed is enforced by dominant queens suppressing worker reproduction through aggression [31], chemical signals [32], and eating eggs laid by workers [33].

Antagonistic interactions are more common as a driver of differentiation within groups, particularly as a result of competition for scarce resources such as food and sites suitable for reproduction [34]. A widespread form of differentiation in social groups are **dominance hierarchies** established via aggressive interactions, which are costly by taking time, energy and the possible risk of injury [35]. The emergence of **producers and scroungers** is another key example of differentiation that emerges from resource competition [36]. Even without competition, differentiation into leaders and followers can emerge spontaneously from stochastic differences in individuals' state of hunger or magnify pre-existing differences [3,5,37].

Differentiation of social roles can also be driven by cooperation within groups, where individuals taking different roles can improve efficiency. Differentiation frequently occurs during cooperative breeding, where a dominant breeding pair are helped by nonbreeding subordinate individuals who assist in rearing young and defence [38,39], improving the reproductive success of the breeding pair [40]. Division of labour is particularly pronounced and common in colonies of social insects [41,42], and has been proposed to be a major benefit to living in groups [43,44]. Differentiation into reproductive queens and unreproductive workers is well documented [45,46], but within a caste of seemingly similar workers, there can be specialisation where individuals perform particular tasks more often than others, for example with workers specialising in feeding larvae, nest maintenance or foraging [47]. While differentiation can be determined by individual-level factors such as age, it can be further regulated by social interactions [31,48,49].

This brief overview demonstrates that conformity and differentiation are a common thread running through seemingly diverse behaviours, and are found across diverse taxa varying in the cognitive ability of individuals and the complexity of their social groups. The mechanisms driving conformity may act more quickly than those driving differentiation. This would suggest that differentiation is more likely in **closed-entry groups** with stable membership as there is a prolonged period of interaction with the same individuals, in contrast to **free-entry groups** where group membership changes frequently. In animals that form groups, conformity is more widespread than differentiation as conformity in at least some behaviours is necessary to form and maintain cohesive groups, whereas differentiation is not a requirement. While differentiation may not be necessary for group formation, it may play an important role in improving group function, for example, in division of labour [42,44]. Investigating and fully understanding the

positive feedback and a cascade in the adoption of the behaviour.
Social learning: learning that occurs through observing, or interacting with, others rather than learning only through personal experience.

patterns and processes that determine how interindividual variation within groups changes with social interactions, however, requires more formal testing across species and populations. This formal testing requires conformity and differentiation to be quantified using a single approach.

Why should conformity and differentiation be defined on the same axis?

By defining conformity as a reduction in interindividual variation and differentiation as the opposing process resulting in greater interindividual variation, both can be considered simultaneously. However, the majority of previous studies have only allowed a binary classification of conformity or not or differentiation or not. This one-sided view can prevent researchers from identifying and hence investigating alternative hypotheses. Consider individuals in a group, such as a bee colony, deciding where to forage. As there can be social interactions that allow individuals to share information about rich foraging patches [50,51], researchers may be interested in whether the foragers show conformity by exploiting fewer patches than expected from random. This effectively is a one-tailed test, considering deviation from random in only one direction. However, it is also plausible that individuals distribute themselves more evenly between patches, differentiating their behaviour to minimise competition; such a pattern would be hidden if only conformity is considered. Similarly, if one is instead interested in whether some individuals disproportionately lead group movements [52,53], researchers could examine the distribution of leadership events between individuals to conclude whether some individuals adopt leadership roles. However, this one-tailed approach could not detect that the distribution of decisions may be more evenly distributed (i.e., egalitarian) than random. By explicitly comparing patterns of interindividual variation, researchers can test alternative hypotheses (i.e., conformity versus differentiation) rather than just attempting to reject a single hypothesis (e.g., conformity or not).

An approach that considers conformity and differentiation as ends of the same scale by considering the change in interindividual variation within groups is similar to the index of dispersion in ecology. These dispersion indices quantify whether individuals within a species are aggregated (clumped), randomly, or uniformly spatially distributed by quantifying the variance in a species' distribution over space [54]. By broadening the definition of conformity and differentiation to be on the same scale, this relaxes constraints of former definitions that require direct observations of behavioural interactions between individuals [55]. The advantage of this breadth is it allows a single definition to be applied across diverse taxonomic groups and a wide range of behaviours and contexts, allowing for comparisons, including in meta-analyses, across populations, species, behaviours, and contexts. This can then facilitate investigation into the evolutionary origins of social interactions affecting interindividual variation, and how this is affected by social and ecological conditions. A common currency for conformity and differentiation allows an objective quantification of social influence on individual variation, which avoids differences in the definitions of conformity and differentiation influencing the conclusions drawn.

A key component of both conformity and differentiation, however, is that the change in variability must be a result of social interactions (i.e., social influence) within the group [56]. Other processes, such as individuals forming groups with phenotypically similar individuals (i.e., assortment [57]) or a shared inheritance of traits within groups of related individuals [58], can also result in within-group variability that is different from a random sample of individuals from the population. However, this would not be considered socially driven conformity as individuals' traits do not change as a result of social interactions. Studying naturally occurring groups without observing the social interactions that result in conformity or differentiation, or without measuring changes in variation across time, can make it difficult to disentangle whether apparent conformity or differentiation is not instead caused by other processes [8].

Approaches to detecting conformity and differentiation

The simplest approach to detecting conformity or differentiation through changes in interindividual variation (and sometimes intergroup variation) due to social interactions is to observe the behaviour of individuals in a nonsocial context and then compare this to the behavioural variation that is expressed when those individuals are in a social setting or after they have had a social experience (Figure 1A,B). However, for **obligately social** species, individuals may not show representative behaviour when tested alone, causing behavioural measurements to be unreliable (and/or unethical if stress is caused). Even in this situation, it may be possible to quantify behaviour of individuals within groups, and hence interindividual variability, soon after group formation and before social interactions have taken place (Figure 1A,B).

A less direct approach, but one that can be used to infer conformity and differentiation through observation of unmanipulated groups, is to compare variation within and among multiple groups sampled at approximately the same time, or to compare changes in variation within groups over time (Figure 1C). This approach has the potential confounding effects of variation within groups

Box 1. Estimating conformity and differentiation using mixed models

Linear mixed models provide a powerful tool to appropriately partition and then estimate variance at different levels, such as the group or individual. These methods can thus be used to directly test whether conformity or differentiation occurs as a result of social experience: increases in among-individual variance would indicate differentiation whereas decreases in among-individual variance (and potentially also increases in among-group variance) indicate conformity. For example, Munson *et al*. [9] used such models to test whether social experience resulted in behavioural conformity or differentiation in three-spined sticklebacks (*Gasterosteus aculeatus*). They first measured each individual's tendency to shoal near a flask of conspecifics in a standardized assay as a measure of shoaling tendency. Then fish were split into two treatments: those that were group-housed and those that were kept in isolation. After 1 month, all fish were remeasured in the shoaling assay. The goal was to test whether such social experience enhanced individual differences (i.e., increase in among-individual behavioural variation) due to social niche specialisation [3,5] or suppressed individual differences (i.e., decrease in among-individual variation) due to conformity [4]. To estimate the among-individual variance components, Munson *et al*. used bivariate mixed models with shoaling tendency before and after the treatment as their response variables in a Bayesian framework (e.g., mod 1 below). By including random effects for both groups and individuals, they could simultaneously estimate the variance due to these effects before and after the treatment. By using the posterior estimates of the before and after treatment variance estimates, they could then estimate the difference in variance (e.g., After Var_{IND} – Before Var_{IND} = ΔVar_{IND}) as a result of the treatment, allowing them to test whether social experience increased or decreased behavioural variation at these different levels. If Munson *et al*. had taken a one-sided approach to test only whether among-individual behavioural variation increased as predicted by the social niche specialisation hypothesis, they would have missed the fact that social experience in this system had the exact opposite effect; social experience increased among-group variation, not among-individual variation, suggesting that individuals are conforming in their behaviour resulting in group-level differences (Figure I).

Example code: Bayesian methods in R (e.g., MCMCglmm [65], brms [66]) are particularly powerful as they often allow for the most flexibility in specifying the model's random structure. Several papers on how to use such models with example code are available for the interested reader [62,67,68]. For example, using MCMCglmm in R (which is what was used in Munson *et al*. [9]), the model would be specified as:

```
mod1 < - cbind(PreBehaviour, PostBehaviour) ~ fixed effects of interest,

random = ~ us(trait):group + us(trait):individual,

rcov = ~idh(trait):units
```

Estimating the change in variance components as a result of the treatment could be done by estimating the posterior mean (or mode or median, as appropriate) difference between the posterior estimates of the behavioural variance before and after the treatment using code such as:

```
mean(mod1$VCV[,"traitPostBehaviour:traitPostBehaviour.group"] - mod1$VCV[,"traitPreBehaviour:traitPreBehaviour.group"])
```

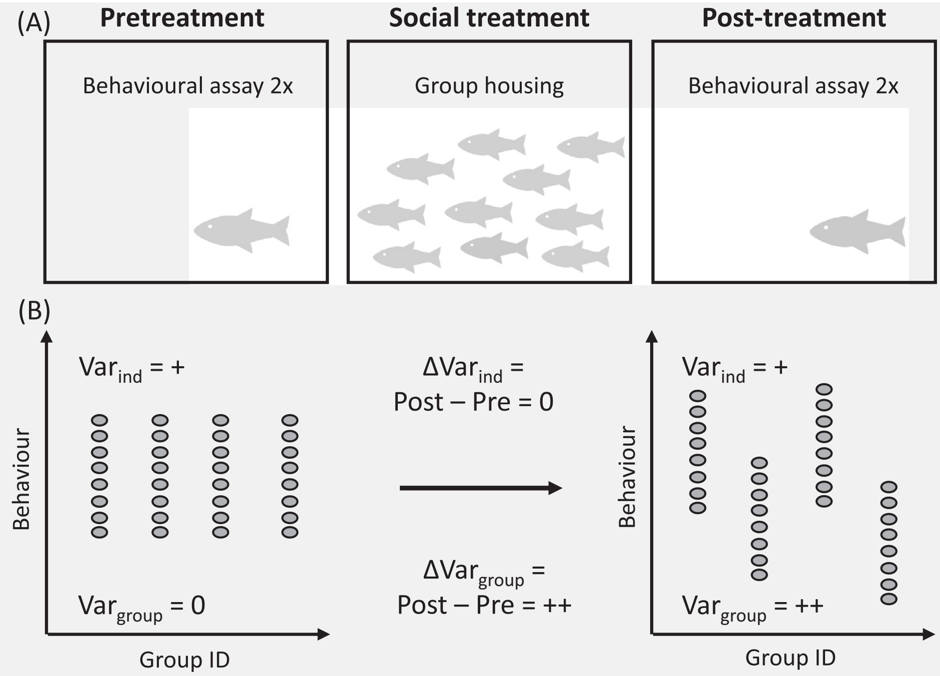

Figure I. Experimental schematic and stylized results of how to measure changes in individual behaviour as a result of social experience. (A) Individual behaviour is repeatedly measured before and after a social experience. Then using mixed modelling techniques, (B) behavioural variation can be partitioned into its among-individual and among-group components; as in Munson *et al*., an increase in among-group variance suggests individuals within groups conformed in their behaviour to generate group divergence in behaviour.

being due to nonrandom assortment or behaviour appearing to conform due to individuals responding to the same ecological conditions if these vary over space and/or time, rather than responding to one another within a group. The latter can, however, be addressed by including fixed effects in the statistical tests to control for possible confounding variables.

Once the data are collected, two approaches are available to statistically determine whether there is conformity or differentiation within groups. Linear mixed or hierarchical models can test for differences in among-individual (and among-group) behavioural variance components (Box 1; [8,9]). A direct comparison of the among-individual variance components before and after a social experience provides the test of whether individuals conformed or diverged in their behaviour. Comparing changes in among-group variance can also be fruitful if multiple groups are part of the experimental design (Box 1). It is important to note that different standardization techniques of the behavioural data and variance components can be used to enhance interpretation. In particular, whereas comparing variance components computed from raw behavioural data can tell us whether behavioural change occurred at all, mean-standardisation of variance components can provide insight into the overall magnitude of behavioural change [59]. We also emphasise that it is good standard practice to always report all variance components in the resulting manuscripts to enable better comparisons across studies and inclusion in meta-analyses [59]. There are several well-developed papers detailing how to run such models and extract the relevant variance components [60–62]. Thus, considering conformity and differentiation as being on the same scale

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Box 2. Randomisation methods to detect conformity and differentiation

Szopa-Comley *et al*. [10] used randomisation tests to test whether pike cichlids (*Crenicichla frenata*) that occurred together within natural river pools demonstrated conformity or differentiation in their predatory behaviour when presented with guppies (*Poecilia reticulata*) in a clear cylinder (Figure I). The R code used for their analysis is included as supplementary data with their paper [10]. In the first randomisation test, the authors calculated the coefficient of variation in the time spent near the prey stimulus among the individual predators observed in each pool; lower coefficients of variation (CVs) indicate individuals from the same pool are exhibiting more similar behaviour. The mean of the coefficient of variation across all pools was then calculated as the observed test statistic. The randomisation procedure randomly allocated the data from individual predators between pools, effectively swapping the individuals between pools *in silica*, and the mean coefficient of variation was calculated for each of the 10 000 iterations of this process. Although the observed variation (mean coefficient of variation) tended to be less than that expected from randomly allocating data from the predators between pools, suggestive of conformity, the observed variation was within the 95% confidence intervals of the expected distribution from the randomisation, thus there was no strong evidence of conformity or differentiation between individual Crenicichla within the same pool.

The second approach used by Szopa-Comley *et al*. is based on the rationale that reduced variability within groups (indicating conformity) results in a positive relationship in behaviour between two randomly selected individuals from the same group, while greater variability within groups (indicating differentiation) results in a negative relationship between them [7]. An individual was randomly selected from each pool as individual 1 and another from the same pool as individual 2. The slope of the relationship between the time spent by individual 1 near the prey stimulus and time spent by individual 2 near the prey stimulus was then determined using a general linear model; the random selection of individuals and extraction of the slope was repeated 10 000 times. Again, the results were suggestive of conformity, with the distribution of the slopes from the randomisation tending to be positive, although the 95% confidence intervals overlapped with zero. The advantage of this approach is that if the slope of the relationship between the two individuals is determined using linear modelling, other variables that could affect this slope can be included as covariates in the model; in the case of Szopa-Comley *et al*., this included canopy cover and the time of day that the observations were made.

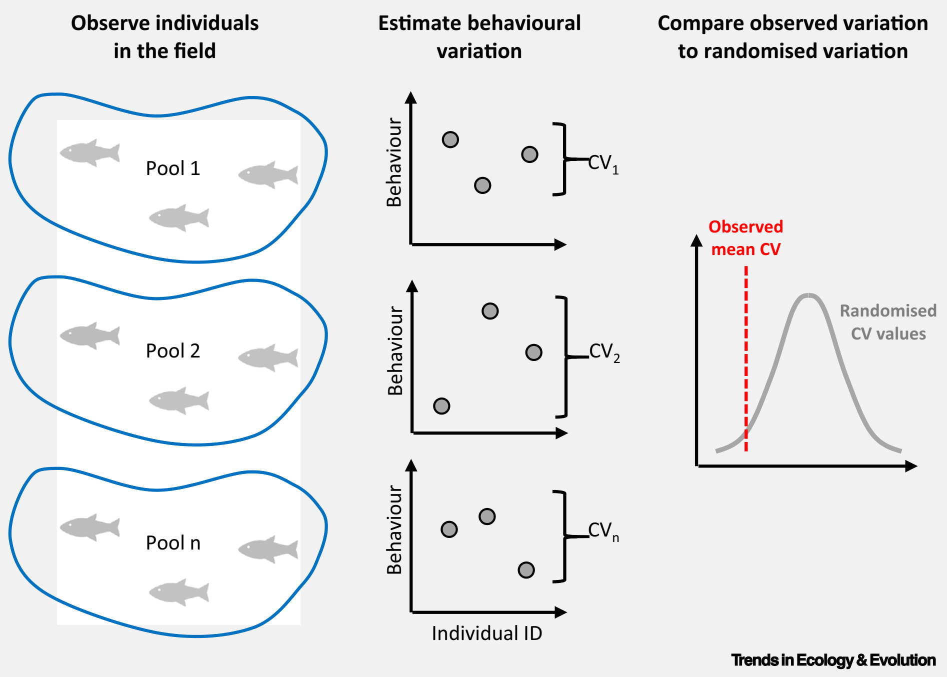

Figure I. Experimental design and stylised results of how to compare observed behavioural variation to randomised behavioural measures. For example, Szopa-Comley *et al*. [10] observed individual predators within pools and estimated the coefficient of variation in individual behaviour within a pool. Using randomisation, they created a null distribution that effectively swapped predator identities across pools and re-estimated these hypothetical CV values. If the observed mean CV across all pools is lower than the randomised distribution this suggests individuals are more similar than expected; if the observed CV is higher, this suggests differentiation.

requires no novel statistical methodologies but rather just an explicit comparison of the magnitude of among-individual, and sometimes, among-group, variance components.

Randomisation methods can also be used to quantify conformity and differentiation on the same scale, which is especially useful when the assumptions of mixed models are not met (Box 2; [7,10]). One approach is to test whether the observed variability between individuals within groups is different to that expected from random. Membership of each data point to a group is randomly assigned to determine the expected amount of within-group variation without the possibility of social interactions. The observed level of within-group variation can then be compared to this randomised distribution; if the observed variation within groups is lower than the 95% confidence interval of the randomised distribution, this suggests conformity, while if within-group variation is greater, it implies differentiation. An alternative is to randomly select individuals from each group and determine whether the behaviour of individuals from the same group is positively (indicating conformity) or negatively (indicating differentiation) correlated. After iterating this random selection of individuals, it can be determined to what extent the relationship deviates from the null, random expectation (Box 2), usually a slope or correlation coefficient of 0.

Concluding remarks

Defining conformity and differentiation in terms of the same quantity (interindividual variation within groups), and thus placing conformity and differentiation on the same scale, allows for a much broader understanding of how social interactions affect interindividual variation in groups. This will allow us to better investigate the ecological, evolutionary and mechanistic drivers of individual and group behaviour, which rely on comparing trends across species, populations and habitats (see Outstanding questions). Not only is our approach able to advance basic research in studying animal sociality, it is especially important in the Anthropocene as it is becoming increasingly recognised that social behaviour is important in responses to anthropogenic environmental change such as avoidance of ecological traps [27,63,64].

Outstanding questions

What are the ecological drivers and evolutionary processes that give rise to conformity, differentiation or neither in animal groups? In other words, when do we expect to observe conformity or differentiation?

Do these factors result in conformity or differentiation being more common in some behaviours, taxonomic groups and environments than others?

Are there common proximate mechanisms that drive conformity, and others that commonly underlie differentiation? Or are their multiple mechanisms that result in each?

Does conformity and/or differentiation result in populations being more or less vulnerable to anthropogenic change?

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Declaration of interests

No interests are declared.

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