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Multilevel Innovativeness and Cross-Species Comparisons

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Behavioral innovativeness—the propensity of an individual organism or higher group to innovate—is frequently invoked as a measurable trait allowing for cross-species comparisons. Individuals or species are often regarded as more innovative or less innovative than others, implying that we can rank order the degree of innovativeness along a single dimension. This paper defends a novel multidimensional understanding of behavioral innovativeness in which innovativeness can be modulated with respect to the generation and capitalization of opportunities, as well as the effectiveness and depth of the innovative behaviors. Besides innovation being multidimensional, it is also multilevel. Here we show how innovativeness at one level (such as the species level) does not automatically translate to innovativeness at another (such as the organism level) and discuss why this matters for cross-species comparisons.

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1. Introduction

Behavioral innovativeness is generally understood as the propensity to innovate (Sol 2015, Griffin 2016). This propensity has long been recognized as crucial for organisms' survival and adaptability in unpredictable environments (Kummer and Goodall 1985; Reader and Laland 2003). While it is widely accepted that species display different degrees of innovativeness (Reader et al. 2016), it is not clear how innovativeness should be described and measured. Characterizing the innovativeness propensity—and linking it to biological entities (individual organisms, groups, species)—is the focus of this article. In particular, we investigate the question of whether innovativeness is a quantitative trait measurable along a single dimension and capable of being used to make comparisons across species. Thus, we are ultimately asking what is being compared—and at which level—in assessing innovativeness across taxa.

The problem of characterizing variation in complex traits among taxa in a way conducive to meaningful comparisons has recently garnered attention from several scholars, particularly in the context of animal consciousness studies (Birch, Schnell, and Clayton 2020) and behavioral innovation (Arbilly and Laland 2017; Brown 2022). This paper aims to further advance discussions regarding the characterization of behavioral innovativeness and to articulate the complications that emerge from a multilevel perspective.

Innovativeness has been linked with many psychological, morphological, and ecological traits, such as advanced cognitive capacities (Shettleworth 2010; Griffin and Guez 2014), increased brain size (Reader and Laland 2002; Lefebvre et al. 2004), colonization success (Sol et al. 2008), and cultural complexity (notably in humans, McBrearty and Brooks 2000; Muthukrishna and Henrich 2016). These traits are used in ranking the innovativeness of taxa: Crows and cockatoos are among the *most* innovative bird taxa (Auersperg 2015). Migratory species among Palearctic passerines are *less* innovative than resident ones, the former being unable to modify or invent new foraging behaviors in the harsh winter months (Sol et al. 2005b). Among primates, apes, capuchins, and macaques are innovation top scorers (Reader et al. 2011). We humans, we like to think, are the most innovative of all. Around 70-50 thousand years ago, we shared the planet with as many as five other hominin species (Galway-Witham et al. 2019), but only one ended up composing sonatas, writing novels, and colonizing ecosystems over the globe. This dominance may to a large degree be due to our innovativeness.

Note how the statements above rely on comparative terms to express varying degrees of innovativeness. This reflects the fact that innovativeness is often treated as having a single dimension, which is usually assumed to be captured by innovation counts (Arbilly and Laland 2017; Overington et al. 2009, 2011; Lefebvre et al. 1997; Lefebvre 2011). This paper challenges the possibility of considering behavioral innovativeness as a unidimensional trait and defends a multidimensional account in the same spirit as that of Brown (2022). Further, it proposes a novel characterization of the dimensions of innovativeness, distinguishing between quantitative and qualitative dimensions. In identifying these dimensions, we refrain from linking innovativeness to specific proximate mechanisms. The conceptual framework in this paper leaves the underlying mechanisms open to discovery rather than specifying them a priori, with the expectation that a more plausible characterization of how innovativeness is modulated can also aid empirical research.

In addition to challenging unidimensional accounts of innovativeness, we also show that the dimensionality problem is complicated by the fact that behavioral innovation can occur—and is frequently defined—at different levels of organization.[1] For example, innovation has been defined at the organism level (Ramsey, Bastian, and van Schaik 2007) and population level (Reader and Laland 2003). When we classify a species as innovative, are we making a claim about how innovative the organisms are in the species? Or are we considering the innovativeness of the groups or populations themselves? This is important since innovativeness at one level does not automatically translate to innovativeness at another level.

One reason for this lack of automatic translation is the complex nature of innovations. As we will see, innovations require both the production and retention of novelty. Thus, if a single organism innovates, it must produce and retain the novelty. But a group of organisms can divide the production-retention labor. Because of this, a group-level innovation can in principle occur without any single organism innovating.

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[1] We recognize that the notion of *levels of organization*, especially in conjunction with the concept of *levels of selection*, needs to be used cautiously (Eronen and Ramsey, 2025). The focus in this paper is restricted to organisms, (higher level) collections of organisms (such as groups or populations), and species.

Interrogating whether the locus of innovativeness is chiefly at the individual or higher level is important for quantifying innovativeness and linking it to animal culture, intelligence, and other features central to species' evolution and ecology. For instance, a species that has highly innovative individuals may respond quite differently to habitat fragmentation than one that is equally innovative, but whose locus of innovativeness lies primarily at a higher level.

We illustrate the implications of a multidimensional, multilevel account of innovativeness in the context of nonhuman behavioral innovation studies as well as hominin evolution and archaeology. We then discuss the consequences of this account for the concept of innovativeness and the potential utility of compressing innovativeness into a single parameter for research purposes. Finally, we consider whether innovativeness should be understood as a singular *trait*.

2. Organism-level innovativeness

To understand behavioral innovativeness at different levels of organization, we will begin with innovativeness at the organismic level before considering higher-level innovativeness.

2.1 Innovation

At the foundation of innovativeness is novelty since an innovation is a novel behavior. Not all novelty involves innovation, however. Ramsey, Bastian, and van Schaik (2007) argue that novel behaviors (novel for an individual organism, not necessarily the group or higher level) can also arise through *social learning* or *environmental induction*[2]. In the case of social learning, an organism can acquire a novel behavior from another member of its population without itself innovating. And just as novelty can be "borrowed" from conspecifics, it can also be "borrowed" from the environment: If a cow indiscriminately eats whatever grass is before it, and if a new species of grass establishes itself in the field, the cow would not be innovating by eating it. The

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[2] Given the focus of this paper and space constraints, we do not revisit the discussion surrounding Ramsey et al.'s (2007) proposal. For a detailed treatment, we refer the reader to the original target article, along with the subsequent commentaries and response.

novel behavior (ingesting the new grass species) would not qualify as a foraging innovation as it is fully induced by the environment.

Two points of caution are worth emphasizing. First, the grain of description, that is, the degree of detail at which we are analyzing or describing a behavior, can affect whether it counts as an innovation. The finer the grain, the more novel the behavior becomes. At the finest grain, every behavioral token is novel. Coarsely describing a cow as simply eating grass will not prompt questions of innovation, but describing it eating, say, a species of wiregrass for the first time will be a contender for innovation. While we acknowledge the relativity of innovativeness to the granularity of the description, this will not be the focus of our analysis. Instead, we will examine how behavioral innovativeness (once a description is fixed) can be assessed across different dimensions and levels.

Second, innovation, social learning, and environmental induction are not discrete sources of novelty, but instead represent points on a continuum. For example, an organism can innovate in such a way that the innovation is spurred by environmental novelty, such as unusually hot weather leading a raven to find a new way to keep cool. In fact, this might often be the case, as we'll see below in discussing the propensity to innovate in response to opportunities. The degree to which the environment plays a role in novelty generation is linked to the degree to which the novelty arises *passively* and *predictably* from environmental triggers, unmediated by organismic action. Agents engaging in novel foraging behavior mediated by active resource searching or tool-assisted techniques present a different case than the cow example. With the ravens, if their behavior is an active response to the heat, where other responses are possible (thus, they are environmentally underdetermined), then it may be considered an innovation.

The same continuum occurs with social influences. Organisms can act as recipients of novelty from others, thus contributing to the behavior's preservation without themselves innovating, or they can use the social environment as an inspiration for innovation, for instance by tweaking or recombining socially learned behaviors (see also Carr et al. 2016). We refer to these latter, transformative behaviors as innovations. As Legare and Nielsen (2015) pointed out in the context of cultural learning, all cultural traditions require at base two fundamental engines: innovation and imitation. With behavioral repertoires, we want to analogously capture the same broad distinction, namely between the production of innovation and its replication/transmission, while acknowledging possible (and well-studied) interplays along the continuum. Importantly,

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this is a conceptual distinction and says nothing about the cognitive underpinnings of preservative and transformative behaviors. It is well understood that preservative behaviors may involve a complex set of perceptual, motor, and cognitive skills, and as such are far from trivial. Further, it should be noted that social learning and copying are themselves graded and multidimensional notions (see Whiten 2022): There is variation in what is replicated by copying and to what degree it is copied. The instances of social learning that are distinguished from innovation are examples of copying that faithfully reproduce the copied behaviors. To what degree faithful copying is rampant in humans—and whether it can be found among animals—is, of course, a vexed issue (see Morin 2016, Allen and Andrews 2024), carrying implications about the extent and degree of innovativeness.

Recognizing the graded character of innovation, Ramsey, Bastian, and van Schaik (2007) offer a novelty triangle with innovation at one corner, social learning at another, and environmental induction at the third (fig. 1). Innovation *sensu stricto* occurs only in the vicinity of the innovation corner of the triangle, with weak to no innovation occurring as we gradually approach the high-fidelity social learning and environmental induction corners.

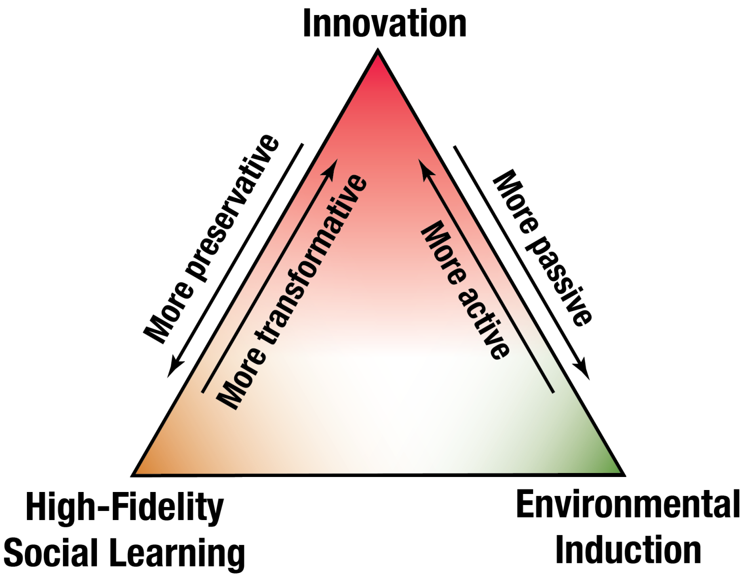

Figure 1. Novel behaviors can result from social learning, environmental induction, innovation, or some combination of these factors. The more innovative the behavior, the less passive and predictable its generation. (Based on Fig. 1 from Ramsey, Bastian, and van Schaik 2007)

Innovative behaviors are thus ones not merely preserved by social learning or determined by environmental induction. But there is a further restriction, one common among characterizations of innovation: the behavior must be learned (Reader and Laland 2003; Bandini and Harrison 2020). By 'learned' it is meant that the innovation must be onboarded, that is, it needs to modify the behavioral repertoire of the organism, either by modifying an existing behavior or by adding a new one. The reason for this restriction in Ramsey, Bastian, and van Schaik (2007) is to differentiate innovation from behaviors that, while novel, have no lasting effect on future behavior. Innovations, in other words, are novelties that are *durable*, that bring about a lasting change in the innovator's behavioral repertoire because the individual learns from them, therefore affecting the probability of their reoccurrence. Behaviors that lack durability but fulfill the other criteria for innovations are best seen as *improvisations*.[3] To go from mere improvisation to innovation, the novelty must endure. Durability also comes in degrees and can be measured by, for example, observing how an organism behaves following the generation of novelty. When it produces a novel response to a given opportunity, if it is innovation and not mere improvisation, then the probability of reproducing the behavior given a similar opportunity should increase.

The extent to which a novel behavior is an innovation thus depends on several factors: To what degree was the novelty a passive result of environmental induction or a behavior preserved through social learning? To what degree is it durable? The complex nature of innovation is carried over into innovativeness, though moving to innovativeness adds additional complexities, which we will articulate below.

2.2 The dimensions of innovativeness

If innovations are behaviors resulting from the process of innovation—a "process that generates in an individual a novel learned behavior that is not simply a consequence of social learning or

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[3] The distinction between "improvised" and "innovative" behaviors may track the "ephemeral" vs. "lasting" innovation distinction, which is used by some (Rachael Brown, personal communication). This difference arguably revolves around where, along the durability continuum, one chooses to label a behavior an innovation.

environmental induction" (Ramsey, Bastian, and van Schaik 2007, p. 395)—then it would seem that innovativeness is a simple propensity to innovate, quantified merely by the frequency with which innovations are generated over time. Innovativeness, however, is not a simple propensity to innovate. There are two reasons for this. One is that not all innovations are created equal. An organism that produces very minor or ineffective innovations is less innovative than one that produces substantial, targeted innovations, even if their frequency of innovation is the same. Second, the *context* of innovation is relevant, as innovations do not arise in a vacuum. When an experimenter wants to know whether an animal is innovative, they don't merely observe it and record innovations per unit of time. Instead, they provide *opportunities* to innovate. Innovativeness is thus often measured vis-à-vis opportunities.[4]

To motivate this idea, consider angling. Angling is the process of using a fishhook, line, and (usually) a rod to catch fish. If we want to determine how good someone is at angling, we shouldn't simply count the number of fish caught per unit of time. Instead, we need to consider their performance when they have the opportunity to angle (other things being equal). Mediocre anglers may fish every weekend, bringing in more fish per year than excellent anglers who fish only during a few weeks each summer. Analogously, the opportunity to innovate is important for assessing the innovativeness of an organism.

Experimental studies of innovativeness often center on problems: the experimenter creates a problem and sees if and how the problem is solved. In fact, the very concept of innovation is often framed as a solution to a problem: the world poses a problem and the organism comes up with a novel solution to it (Kummer and Goodall 1985). But we resist such restrictive definitions of innovation. Innovations can occur in the absence of preexisting problems and can arise from a variety of triggering mechanisms (Reader et al. 2016; van Schaik et al. 2016; Bandini and Harrison 2020). Necessity is not the sole mother of innovations, although debates persist over the importance of the various mechanisms (Greenbaum et al. 2019).

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[4] The use of metrological language here does not mean we are endorsing an operational definition of innovativeness. Instead, it is that describing how innovativeness can be measured sheds light on how the propensity is conceptualized.

We thus prefer the more open language of *opportunities* instead of problems. While the notion of opportunities is not trivial, we don't think it requires overly complex metaphysical commitments. Opportunities can be adaptive challenges but also occasions to differentially exploit available environmental options and affordances (Tebbich et al. 2016). Innovations can be playful behavior (Bateson 2015), not driven by an immediate necessity or problem to be solved, such as Japanese macaques rolling snowballs to play with (Eaton 1976, Laland 2017). Aesthetic expressions in hominin species—such as the use of body ornaments, pigments, and new materials (worked ivory, bone, or antler)—can be innovations that explore, among other things, novel sensorimotor and perceptual possibilities (McBrearty and Brooks 2000). Social behaviors and forms of communication can also undergo innovation, like sperm whales innovating their vocalizations to signal belonging to a whale clan (Hersch et al. 2022). Opportunities can vary in terms of degrees of accessibility, their profitability, or their recognizability based on their resemblance to previously exploited ones.

Further, explicitly considering opportunities (as in Tebbich et al. 2016) is useful for tempering expectations of innovations where there is no need, no occasion, or differing opportunities for them to emerge (as in the angling example). This helps prevent premature judgments of one organism (or species) as more innovative than another without considering whether and how their immediate opportunity niche differs.

A measure of innovativeness is thus a measure of both the organism's propensity to create innovation opportunities and what it does in the face of opportunities. Does the organism exhibit behaviors in a stereotyped way from a fixed repertoire? Does it innovate? If it innovates, how novel are the responses it produces and how frequently does it produce them? Let's use these questions to articulate the way that innovativeness can be modulated. As the array of innovative behaviors can be indefinitely large, there can be multiple dimensions along which innovativeness can express itself. However, we hold that there are four key, conceptually non-redundant dimensions of innovativeness, two related to the *quantity* of innovations, and two related to their *quality*. Both the quantitative and qualitative dimensions are graded, meaning that there are varying degrees at which an organism's innovation propensity can be expressed and measured along each dimension. Thus, the qualitative dimensions (without being misled by the term) can be assessed quantitatively.

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Quantitative dimensions of innovativeness:

Opportunity capitalization. This dimension of innovativeness concerns the disposition to innovate given an opportunity to do so. This can be thought of as the conditional probability of producing an innovation given an opportunity, measured by the opportunity-relative rate of innovation. Sometimes opportunities are clearly defined—such as a preexisting problem posed by an experimenter in a controlled setting—but other times they can be recognized or indirectly inferred from various domains (such as food and resources availability and the environmental, material, and social context). To measure frequency, then, no global partitioning of opportunities is necessary. What is important is to identify opportunities and then see how the organisms respond to them.

Opportunity generation. Innovations are responses to opportunities. Sometimes these opportunities are simply part of the furniture of the environment and are not created or amplified by organismic activities. But organisms can also have dispositions to create opportunities. A more neophilic organism may tend to create more opportunities to innovate, as curious individuals who are eager to interact with novel stimuli will tend to expose themselves to increased possibilities of crafting novel behaviors. Thus, even if two individuals capitalize on opportunities at the same frequency, if one has a more pronounced disposition to create opportunities, overall innovativeness can be increased.

Qualitative dimensions of innovativeness:

Effectiveness. Novelty can be mere noise, sloppiness, or a mistake. In a problem-solving or goal-oriented situation, behaving sloppily is not innovating (though mistakes and accidents can lead to innovation, provided that the accident modifies the behavioral repertoire). Thus, the degree of *effectiveness* of a behavior for what it is supposed to do is an important factor in innovativeness. If the novelty is generated in response to a well-defined problem, then effectiveness is the degree to which the behavior helps to solve the problem. For example, dolphins from Shark Bay (Western Australia) have been observed using sponges over their beaks (rostra) when fishing on the seafloor (Patterson and Mann 2011). This has been interpreted as an effective behavioral innovation that allows dolphins to protect their beaks from sharp rocks and chunks of coral while digging up prey.

In the case of the snowballs, snow offers an open opportunity for play. Rolling the snowballs is imaginative, exploratory, and creative, not a solution to a preexisting problem. If the behavior is more of an open-ended response to an opportunity, such as playful or aesthetic-artistic behavior, effectiveness requires a more circumstantial evaluation. In some circumstances, as in human playful behavior, a problem or an unnecessary challenge is created for the purposes of play (such as building a tower of cards or hopping between lines on a sidewalk). Although play is often defined as a behavior that is not completely functional in the context in which it occurs (Burghardt 2005), it can certainly be an effective way to train hunting or fighting skills, establish or strengthen social relationships, and so on, providing long-term benefits (Bateson 2015)[5]. In this context, the effectiveness of playful behaviors can be assessed on a developmental scale, when the relative payoffs become visible. In other contexts, no immediate or correlated function seems to be linked to playful behavior. In such cases, innovative playful behavior could still be assessed as more or less effective in eliciting the reward pathway to satisfy the actor (Vanderschuren et al. 2016).

Depth. Not all novelty is equivalent in its profundity. Novelty ranges on a continuum, from being shallow (subtle variations on existing behaviors) to being multi-step, to quasi-saltational (not mere incremental novelty building on existing behaviors, but new behaviors). This dimension shares similarities with Arbilly and Lala's quantitative measure of innovation *magnitude* (2017). Here depth can be quantified in terms of the number of steps required to produce the novelty from existing behaviors or the amount of information and skill required to produce the behavior. Performing an existing behavior in a slightly new context—like foraging at a new food patch—is a shallow innovation. Producing a new multi-step foraging method is arguably a more profound and complex innovation. An example of this could be the opening of household waste bins by sulphur-crested cockatoos, a social parrot increasingly

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[5] It is plausible that playful play can be a facilitator for innovativeness by encouraging plastic responses to environmental and social circumstances that can modify the behavioral repertoire of the individual or its group. See Bateson (2015) and Bateson and Martin (2013) for a discussion of the role of playful behavior in promoting novelty and creativity in evolution.

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common in cities (Klump et al. 2021)[6]. This foraging innovation requires multiple steps with various options: pry, open, hold, walk, and flip. Another example is provided by tool hafting among hominins (that is, the process of attaching a sharp object, such as a stone blade or bone point, to a handle or shaft to create a more effective and versatile tool). This involves several steps: the selection of the components, the preparation of the tool head and handle, the use of adhesives, and the reshaping and finishing of the composite tool. With behaviors not easily falling on a single qualitative scale, it might be possible to distinguish *combinatorial* depth (the combination or recombination of multiple steps building on existing behaviors) and *saltational* depth (the introduction of new themes in the behavioral repertoire, which may sometimes require only a few steps).

Having sketched these four dimensions (see fig. 2), let's discuss how they relate to each other. Each of these dimensions can vary quasi-independently of the others. In principle an organism can frequently capitalize on opportunities to innovate, but tend to do so only superficially, producing shallow innovations. It could create many opportunities to innovate but rarely take advantage of them. An organism may also engage in effective but shallow innovation (sometimes for good reasons: effectively solving a problem does not necessarily require a deep and complex innovative solution).

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[6] Klump et al. (2021) also analyze the spread of this innovation from three suburbs to 44 across Sydney, leading to the emergence of geographically distinct subcultures. This may therefore represent a case in which social learning—alongside geographic barriers, founder effects, and drift—not only facilitated the establishment of the innovation but also gave rise to novel variants of it.

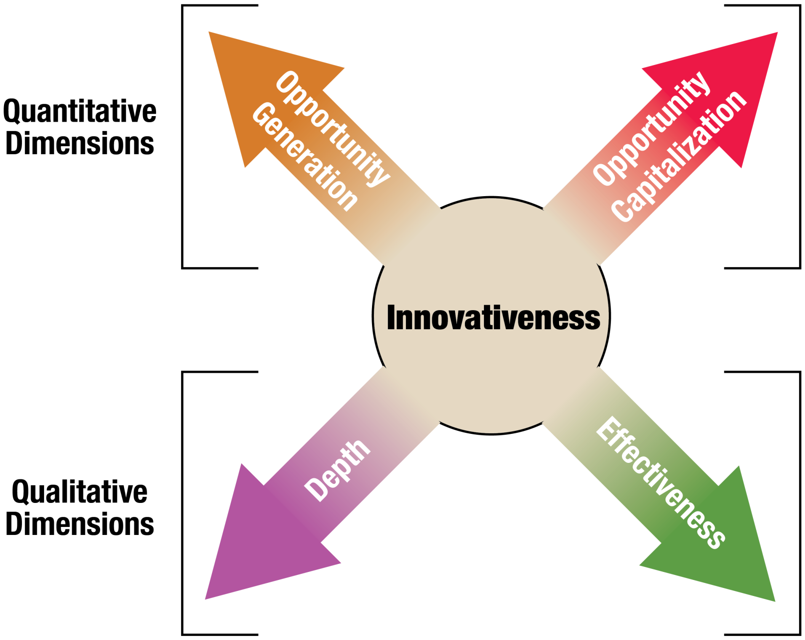

Figure 2. Four key dimensions of the innovativeness propensity. For organism-level innovativeness, innovativeness depends on the magnitude of these dimensions of the organism's propensity. For group-level (or higher) innovativeness, not all the dimensions need to be manifested by one organism, but there can instead be a division of innovative labor.

While these dimensions are conceptually distinct—they do not describe the same axis of innovative variation in different terms—empirical results on interindividual differences in innovativeness suggest how these dimensions may be modulated separately in real-world settings. In some taxa in which juveniles are more explorative than adults, there is no evidence that the juveniles are better problem-solvers (these include raptors, great tits, Indian mynas, satin bowerbirds, hyenas, and meerkats, see Griffin and Guez 2014). This indicates that in some taxa, juveniles may well be good opportunity capitalizers but less (or un-) effective innovators, likely due to a lack of relevant motor competencies (among other things). Humans, particularly in the context of innovation of epistemic resources like scientific knowledge, provide compelling examples of how the dimensions of opportunity generation and capitalization can diverge. Within research communities, individuals often vary in their propensity to produce opportunities for innovation and their capacity to capitalize on those that arise: the history of scientific and technological discoveries illustrates this dynamic vividly. Alexander Fleming—an opportunity generator—famously discovered that mold on a Petri dish of *Staphylococcus* bacteria inhibited bacterial growth, leading to penicillin, but he did not fully capitalize on its potential. In contrast, good opportunity capitalizers (Howard Florey and Ernst Boris Chain) effectively transformed penicillin into a widely used therapeutic strategy. An empirical correlation between two or more dimensions—such as organisms that are systematically good opportunity generators tending to be deep innovators—does not pose a problem for our account but rather suggests interesting research avenues.

One of the implications of our multidimensional account is that comparing the innovativeness of different individuals without considering or making explicit the various dimensions of innovativeness is not particularly informative nor helpful in shedding light on the drivers of the innovativeness propensity. One individual could in principle innovate infrequently but produce quasi-saltational innovations, while another innovates frequently but superficially. Which is more innovative? Unless we have a way of finding a common currency that spans frequency and depth, we cannot rank one individual as more innovative than another. Things get even more complex if we move from the organism level to assessing the differential innovativeness of *species*. We will consider in detail the complexity of multilevel innovativeness in sections 3 and 4. But before we get there, let's consider Brown's (2022) multidimensional account of innovativeness and analyze how our proposal differs from hers.

2.3 Brown's framework

Brown (2022) offers a five-dimensional account of innovativeness in response to Arbilly and Laland's discussion of the magnitude of innovation, defined as "a deviation of the population's mean behavior" (2017, 2). Brown approaches the problem of innovativeness by examining an individual case of innovation produced by Betty, a New Caledonian Crow. Betty's most notable innovation was that she took a garden wire and bent it into a hook, then used the hook to retrieve food that would not have been otherwise accessible. Drawing on discussions in Weir et al. (2002) and Rutz et al. (2016), Brown argues that there were three variables relevant to the assessment that Betty's behavior is a high-magnitude innovation:

> (i) Her apparent lack of experience with the wire (and other pliant material),
> (ii) the apparently novel behavioral action (bending) she performed, and
> (iii) the novelty of the problem she solved. (1181)

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She also points out two additional important features of the Betty case:

(iv) the spontaneity of the behavior (i.e., that it arose without extensive trial and error), and
(v) that it was robustly repeated (i.e., suggesting that it was not an accidental, or undirected, action). (1181)

From these features of Betty's innovation, Brown extrapolates a five-dimensional space for quantifying degrees of innovativeness:

(i) Experience with material being manipulated
(ii) Novelty of the motor action being performed
(iii) Novelty of the problem being solved
(iv) Spontaneity of the behaviour
(v) Robustness of the innovation (1182)

Brown's framework rightfully emphasizes the need to break innovativeness into its components. However, her account is tailored for cases of foraging innovations—the other cases considered are Japanese macaques washing sweet potatoes and British tits opening milk bottles—which constrains broader applicability. As we discussed above, restricting innovations to solutions to problems is overly limiting, and there's much more to behavioral innovation than resource-acquisition innovations. Our opportunity dimensions can be applied to foraging behaviors (e.g., capitalizing on a difficult-to-retrieve food source for a novel resource acquisition strategy) and thus can be used to ensure meaningful comparisons, without the need to conceptualize innovativeness idiosyncratically for each domain.

Another limitation of Brown's framework lies in the fact that the dimensions she specifies do not appear to be conceptually independent. We take conceptual independence to be a desideratum of an account of innovativeness since, if they are not independent, there is a risk of overrepresenting the same components of innovation, leading to inflated assessments. While we agree that dimensional independence needs to be tested empirically (Brown, personal communication), we believe that if behaviors are seen to strongly covary along specific dimensions (or vary independently) for reasons that are more conceptual than empirical, this should guide the compression (or subdivision) of the relevant dimensions.

The first three dimensions of Brown's account concern the degree of novelty: the novelty of the material, the motor action, and the problem. All of these can be related to our single dimension of *depth*. Brown holds that the novelty of the problem being solved, while

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acknowledging a degree of ambiguity in this parameter, is a separate dimension from the organism's experience with the material used, as well as the action being performed. We feel that the novelty of the problem is not specifiable independently of the organism's abilities and experiences. If Betty's "tool bending" (the motor action) is already part of the natural behavioral repertoire of her species (as it seems to be, Rutz et al. 2016), her application of this behavior to a different material (the wire) and a different context (retrieving food from a tube—itself interpretable as a variation on other extractive foraging puzzles), makes the problem itself less novel. Similarly, if we discovered that Betty commonly interacts with wire (that is, she has experience with the material), the problem itself would be classified as less novel. The way the original and later assessments of Betty's case are represented in Brown's multidimensional space (2022, Fig. 2) seems to imply a lack of conceptual independence. Rutz and colleagues' (2016) discovery about the motor action being a species-typical behavior, expressed in bending sticks in the wild, is shown as not only affecting the motor action dimension, but also changing our assessments along other dimensions: the novelty of the problem, the experience with the material, and spontaneity of the behavior. Nevertheless, Brown represents these as distinct dimensions[7].

Given the intertwined nature of the novelty of the problem and the prior experiences and normal behaviors of the subject, we hold that it is more fruitful to propose a single dimension ranging from minor innovations ("variations on a theme") to "saltational" innovations (introducing new themes). Under our account, Rutz et al.'s (2016) results suggest that Betty's case is closer to the first, thus implying a level of innovation less deep than initially interpreted.

Brown's *spontaneity* dimension is related to both our *opportunity capitalization* and *effectiveness.* We hold that it is important to distinguish the disposition to capitalize on an opportunity from the effectiveness of the capitalization. A behavior could be spontaneously performed but not performed well. Or it could be performed well, but with less spontaneity. Thus, we agree that spontaneity is important but feel that there are different components to it: the

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[7] Our dimension of 'depth' can therefore be interpreted by some as a compression of different dimensions. We believe the compression vs. separation issue ultimately comes down to what level of granularity is useful for the specific research questions at hand.

ability to immediately recognize and capitalize on an opportunity is distinct from an effective response to it.

Finally, Brown's *robustness* dimension is related to the very definition of what it is to innovate, that is, the production of novelties that stick. Thus, because we conceive of innovativeness as the disposition to innovate, some threshold degree of robustness must be in place for the disposition to be a disposition to innovate.

3. Innovativeness at higher levels

Let us consider now how innovativeness can be realized at higher levels of organization. A fleet herd of bison must be composed of fleet bison. But a herd of fleet bison does not necessarily make for a fleet herd, since this requires both fleet organisms and herd coordination.[8] Fleetness at the herd level is thus due to properties of organisms (organism-level fleetness) as well as higher-level properties (within-herd coordination). If we say that bison are a fleet species, there is thus some vagueness. Unless specified, it is unclear what level is being described. Now consider a slightly more complex example: group hunting. When bottlenose dolphins hunt together, some individuals (the drivers) herd fishes in a circle toward barrier dolphins. There is thus division of labor and role specialization (Gazda et al. 2005). Successful hunting at the group level doesn't require that every organism be a proficient hunter. In fact, fish capture rates have been observed to differ between the drivers and the barrier dolphins in some groups. But through coordination and cooperative work, the group manages to secure a better result than what could be accomplished individually.

Innovativeness, like fleetness or hunting proficiency, can be ascribed to various levels of organization. If we say that crows or chimpanzees are innovative species, what does this mean and what evidence supports such claims? Much work in animal innovation studies derives its inferences about group (or other higher-level) innovativeness from observational case studies or controlled experiments on individual agents, which are obviously easier to manipulate. The implicit assumption is that innovative individuals build innovative groups and species. But because of the multidimensional character of innovativeness, social species may distribute the

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[8] Pace Williams (1966), who said individual selection for fleet deer implies, "not only that it is a herd of fleet deer, but also that it is a fleet herd" (16).

innovative labor, such that innovations are produced not by a single individual, but as a team. Thus, while a fleet herd requires individual fleetness, an innovative group doesn't necessarily require individual innovativeness. Let's now consider the disposition to innovate and how this can be realized at different levels of organization.

We will begin with a single organism. Its disposition to innovate is its disposition to generate and learn behavioral novelties that are not simply a result of environmental induction or social learning. The individual can vary in the degree to which it generates opportunities to innovate as well as the degree to which it capitalizes on opportunities. The innovations can be more or less effective and can vary in their depth. What should be noted here is that when it is a single organism, that individual must realize *all* parts of the innovative process, including the retention of the innovation in her behavioral repertoire.

When we ask if a population or species is innovative, we may simply be asking about the degree to which the constituent organisms innovate. But we could also be asking about the innovativeness of the higher level itself (independently of the innovativeness of the constituent organisms). As we will see, the interpretation of various dimensions above the organism level raises important implications for the cross-taxa comparability of innovativeness.

Consider a group containing some skilled improvisors. They improvise, but don't recognize the potential of their novel behaviors and don't learn from them. So, the improvisations do not stick in the improvising organisms—they don't modify their behavioral repertoire. Other individuals in the group don't have the same disposition to improvise but are keen observers. They recognize the potential of some of the improvised behaviors and learn from them, thereby modifying their behavioral repertoire. The new behavior could bring some important advantages and could spread through the population. In this scenario there is, strictly speaking, no individual organism that innovated: no individual did the whole job of generating a novel, learned behavior. Nevertheless, the group as a whole did innovate. It did so since it produced a novel behavior that was neither environmentally induced nor socially learned (i.e., not learned from another group). In this case, the group acted as an individual, producing the novelty and committing it to (communal) memory.

In a similar manner, the four innovativeness dimensions we described earlier can to some degree be distributed within groups. Some individuals might be good at generating opportunities for innovation (by encouraging the group to explore or experiment with novel materials) but may not capitalize on the opportunities. Others in the group may do little in the way of generating opportunities but may be skilled at capitalizing on the opportunities. In this case, it is not that no individuals innovate, but that the synergistic effect of the opportunity-generating individuals and the opportunity capitalizers combine to create a group-level innovative performance that exceeds that at the organism level. This need not imply active coordination or division of labor (as in the bison or dolphin hunt example) but may instead emerge from structural features of a social group.

Wild orangutans nicely exemplify apparently paradoxical links between individual and group-level innovativeness. Orangutans are semi-solitary, large-brained arboreal apes and among the best primate problem-solvers. As van Schaik and colleagues have shown (2016), young orangutans in the wild are highly neophobic: they are novelty averse and avoid independent exploration (in contrast to orangutans in captivity). So, they arguably have little propensity for opportunity generation and infrequently capitalize on given opportunities. Nonetheless, most wild populations display large innovation repertoires because orangutan populations do a good job in retaining innovations that arise accidentally and opportunistically. Species with "reluctant" individual innovators (as van Schaik and colleagues defined orangutans) can nonetheless score high in innovativeness at the species level. Another interesting example is provided by collective navigation problems in homing pigeons (*Columba livia*) (Sasaki and Biro 2017). Here innovations in route efficiency—improvements in reducing the distance between release site and home—emerge across generations at the collective level, with group homing solutions outperforming those of solitary agents.

Humans are an extreme example of how complex the interplay between organism-level and higher-level innovativeness can become. Large-scale social configurations and information pooling increase the probability of accidentally producing novelties that can then stick and become group-level innovations. Such innovations can then be incrementally improved and culturally recombined. This means that deeper, more complex innovations that are more effective in solving specific problems or providing other benefits can be built from shallower and less effective individual innovations. Extraordinary individual insight is not required for high-magnitude group-level innovativeness.

This idea resonates with work on the cultural evolution of group-level properties (Smaldino 2014; Muthukrishna and Henrich 2016). In formulating their "cultural brain hypothesis," Muthukrishna and Henrich resist the idea that innovations are best understood as the work of a talented few, emphasizing instead how cultural evolution results in technologies and information that not only could not be recreated by any individual in a lifetime but do not even require that single individuals understand how they work. And in Ramsey's (2013) definition of culture, he includes group-level cultural transmission to be able to include "cultural variants that are only ascribable to groups, and not possessed (in whole) by any one of the individuals in the group" (464).

An important feature of human innovativeness is their unrivaled capacity for collective opportunity generation. This is achieved by structuring the environment in which their offspring develop and learn (Sterelny 2011), thus building scaffolds that inspire and support innovation. Modern research institutions are an extreme example of how humans actively engineer opportunity-rich environments to promote higher rates of innovation. Although this dimension of innovativeness and the related ability to innovate social tools (Sterelny 2016) tend to be overlooked by experimental animal behavior research—since in those cases the opportunities are provided by the researcher—they are fundamental aspects of social species. Therefore, as group-level innovativeness can build on organismic innovativeness, the converse also holds. Scaffolded learning environments can encourage and support organismic innovativeness, with individuals having the possibility to draw upon a larger pool of opportunities to tinker with behaviors and exert their creativity. The various dimensions of innovativeness can behave quasi-independently at the same level, but at higher levels—particularly among social species—these may create important between-level feedback loops.

4. Does it still make sense to speak of "innovativeness"?

The multidimensional, multilevel account of innovativeness offered here implies that unqualified cross-taxa comparisons that treat innovativeness as a simple scalar quantity risk overlooking crucial differences among taxa. Moreover, such comparisons may bias research toward specific hypotheses. For instance, if we implicitly value individual problem-solving abilities (effectiveness) as the sole relevant dimension of innovativeness, we could be tempted to draw conclusions about the adaptability of a species based on this component alone, downplaying other important components, such as the disposition to create novel opportunities.

Given the complexity and multidimensionality of innovativeness, a reaction one could have to our framework is to see our conclusion not as explicating innovativeness, but as expunging it: We should not speak of "innovativeness" but should instead concern ourselves with the constituent dimensions—how opportunities are capitalized or the depth of novelties—not innovativeness simpliciter. While we acknowledge that our account undermines simplistic understandings of innovativeness, we nevertheless hold that there is still a place for the innovativeness concept. Similarly, multidimensional frameworks that have argued against a single-scale approach to the study of other complex phenomena—such as animal consciousness—have not resulted in the elimination of the concept. Instead, they advocate for understanding variation between species in terms of multidimensional profiles rather than degrees on a single scale (Birch et al. 2020). Analogously, our argument can be taken to promote an understanding of innovativeness via multidimensional and multilevel profiles.

Any singular measure of innovativeness is a measure of only one of the innovativeness dimensions or is a result of compressing multiple dimensions into one. While dimensional compression involves a loss of information, such compressions are sometimes useful. To see the usefulness of dimensional compressions, we can examine other fields and how they have dealt with the problem of collapsing many dimensions—once adequately specified—into one. One area in which this is frequently done is sports. We often want to compare how good particular players or teams are without necessarily being concerned with what makes them good. Take player efficiency rating (PER) in basketball as an example. This is a scalar quantity for the "efficiency" of players based on a set of dimensions including the number of field goals made, defensive rebounds, offensive rebounds, assists, blocks, and so on (Hollinger 2007). These dimensions are not simply averaged, but are plugged into a complex equation for obtaining the PER. There are some parallels between player efficiency and innovativeness (though the analogy is only illustrative). For example, our opportunity generation dimension is like creating a basketball shot opportunity, opportunity capitalization parallels taking the shot, the effectiveness is like field goal percentage, and depth is like the payoff of the shot (in this case one, two, or three points).

PER has many uses, such as predicting team performance and recruiting players. While it is more informative to know why a particular player has a high PER (exceptional rebounding, for instance), PER nevertheless has usefulness without knowing these details. We think that the same can be the case for innovativeness. Though it is beyond the scope of this paper, we feel that, depending on the research question, exploring the complex interplay of these dimensions to come up with a way of compressing innovativeness onto a single dimension (along the lines of the PER) could help, for instance, to visualize data via a simpler representation.[9]

Does this imply that innovativeness can be treated as a singular trait? While a complete response to this question is reserved for future research—especially since the fundamental question *what is a trait?* is itself a difficult one (Meneganzin, Ramsey, and DiFrisco 2024)—it is worth offering some preliminary thoughts based on the framework presented here. In the past decade, much research has indeed treated innovativeness as a direct reflection of cognition and as a trait able to undergo selection, prompted by studies framing innovativeness as an adaptive specialization to specific environmental demands or by evidence of links between innovation and fitness (Healy and Rowe 2007; Cauchard et al. 2012—but see Griffin 2016 and Sol 2015 for criticism). And it is easy to see how the different dimensions of innovativeness outlined here can be linked with distinct cognitive, psychological, ecological, and social factors. We previously mentioned neophilia, a personality trait, as a possible catalyzer of novel opportunities to innovate. Similarly, learning can be linked to both qualitative and quantitative dimensions of innovativeness at higher levels.

Previous work has shown patterns of covariation of innovation with a set of social, technical, and ecological abilities among primates (Reader et al. 2011). This suggests that innovativeness likely does not vary independently from these other traits. Thus, innovativeness is not likely to be a direct target of selection, but rather the outcome of selection on a suite of traits that have evolved to cope with environmental complexity and variability. Sol (2015) speculates that even if innovativeness shouldn't be understood as a unitary process or a genuine trait, traits underlying innovativeness may be expected to evolve together in highly innovative animals that show "creative lifestyles"—possibly the result of selection for combinations of innovativeness-related traits via complex social and ecological opportunist-generalist lifestyles. If

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[9] One possible use of a PER-like measure for behavioural innovativeness would be to quickly track variation in innovativeness within an individual or group over time. It could also allow researchers to examine whether the same overall level of innovativeness can be multiply realized—manifested through different patterns of performance across underlying dimensions.

innovativeness is indeed best seen as an evolutionary byproduct—a "syndrome" (Sol 2015) or "emergent property" (Griffin 2016)—measuring it without reifying it as a trait can shed light on its underlying constraining and enabling traits. In this regard, our multidimensional, multilevel account opens the possibility of testing intriguing hypotheses about how innovativeness is manifested across taxa—about its ecological roles and evolutionary history. We will now consider how our account of innovativeness can be measured and used in comparative studies.

5. Measuring and comparing innovativeness

The complex ways that innovations can occur at higher levels have important implications for how we should understand and compare the innovativeness of species. A species, as we have seen, can be innovative (along some relevant dimension) without the individuals that compose it innovating, so unqualified references to a species as innovative will not tell us where the locus of innovativeness lies. There are also metrological implications. If we measure the innovativeness of a species in terms of the production of population-level novelty, this will have only an indirect link to innovativeness as an organism-level disposition. Similarly, measuring the innovativeness of individual organisms may be a poor proxy for measuring the innovativeness of species.

Griffin (2016) identifies two traditions in the study of animal innovation. The first adopts field innovation counts using anecdotes—of, for instance, novel feeding behavior observations—as proxies of species-level innovativeness. The second largely relies on organism-level proxy measures of innovativeness focusing on experimental problem-solving performance. However, both approaches come with problems in light of the multidimensional, multilevel nature of innovativeness, as we will now see.

First, species-level innovation counts, in addition to the problem of how innovations are defined and identified for the comparability of results (Bandini and Harrison 2020), risk ignoring the qualitative dimensions of innovativeness. If these dimensions are ignored, the complex bin-opening behavior among sulfur-crested cockatoos and a bird species merely foraging at a new patch would be given equal weight. Such innovation counts would thus fail to differentiate between shallow and deep innovations and would not be sensitive to the effectiveness of innovations. Moreover, mere tallies of innovations don't tell us much about the innovativeness propensity itself. For instance, is a higher rate of innovation due to a higher propensity to capitalize on available opportunities to innovate? Or is it due to individuals actively shaping the opportunity landscape? Also, how should we disentangle the role of social learning (in social animals) in passing on and maintaining innovations? Populations with the same innovation rate can differ in how frequently we observe innovations, but this could be merely due to how well innovations are retained through social learning.

Second, addressing innovativeness solely via experimental problem-solving performance misses higher-level, emergent features of the innovation propensity in social species, as well as important scaffolds for individual innovativeness. We've already seen that evidence of tool-bending behavior among New Caledonian crows impacts the assessment of Betty's innovativeness in terms of depth. Attending to the increasing evidence of New Caledonian crows developing their tool skills in highly scaffolded environments (Holzhaider et al. 2010) raises the possibility that NC crows have a high degree of population-level innovativeness based on their opportunity generation, with individual innovativeness potentially being more inspired by the social environment than by extraordinary insight. This highlights how difficult it can be to discriminate experimentally between the group- and organism-level innovativeness and helps account for why this is such an important gap in nonhuman animal innovation research (Griffin 2016). Further, individual innovativeness measured against foraging puzzles is often reduced to ungraded assessments of effectiveness in a context in which the opportunity is predefined and offered by the researcher.

An illustration of the implications of the multidimensional, multilevel character of innovativeness is offered by hominin evolution. Neanderthals, a sister lineage of *Homo sapiens*, have a longstanding repute as lacking our species' innovative proficiency. The claim is not that they weren't innovative, since it would be implausible to think otherwise with a species that successfully adapted to and persisted in vast and varied niches in Eurasia. Rather, the claim is that their capacity for innovation was lower than that of our species (e.g., Mellars 1998; Wynn and Coolidge 2008; Tattersall 2012). Neanderthals, some have claimed, "made the same kinds of tools for 200,000 years without ever tinkering with the basic components" (Wynn and Coolidge 2008, p. 45). The Middle Paleolithic has long evoked a time of comparatively little technological innovation and creativity, especially in the design of implements (Kuhn and Stiner 1998). While more recent evidence increasing showcases instances of Neanderthal behavioral and cultural sophistication (Villa and Roebroeks 2014; Nowell 2023) and suggests a higher degree of cultural variability during the Middle Pleistocene (Kuhn 2020), the problem of comparative innovativeness remains.

Some attempts to explain the disparity in the archaeological signal have looked for a biological basis, turning to differences between *Homo sapiens* and Neanderthals in the genetic architecture underlying the capacity for 'creativity' and innovativeness (e.g., Zwir et al. 2022) or neuroanatomical differences (e.g., Kochiyama et al. 2018). Other discussions emphasize the lower frequency of items related to personal ornamentation (Wynn et al. 2016). These approaches assume that the record reflects species-specific constraints on an individual-level innovation propensity. However, we think that the dimensions of innovativeness articulated above highlight the challenges in inferring degrees of individual innovativeness from the archaeological record.

Given our framework, how should comparative innovativeness claims between Neanderthal and *H. sapiens* be interpreted?

First, recall that innovations require both the production and the retention of novelty. In the archaeological record, the number of innovations that survive the preservation lottery does not allow us to infer a general rate of innovation, but only (and very indirectly) the propensity of some non-perishable innovations becoming established in a region. More specifically, the archaeological visibility of an innovation correlates with a higher percentage of adoption by the larger population: the more widespread the innovation, the higher its chances of being established in the record. A difference in this number across species does not provide a simple reflection of differences in the innovativeness of the members of the species. Archaeologists have no direct access to individual innovativeness. Instead, it could be that archaeological variations across species are, at least in part (and when dramatic erasure by climatic or preservation factors can be excluded), due to one species being better at retaining or sharing innovations. In the division of the production-retention labor, even under idealized conditions of identical or comparable production rates, if one species or population plays the retention game better, the archaeological visibility of its innovations would be higher.[10]

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[10] It should be noted here that what appears to be a higher uptake of innovations does not immediately speak to a higher effectiveness of innovations. In hominin species, the adoption or

Second, consider the opportunity landscape—the physical or social environment providing affordances for innovative behaviors. In principle, if one species has a richer set of innovation opportunities it can capitalize on, it could generate more innovations per unit time without being more innovative (or being more innovative in all respects). This should be accounted for when comparing species that have long occupied different geographic (and social, as we'll see below) niches—a case exemplified by *H. sapiens* (a species that evolved largely within the African continent between ca. 300kya and 70kya) and the Neanderthals (which evolved in Europe and Asia). These niches and their stability may have come with different innovation pressures[11]. Further, innovation opportunities can also be generated by the species (by structuring innovation-supporting environments), so that variation in the archaeological record could in part be due to variation in the opportunity generation propensity.

Paleoanthropological and contextual information about the opportunity landscape of Neanderthals (their demographic, social, and ecological niche) can be leveraged to attempt to disentangle different innovativeness dimensions in comparative assessments. Neanderthal demography and their sociocultural niche differ from ancestral *H. sapiens*. The former's widespread but disconnected metapopulation, low population densities (Prufer et al. 2014; see also the overview in Currie and Meneganzin 2022), and "inwardly focused" society (Spikins et al. 2017) may imply a differently shaped opportunity horizon, such that some kinds of innovations are less likely to appear and be retained, like those linked to exchange practices involving specific artifacts (like portable figurines or ornaments) to ensure connectivity over large cooperative networks. That is, archaeologically visible species-level innovativeness can in principle vary due to population structure and the specific demands of a sociocultural niche, providing different information pools for innovators to draw from, different innovation demands,

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rejection of new practices is also complexly mediated by the dynamics of power and by the reputation of the innovators (Henrich and Gil-White 2001).

[11] Studies of the drivers of technological evolution in archaeology have suggested correlations between toolkit richness and environmental risks (Buchanan et al. 2016). This again suggests that looking at the variation between the toolkits of foraging groups living in different environmental contexts, which require and support distinct innovative repertoires and rates, may give the misleading impression of different innovation capacities between groups.

and differential retention probabilities, without necessarily positing dramatic differences among individual-level innovative propensities. While in our characterization of organismic innovativeness, high-fidelity social learning was distinguished from genuine innovative behavior, in social species social learning plays crucial roles both in shaping the opportunity landscape and in the dynamics of the retention and diffusion of novelty.

When it comes to the Middle Paleolithic repertoires and technocomplexes (and the debated issue of their dynamism, cf. Kuhn and Stiner 1998; Stiner 2013; Kuhn 2020), it could be tempting to conclude that where technological continuity is still to be seen, this automatically translates into low scores across all innovativeness dimensions. However, technological continuity is anything but anomalous in hominin evolution (Kuhn and Stiner 1998). The real anomaly is the diversity of the Upper Paleolithic record of *H. sapiens*. So, the purported lower degrees of change in the technological record of regional Neanderthals may, on the contrary, signal a good degree (or a local optimum) of effectiveness of their utilitarian tools for their uses within their specific social and economic landscapes—a signature of a successful, stable, well-tuned system (Stiner 2013) (before subsequent disruptions caused by the arrival of a new species). In other words, we should expect technological change to reflect functional factors as well as the size and structure of cooperative social units.

The paleoanthropological case provides an extreme example of the extent to which mere innovation counts, especially counts filtered through the archaeological record, can lose important layers of complexity that are otherwise captured through a multidimensional, multilevel account. Even when the accuracy of the signal is not debated, inferences from artifacts to innovation rates to potential biologically mediated constraints on innovativeness are shown to be much more difficult than it might otherwise seem. Nevertheless, our multidimensional, multilevel account does more than draw into question such inferences. It also helps to show what kinds of inferences can be drawn and what kinds of data we would need in order to make interspecific innovativeness comparisons possible.

6. Concluding remarks

Characterizing innovativeness, delineating its key components, and exploring the interplay between organisms and higher levels is a fundamental step toward enabling cross-species comparisons in innovativeness. Our multidimensional, multilevel account of innovativeness serves both as a cautionary reminder of the complexity of this propensity as well as a framework to aid in quantifying and comparing innovativeness.

We hope that our framework will be useful in studies of innovativeness, prompting discussions about how innovativeness can and should be operationalized. If a multidimensional, multilevel innovativeness framework is on the right theoretical track, we welcome future discussions on the exciting project of how best to implement it. We also hope our framework will help to foster connections between studies from a diversity of taxa. For instance, much work on animal innovation is disconnected from theoretical work on the role of social environments in hominin evolution (Sterelny 2016). While the perceived differences between the ways humans and animals innovate provide some justification for this separation, we hope that the framework proposed here can foster fruitful discussions about how human and nonhuman animals innovate. By fracturing innovativeness into multiple dimensions and analyzing its emergence at higher levels, we encourage a more detailed, instructive comparison of innovativeness across the human-nonhuman animal divide.

One interesting consequence of our account is its potential relevance to ongoing discussions in comparative culture research, such as those centered on the Zone of Latent Solutions (ZLS, Tennie 2020; see Whiten 2022 for criticism)[12]. According to the ZLS, ape cultures consist largely of latent solutions that are not the result of copying via social learning mechanisms, but rather are socially mediated re-innovations. If this is right, it implies relatively high scores on apes' individual opportunity capitalization dimension (mediated by socially directed attention and environmental induction) and relatively low scores on the species-level depth dimension. Once more, the role of social learning and social environments needs to be carefully unpacked due to their diverse implications for both the retention and prompting of innovation.

Another important consequence of the proposed account relates to conservation. Tracking the locus of innovativeness and understanding the relationship between the individual and higher levels is crucially linked with the potential resilience of a species in the face of environmental disturbances, habitat degradation, or population fragmentation. For instance, species whose viability relies on individual repositories of knowledge (such as elephant

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[12] We are grateful to Simon Fitzpatrick for raising this point.

matriarchs) would require different conservation policies than others whose reproductive and foraging success seems to be linked to clan structure (such as sperm whales) (Brakes et al. 2021). Conserving the capacity for innovation may thus rely on conserving specific individuals or it may be more important to maintain or promote certain group-level features and dynamics.

When we can't observe the innovation process, as is the case for the archaeological record, unqualified cross-taxa comparisons in innovativeness may hinder the appreciation of local cultural and technological trajectories, in which some dimensions of innovativeness were more likely to be expressed than others, as Neanderthal evolution plausibly exemplifies. Flat judgments of our species simply being "more innovative" than our evolutionary cousins won't take us far in understanding the specific mechanisms that shaped the evolution of innovativeness in the two lineages.

The study of innovativeness is clearly a challenging and complex undertaking. We hope that the framework offered here will help to further the study of this important phenomenon, that it will prompt research along more productive and informative directions, while also opening new avenues for comparative research.

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