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Opinion

Keystone individuals – linking predator traits to community ecology

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Individual behavioral plasticity enables animals to adjust to different scenarios. Yet, personality traits limit this flexibility, leading to consistent interindividual differences in behavior. These individual behavioral traits have the potential to govern community interactions, although testing this is difficult in complex natural systems. For large predators who often exert strong effects on ecosystem functioning, this behavioral diversity may be especially important and lead to individualized ecosystem roles. We present a framework for quantifying individual behavioral plasticity and personality traits of large wild predators, revealing the extent to which certain natural behaviors are governed by these latent traits. The outcomes will reveal how the innate characteristics of wildlife can scale up to affect community interactions.

Highlights

Animal personality traits and individual behavioral plasticity can lead to individual differences in ecosystem roles and biotic interactions.

The ecosystem-level consequences of individual variation are likely particularly important for large, apex predators who can strongly influence community interactions, yet are understudied.

Human activities may favor certain traits within populations and the displacement or loss of certain phenotypes may alter the structure of food webs and reduce ecosystem resilience.

We provide a framework for identifying these traits and individual plasticity in wild predators. The outcomes should allow for an exploration of how behavioral diversity can translate to individualized ecosystem roles.

Animal behavioral diversity and community ecology

Animal personality (see Glossary) research has grown enormously over the previous two decades, with efforts focused on elucidating the mechanisms by which consistent individual behavioral differences arise. Specific **personality traits** (e.g., boldness and aggressiveness) affect life history characteristics, the distribution of individuals over landscapes, social dynamics, and transmission of information or infectious disease within groups [1–4]. The ecosystem-level consequences of variation in these traits may be especially pronounced for Earth's megabiota, which often disproportionately impact landscapes and ecosystems [5]. Among these species, large predators can regulate prey populations and smaller competitors, limit the spread of diseases, induce **risk effects**, and provide nutrients and energy from carrion [6]. Predators that alter prey density or induce fear, can affect herbivore distributions (i.e., **landscapes of fear**), leading to cascading effects for plants and numerous smaller organisms [7,8]. The strength of these interactions are highly context dependent within and across ecosystems [9,10]. We argue that within-species behavioral diversity, in the form of personality traits, should be considered among these contexts.

While research on wild predators has investigated behavioral **repeatability** (personality in its broadest sense), specific traits should be considered latent characteristics (e.g., derived from gene–environment interactions) [11]. Combinations and degrees of traits will then have behavioral consequences and drive ecosystem role diversity. Here we present a framework for how researchers can quantify independent personality traits and individual behavioral **plasticity** and use derived estimates to examine individualization to ecological roles of wild predators. We then present examples of hypothesized pathways by which individual traits can govern community interactions and how identification of these traits may help us better understand and predict individual responses to environmental change.

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A framework for identifying the individual behavioral traits of predators

Although personality has been explored in wild and captive predators [12,13], no research has so far used the full array of validity tests required to infer specific and independent personality traits [14]. This oversight is coupled with a trend for research to label any behavior exhibiting repeatability as personality generally, and to speculate on which traits these behaviors are linked to. For example, in brown bears (*Ursus actos*), daily displacement has been used as an indicator for **exploration**, while diurnality and selection for roads and open habitats have been used as indicators for boldness [15]. Similarly, selection of roads and human infrastructure has been used as a proxy for boldness in dispersing grey wolves (*Canis lupis*) [16]. This approach can be misleading as repeatability is calculated over time domains that make it challenging for researchers to know what ecological scenarios underpin these behaviors.

For a behavior to be considered a reliable indicator for a latent personality trait, it must exhibit both among-individual variation (i.e., repeatability) and within-individual consistency (i.e., low individual plasticity and high **predictability**). Crucially, the behavior must also exhibit: (i) **ecological validity**, (ii) **convergent validity** with at least one other distinct and repeatable behavior, and (iii) **discriminant validity** with the remaining behaviors under investigation [17]. In this context, a personality trait has downstream effects on behavior (i.e., behaviors are symptoms of traits). Importantly, a behavior may be repeatable without being a valid proxy for a latent personality trait, and therefore **validity testing** is required to identify distinct personality traits [17]. In this approach, ecologically valid experiments are used to control the ecological scenarios underpinning behavioral responses; thus, covariation (or lack of) between individual behaviors (recorded from different tests) represents an unambiguous assessment of the presence/absence of specific traits [17].

Research aiming to link information about personality traits to natural patterns of behavior typically use a two-step approach in which individual variation in experimental responses is linked to variation in natural behavioral patterns [18]. The errors associated with these behaviors is typically lost when datasets are combined for analysis, potentially yielding misleading results [19]. Later, we present a framework that combines ecological (i.e., variance partitioning) [20] and psychological (i.e., validity testing) [17] approaches to determine whether specific behaviors reflect situational (or plastic) responses to external stimuli or latent personality traits. Our framework retains the error related to experimentally elicited and natural behaviors, allowing exploration of the individual covariances of these behaviors. The outputs can be used to develop a mechanistic understanding of how innate attributes combine to govern individualization to animals' ecosystem roles.

Defining personality traits

In behavioral ecology, five main personality traits have been presented: boldness, exploration, **activity**, **sociability**, and **aggression** (Table 1) [1]; however, operationally defining certain traits and designing ecologically valid tests for these traits has been challenging [17]. Boldness has been defined as the propensity to take risks, excluding novel scenarios [1], or, conversely, interpreted as the propensity to take risks, especially in novel situations [21]; yet, responses to novel foods have also been considered to represent a **neophilia** trait [22]. Flight initiation distance (FID) methods have also been used as a proxy for boldness [23,24], but given that many species now encounter humans on a consistent basis, approaches by humans may instead be an ecologically valid measure of a distinct **human-tolerance** trait [25]. Similarly, open-field tests are used to measure exploration; however, the context of whether exposure to the novel environment is forced (Table 1) determines whether the test is more likely to measure **risk taking** versus exploration [17]. We solve these issues in our framework by presenting

Glossary

Activity: the extent of an animal's activity generally, that is, in non-risky, non-novel scenarios specifically.

Aggression: the propensity to be agonistic towards conspecifics.

Animal personality: among-individual behavioral differences that are consistent through time and contexts, measured as the variance of a random intercept in a mixed-effects model.

Bio-geochemical hotspot: discrete areas of heightened nutrient availability on the landscape. Several abiotic and biotic processes affect soil nutrient content, including carcass deposition from predation.

Convergent validity: testing whether two distinct behaviors hypothesized to measure the same trait actually measure the same trait (i.e., two behaviors covary).

Discriminant validity: testing whether two distinct behaviors hypothesized to measure different traits actually measure different traits (i.e., two behaviors do not covary).

Ecological network: visual representations of the food web or symbiotic species interactions found within biotic communities. Typically, species or individuals are nodes, while interactions are the links in these networks.

Ecological validity: ecological situation (e.g., competition with a conspecific for food) must be relevant to the behaviors (e.g., latency to attack) measured and the trait (e.g., aggression) being investigated.

Exploration: tendency to explore new environments, alternatively labeled avoidance if a population/group tend towards avoiding new environments.

Human tolerance: tendency to endure the proximity and sounds of humans, alternatively labeled human intolerance.

Landscape of fear: animal space use can be shaped by variation in where and when individuals perceive themselves likely to encounter predators – dependent on predator hunting mode/predictability, habitat heterogeneity, and predator/prey active periods.

Neophilia: tendency to inspect/interact with novel items/foods, alternatively labeled neophobia.

Personality trait: latent characteristic inferred from among-individual variation and within-individual consistency in a behavior. An individual's position on one

Table 1. Tests and measures for quantifying distinct personality traits in wild terrestrial predators. Also included is a summary of ethical and methodological considerations, including how certain tests can measure or conflate with other tests unless designed robustly

Experimental/field tests	Behavioral measures	Important considerations
Risk taking [1]		
Trapability: tendency to investigate/enter traps [57]. Emergence: an animal is captured and released into an enclosure [58]. Predator/threat simulation: the animal is startled using a mock predator/dominant heterospecific visual stimuli or audio playbacks (e.g., sirens, animal roars) [14]. Moving objects (e.g., pop-up flag), flashing lights, or scents are also options.	Trapability: number of times captured per temporal period (e.g., month). Emergence: latency to emergence and time spent moving. Predator/threat simulation: flight time/distance and latency to return or to resume previous behaviors. Threatening scents: attraction/avoidance of the area, time spent interacting with the scented substrate, and whether the individual marks with their own scent.	Ethical: trapping exclusively for these purposes may be considered unethical, especially if also released into an enclosure. Efficacy: many species/individuals may be trap shy. Emergence test: to ensure this 'measures risk taking and not exploration', the animal's decision to enter the arena must be forced (i.e., it has no other option, see Open-field test later). Minimize novelty in the enclosure. Encountering threatening stimuli: this test must be free, that is, animals should encounter these while ranging freely and not after trapping or in an enclosure. Scent-marking responses: scent stations must be cleaned and refreshed regularly to avoid biases. Habituation: simulation tests must be moved and rotated through test and control stimuli frequently. Conflation: these tests may also measure aggression.
Neophilia [22]		
Novel object: the animal is presented with a novel food [22] or object [14]. Novel sound: audio playbacks of unfamiliar novel potential prey items (e.g., a call from a South American primate to an African carnivore). Novel scents: novel scents are applied to a natural substrate.	Novel object: latency to and time spent interacting with the stimulus. Novel sound: time spent investigating the area (i.e., sound). Novel scents: attraction/avoidance of the area and time spent interacting with the scented substrate.	Vision: many predators lack trichromatic color vision. Ethical: provisioning food may be considered unethical or risks future conflict with humans. Vital that animals do not learn to associate humans with food. Encountering stimuli: these tests must be free. Habituation: tests must be moved, and objects/food frequently changed to ensure novelty. Few objects/foods may be novel to some animals. Scent-marking responses: see risk-taking. Conflation: risk-taking or exploration.
Exploration [17]		
Open field: the animal is presented with an unfamiliar environment to explore [59,60]. The environment should have external 'walls' made from materials that match the general color of the environment (e.g., brown or dark green tarps in forests), while contents may include log- or stone-piles and branches tied into tripods.	Time spent in the arena, distance travelled, time spent moving and inspecting (e.g., sniffing) walls or objects within the arena.	Entry decision: test must be free, that is, the animal can choose whether to enter and explore the arena [17]. Minimize novelty: as these environments will always be slightly novel in nature it is important to avoid using unfamiliar objects, materials, and colors. Human scents: minimize transfer of

(continued on next page)

trait axis should not predict its position on another independent trait axis.

Plasticity: changes in an individual's behavior in response to different stimuli – assessed as a gradient to the reaction norm slope.

Predictability: between-individual differences in residual intra-individual variation, that is, the variation that is unexplained by individual differences, individual plasticity, and environmental factors.

Repeatability: presence and extent of among-individual variation in average behavioral expression, standardized into the interval 0–1 (i.e., the proportion of phenotypic behavioral variance that can be attributed to among-individual differences).

Risk effects: nonlethal costs of predator avoidance (e.g., nutritional or physiological) which may sometimes affect reproductive success.

Risk taking: propensity to take risks in the absence of novelty, alternatively labeled anxiety/fearfulness.

Shared-method variance: behaviors recorded using similar methods exhibit artificially higher correlations than behaviors recorded with different methods. This includes different approach methods [e.g., flight initiation distances (FIDs) on foot vs. vehicles], audio playbacks (e.g., bear roars vs. human speech), threatening visual stimuli (e.g., human vs. predators), and scents from different species.

Sociability: propensity to remain close to conspecifics.

Trophic cascade: when apex predators control the density of herbivorous prey or affect the spatial distribution of where prey browse, altering the abundance and community dynamics of primary producers.

Validity testing: testing for both convergent validity and discriminant validity. Covariation above 0.5 may signify moderate confidence that two behaviors covary.

Table 1. (continued)

Experimental/field tests	Behavioral measures	Important considerations
		human scents to novel environment materials/objects (e.g., cleaning and wearing coveralls, face masks, and gloves). Conflation: risk taking, neophilia, or activity. Adaptation to social species: attributes of the social environment are likely important to consider (e.g., the sequence of individuals entering a new environment).
Activity [1]		
Activity: an animal roaming its typical (i.e., familiar) environment [1].	Time spent moving or distance covered.	Familiarity: an experimental test for ‘activity’ likely requires captive animals exploring familiar enclosures [55]; it may be challenging to recreate this stimulus in natural settings. Thus, remotely sensed or observation data may be more effective in wild individuals.
Human tolerance [25]		
FID: the distance an animal displaces away from an approaching experimenter or vehicle approaching at a constant velocity [61–63]. Encounter simulation: the animal is exposed to mock human visual stimuli (e.g., cardboard cutout), audio playbacks (e.g., human speech), or scents.	FID and encounters: flight time/distance and latency to return or to resume previous behaviors. Human scents: avoidance of the area and time spent interacting with the scented substrate.	Safety: for some species, populations, or individuals FID approaches on foot will not be safe. Tangential approaches may offer a viable alternative where direct approaches are not feasible. Encountering stimuli: these tests must be free. Conflation: risk-taking or aggression. Ecological validity: although FIDs can also be conducted with vehicles, animals may not associate the vehicle with humans specifically. As such, a vehicle FID may be a better measure for risk taking. However, the two methods may exhibit shared-method variance. Adaptation to social species: these methods have been used on social animals [30]. Individuals of social groups should be measured in (relative) isolation, with contextual factors such as distance to conspecifics and whether they flee first accounted for.
Sociability [64]		
Field mirror: an animal encounters a mirror [60]. Encounter simulation: the animal is exposed to audio playbacks of unfamiliar conspecific calls [60] or unfamiliar conspecific scents.	Mirror: time spent inspecting (e.g., sniffing) mirror without showing any aggression [62]. Encounters: flight time/distance and latency to return or to resume previous behaviors. Conspecific scents: avoidance of the area, latency to and time spent interacting with the scented substrate.	Injury: mirror must be able to withstand attacks, for example, acrylic. Inappropriate for aerial predators or where smaller birds may collide with surface. Encountering stimuli: these tests must be free. Scent-marking responses: see risk taking. Conflation: aggression and risk taking (e.g., the animal may hold its ground and vocalize).

Table 1. (continued)

Experimental/field tests	Behavioral measures	Important considerations
		Adaptation to social species: direct observation of these behaviors (e.g., from a field vehicle) may be easier to measure in social groups in certain species.
Aggression [1]		
Field mirror: described earlier. Encounter simulation: described earlier.	Mirror: latency to attack or number of attacks (e.g., swiping) [65]. Encounters: number of aggressive behaviors (e.g., vocalizations, threatening gestures). Conspecific scents: latency to and time spent interacting with the scented substrate.	Injury: see sociability. Encountering stimuli: see sociability. Scent-marking responses: see risk taking. Conflation: sociality and risk taking. Adaptation to social species: see sociability.

operational definitions focused on specific behaviors and contexts (see Glossary and Table 1). Importantly, we divide the popular boldness trait into risk taking, neophilia, and human tolerance, with the remaining traits defined such that they are clearly distinct.

Designing ecologically valid methods

Ecologically valid experiments offer the greatest scope for controlling scenarios and testing animal responses across a range of realistic conditions, and are the most powerful option for inference [13]. Undertaking an entirely experimental approach may be unrealistic or disruptive for some wildlife, but there are several ways of designing ecologically valid tests (Table 1). We offer suggestions (see Figure I in Box 1) for collecting observational data (e.g., direct observations, camera traps, dietary data, and GPS/drone data) and organizing into temporal periods (e.g., blocks) that mimic the trial number structure of repeated experiments, thus allowing for validity testing (Box 1) – with measurement-error models used to retain the error within each

Box 1. Investigating personality traits and plasticity in apex predators

Integrating variance portioning and validity testing

First, for each natural and experimentally elicited behavior, a univariate double-hierarchical model (DHGLM) should be implemented that includes a random intercept for individual identity, with intraindividual residual variance (i.e., predictability) and correlation components also defined [18,20]. DHGLMs concerning natural behaviors (Figure I) also require a measurement-error component if averages are used (e.g., averaging daily travel distance per week/month). All-important confounding variables (i.e., alternative hypotheses) should be included as random terms or as fixed effects, and as slopes over individual identity (i.e., reaction norm slopes). Alternative hypotheses and model structures should be devised using an information-theoretic approach [51], thus ensuring that the variance partitioning components of repeatability, reaction norm slopes, predictability, and the correlation between individual intercepts and their reaction norm slopes [18] are all estimated with the least bias [52]. Second, the same model structures used in the univariate DHGLMs should be implemented as bivariate models for validity testing between behaviors [18,19,52], allowing the variance components to be estimated according to the covariance between both behaviors.

Sampling requirements

To accurately estimate all of the variance components, a study with ≥50 individuals would require four samples per individual in each ecological scenario [20]. Given that predator populations are often widely dispersed, a study of 15 or 20 individuals would require at least 18 and 12 samples (respectively) per individual for each experiment/behavior. If multiple random terms (e.g., for among-habitat or -experimental design effects) and reaction norm slopes are required, then individual replicates may need to increase by a factor of two per additional term. We recommend therefore that datasets and analyses are simulated before data collection to determine sampling requirements. Some process of identifying the most parsimonious model or the model with the greatest predictive precision may be required during the final analysis to minimize over-fitting issues (e.g., stacking of predictive distributions and assessing R^2 values).

Quantifying individuals according to personality traits and plasticity

Each DHGLM will calculate the difference between the predicted mean population-level response (for the set of fixed effects) and the predicted responses for each individual. These individual-specific intercepts (i.e., conditional modes or best linear unbiased predictors) infer the extent to which each individual differs from the population mean, and thus, represent individual positions on particular personality trait continua [19]. Similarly, individual-level estimates for reaction norm slopes represent each individual's relative plasticity across the gradient of interest.

Figure I. Personality/plasticity – methods and measures. Examples of behaviors that can be linked with personality traits and individual plasticity. Responses to natural or experimental scents (top left), sounds, or visual cues can be used to infer risk-taking, neophobia, sociability, aggression (towards conspecifics), or human tolerance. Tendencies to use novel objects (e.g., deer bait stations) may indicate neophilia (top left center). Regularly killing prey with defensive weaponry may indicate risk taking (top right center and bottom center), as may scavenging from another predator (bottom left). GPS collars can be used to measure behaviors that may be proxies for personality traits (top and bottom right). Movement within anthropogenic/unfamiliar areas (bottom right – Eurasian lynx in front of a wooden fence) may infer human tolerance or exploration. Collar metrics such as day journey length, activity rates, or path linearity provide data on the activity trait (photos credits: top, bottom left, and center: Miha Krofel, bottom left: Max Allen).

temporal period. For each ecologically valid behavioral measure, researchers must carefully record data on confounding variables (i.e., alternative hypotheses). Examples include methodological (e.g., observer effects, familiarity with experiment, scents from humans/other wildlife), abiotic (e.g., weather and seasonality), ecological scenarios (e.g., prey density, competitor presence, and kill size), and individual phenotypic confounds (e.g., reproductive status, age, sex, and body size). Deciding whether and how to center these variables is vital to ensuring models have meaningful values for zero [20].

A combined approach for identifying personality traits and plasticity

We propose that researchers initially perform variance partitioning [18] on natural and experimentally elicited behaviors (Box 1). Any behaviors exhibiting repeatability and within-individual consistencies (i.e., relatively flat reaction norm slopes and high predictability) can then be taken forward for validity testing to infer personality traits. Validity testing using multivariate models ensures that individual variances are brought forward through every level of analysis [26]. Validity testing therefore requires at least two distinct behavioral measures – one of which should be derived experimentally – for each personality trait under investigation; otherwise, it is unclear whether certain behaviors are narrowly applicable to specific scenarios [17]. This distinguishes validity testing from behavioral syndromes (which considers only correlated suites of behavior), allowing researchers to identify specific personality traits governing behavioral patterns. If all the experiments designed to test a specific trait fail to elicit repeatability and within-individual consistency, then validity testing is not needed, and researchers can reject the hypothesis that a certain trait is present.

Labeling behaviors and traits

We recommend that the traits we define (Table 1) are initially used to design a range of ecologically valid tests, but the final labeling of traits is only done once results are known. For instance, neophilia and exploration may be best described as neophobia and avoidance if a study group/population typically avoid novel objects or environments (but among-individual variation remains). If researchers cannot achieve robust sample sizes (e.g., low density populations) then identifying distinct traits may be out of reach. However, our framework still allows for within- and among-individual variation to be quantified in a single behavior (Box 1) and model-derived individual estimates used in subsequent ecological analyses (Box 2). This will still offer insights into how among-individual variation in a single behavior (i.e., behavior type) may contribute to varied ecosystem roles, but will not yield a mechanistic understanding of how innate characteristics combine to create heterogeneity in individual roles. Note, however, that failure to sample individuals across a full range of conditions can artificially inflate repeatability – known as pseudo-repeatability [20]. The accuracy of repeatability estimates also depends on the total sample size (number of individuals × number of repeats) and the extent of repeatability. For example, low repeatability values (~0.1) require ≥100 individuals with ≥4 repeats [20]. As a result, even in its most general sense, personality inference still requires robust sampling designs.

Box 2. Using personality findings to understand individual ecosystem roles

Individual-level predictors in ecological analyses

It is vital that the error associated with conditional modes or individual-reaction norm slopes is carried forward when investigating the correlations between individual behavioral traits and biotic interactions; to achieve this, we again recommend measurement-error models. These individual-specific estimates (and errors) can be used as covariates (i.e., population-level effects) in models exploring interindividual variation in carrion subsidies, habitat selection, prey landscapes of fear, or intraguild competition, or used as node-level attributes (i.e., phenotypic traits) in **ecological networks** [53]. Such analyses could reveal how innate characteristics can have downstream consequences on ecosystems or help predict how heterogeneous individuals respond to environmental change.

Phenotypic clustering

Animals with particular traits may cluster non-randomly across landscapes. Western bluebirds (*Sialia mexicana*) have been shown to sort into distinct breeding habitats based on individual aggressiveness [3]. Even within a habituated social group, chacma baboons' positions in proximity and contact networks are affected by human presence according to each individual's level of human tolerance [19]. The same principal may apply to animals across much broader spatial scales, resulting in humans redistributing key biotic interactions. For example, brown bears (*Ursus arctos*) show evidence of personality (in its broadest sense) [15], with interindividual differences in their movement patterns. While brown bears are considered dietary generalists, certain individuals will specialize, sometimes occupying distinctly herbivorous or carnivorous trophic positions within the same habitat [54], which we hypothesize are partly underpinned by specific personality traits. Individual brown bears can also respond in divergent ways to human presence where some mothers with cubs will use humans as a shield to avoid infanticide [55]. This human-caused redistribution may similarly occur for individuals depending on their specific personality traits, independent of reproductive status (Figure I). It is therefore possible that human presence may redistribute bear patterns of seed dispersal [56] or predation. Once researchers have identified the traits present in their study population, mapping individuals' ranges or occurrence distributions should reveal spatial patterns of phenotypic clustering – particularly if trapping uses methods unlikely to select for particular traits (see Table 1 in main text).

Applications to science communication

Finally, researchers might label trends graphically instead of conducting further statistical analysis (e.g., color coding individuals according to phenotypes) – such an approach should enable numerous opportunities for science communication. By emphasizing that these animals are individuals with different preferences and stories, researchers may help gain enthusiasm for conservation plans that allow behavioral heterogeneity to be protected.

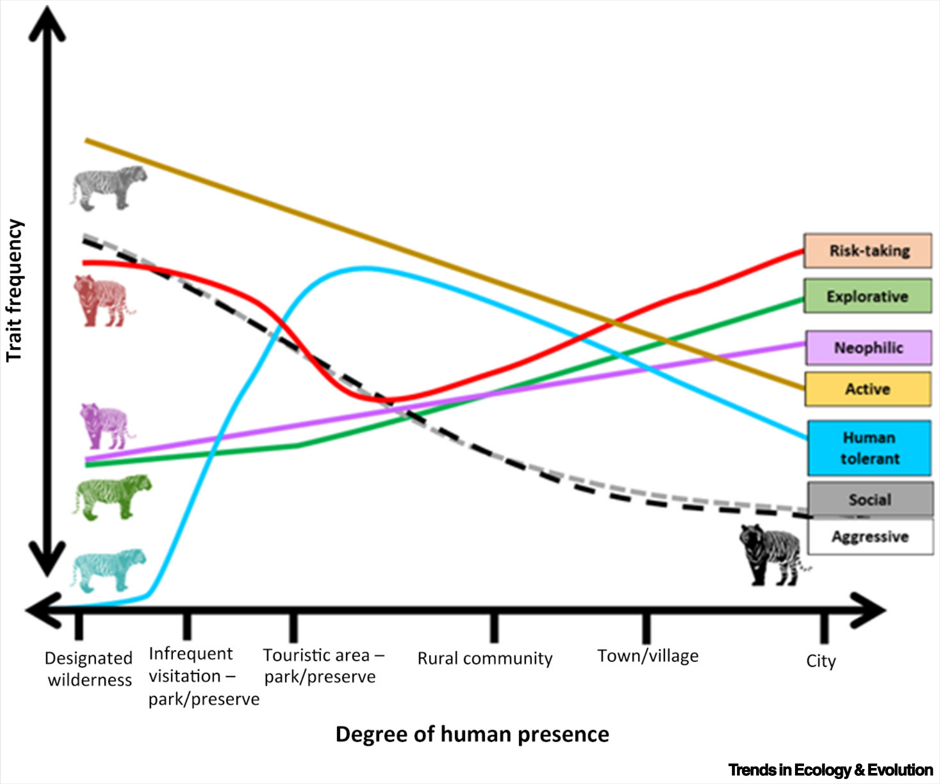
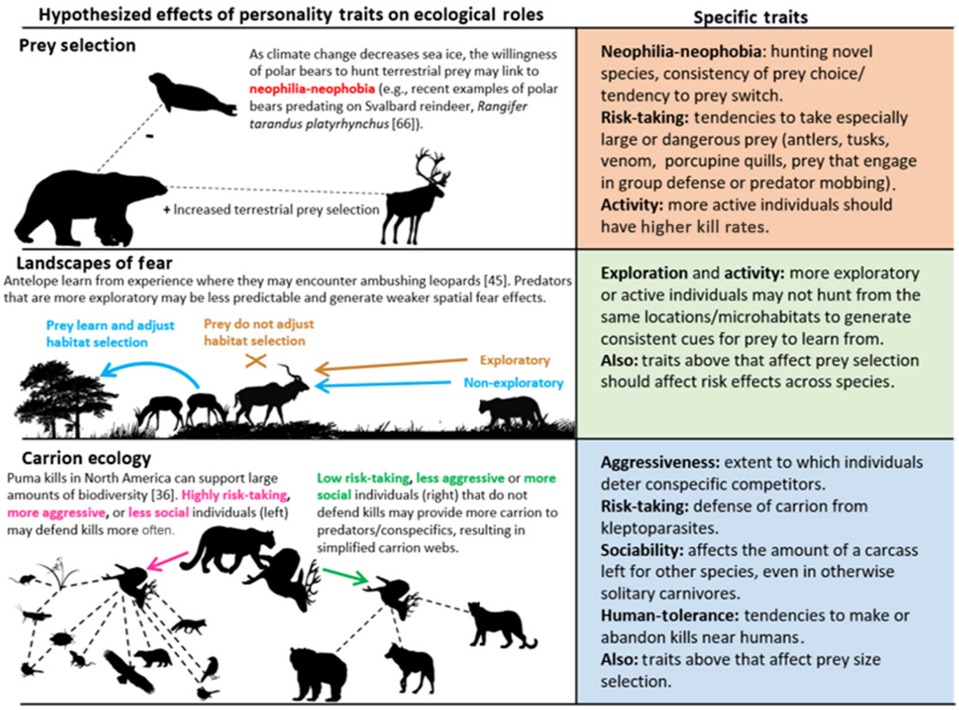


Figure I. Hypothetical trait frequencies across a gradient of human disturbance. Filtering due to phenotype-specific habitat selection and differential mortality risks across various habitats. In this nonexhaustive example, risk-taking individuals who take large prey prefer wilderness over touristic areas of a protected area. Animals avoiding risks from intraguild predation or competition might use proximity to humans as a buffer. This does not necessarily imply a correlation with human tolerance, but more tolerant individuals should also occur near benign humans. As risk from vehicles and other dangers increases towards cities, the risk-taking proportion of a (sub)population may increase. Alternatively, human tolerance and risk taking (and neophilia) may be one trait in certain species (i.e., boldness). Individuals who are less aggressive towards conspecifics may use altered landscapes as a refuge, and as the number of social partners decreases, aggressive and highly social individuals should be less common. By contrast, individuals who are explorative and more neophilic may be proportionally more common nearer humans as these landscapes may shift in unfamiliar ways with novel infrastructure. Human presence may therefore reassort the spatial distribution of biotic interactions linked with specific phenotypes.

Sacrificing testing for one or more personality traits (Table 1) may unintentionally reduce the certainty that the remaining traits are fully distinct. We recommend attempting to identify the full array of hypothesized personality traits in a single, consolidated framework. Although it could be argued that such an approach increases the odds of producing a 'jangle' fallacy (i.e., different trait labels actually measure the same trait) [17], running validity tests between every combination of behaviors (except for those with **shared-method variance** or that fail to exhibit repeatability, relatively flat slopes, and predictability) will ensure against this (i.e., a fully crossed design). Outcomes can then guide labeling decisions. For example, if behaviors used to measure neophilia covary with the behaviors used to measure the remaining hypothetical traits, researchers could reasonably argue evidence for a single boldness trait [21].

Personality traits as drivers of ecosystem role diversity

Species functional traits can shape their biotic interactions [27,28] and we argue that latent personality traits should drive consistent variation in species interactions [29], but predictions about how they will govern community interactions are specific to the trait composition within each population or species (Figure 1). Certain trait combinations should produce individuals who exert stronger effects on interacting species. For example, individual predators who are highly risk taking may more regularly hunt prey larger than themselves [30,31]. This carrion can serve as a critical source of energy and nutrients to smaller organisms [32–34] and rare or endangered scavenger species (e.g., *Puma concolor* providing for Andean condors*, Vultur gryphus* [34–36]). The effect of individual traits for this interaction is likely more pronounced in solitary species as social groups will consume more of a kill [32,37]. Yet even within solitary species, the tendency to share kills [37,38] should be connected to specific traits (e.g., sociability or aggressiveness), indirectly affecting scavengers/decomposers. As carcass size and human presence affect scavenger abundance [39], their distributions could track those of predators with specific traits, especially in anthropogenic landscapes (e.g., risk taking or human tolerant). Certain individuals should then play a disproportionate role in creating **bio-geochemical hotspots** where nutrients and moisture added to soil benefit plants and soil communities [33]. Considering highly



As climate change decreases sea ice, the willingness of polar bears to hunt terrestrial prey may link to **neophilia-neophobia** (e.g., recent examples of polar bears predating on Svalbard reindeer, *Rangifer tarandus platyrhynchus* [66]).

Neophilia-neophobia: hunting novel species, consistency of prey choice/ tendency to prey switch.
Risk-taking: tendencies to take especially large or dangerous prey (antlers, tusks, venom, porcupine quills, prey that engage in group defense or predator mobbing).
Activity: more active individuals should have higher kill rates.

Antelope learn from experience where they may encounter ambushing leopards [45]. Predators that are more exploratory may be less predictable and generate weaker spatial fear effects.

Exploration and **activity:** more exploratory or active individuals may not hunt from the same locations/microhabitats to generate consistent cues for prey to learn from.
Also: traits above that affect prey selection should affect risk effects across species.

Puma kills in North America can support large amounts of biodiversity [36]. **Highly risk-taking**, **more aggressive**, or **less social** individuals (left) may defend kills more often.

Low risk-taking, **less aggressive** or **more social** individuals (right) that do not defend kills may provide more carrion to predators/conspecifics, resulting in simplified carrion webs.

Aggressiveness: extent to which individuals deter conspecific competitors.
Risk-taking: defense of carrion from kleptoparasites.
Sociability: affects the amount of a carcass left for other species, even in otherwise solitary carnivores.
Human-tolerance: tendencies to make or abandon kills near humans.
Also: traits above that affect prey size selection.

Trends in Ecology & Evolution

Figure 1. Hypothesized effects of potential personality traits on specific ecological roles. Along with more commonly considered individual traits (e.g., body size and reproductive status), specific personality traits should govern individual behavior, including interactions with other species. Listed here are a few example hypotheses to guide future research. Traits such as neophilia-neophobia could drive interindividual patterns of prey selection in a changing environment [66]. Risk taking could affect individual willingness to hunt large, or especially dangerous prey and (along with aggression and sociability, among others) result in substantial differences in individual carrion networks. Traits governing predator behavior may also affect the strength of fear effects. In addition, the traits of one species may interact with another in dynamic ways. For example, the traits of individual prey or the composition of personality traits found in a prey social group may affect their responses to predation risk [67]. This should similarly be true for competing predators (e.g., spotted hyena; *Crocuta crocuta*) show individual differences in response to risks from lions (*Panthera leo*) [68]. When and where human tolerance is found to be a personality trait, this will affect the nature and strength of biotic interactions within shared landscapes. Individual differences in human tolerance could result in the redistribution of certain phenotypes, but nonrandom spatial patterning (clustering or avoidance of similar phenotypes) may also happen naturally, leading to variation in where key ecosystem roles take place (see Box 2 in the main text). See [36,45].

connected or ecosystem engineering species are often termed keystones, we argue that certain individuals within a species can similarly produce outsized ecosystem effects (Figure 1).

The composition and spatial patterning of personality traits found in a predator population may further amplify or attenuate ecosystem-level effects and may be particularly consequential for predator–prey interactions. For example, in aquatic mesocosms, the composition traits can determine if predators induce density-mediated **trophic cascades** [4]. Prey selection may also be tied to personality and has been linked with beaver (*Castor canadensis*) predation by wolves (although not to specific traits) [40]. Similarly, some pumas select beavers more than expected [41], which could also be underpinned by personality. As beaver predation patterns can shape wetland distributions [42], it is possible that predator personalities have a major impact on landscape structure and human-centered ecosystem services [40]. When predators specialize on certain prey, regardless of availability, this can also negatively affect endangered prey viability [43]. In these cases, a predator's unwillingness to hunt different prey may be underpinned by neophobia or a lack of plasticity, rendering individuals particularly consequential for conservation.

The fear that predators induce in their prey can be affected by species-level traits, such as hunting mode [9,10]. Ambush predators that consistently hunt from certain locations or microhabitats tend to induce stronger landscapes of fear than coursing predators that chase prey across great distances [9,10,44,45]. Yet, within a single species, individual behavioral traits could also affect prey fear. Within a single predator species, highly active, explorative, or plastic individuals may be less consistent in their hunting habitat selection, generating fewer reliable cues that allow prey to avoid risky places. The converse might also be true for individuals who tend towards the opposite extremes with less explorative or active individuals inducing stronger fear responses and spatial avoidance (Figure 1).

Concluding remarks

Individual behavioral traits can govern ecological roles [4,14,40,46,47], but extending this research to megafauna inhabiting complex natural systems is a challenge. We have provided a framework for how researchers might tackle questions on large terrestrial predators, but these experimental and observational methods should be adaptable to a variety of taxa and systems. These ideas may help us understand how communities evolve in response to both global change – and conservation efforts. In Europe and North America, apex predators are recolonizing areas of their former ranges and dispersers who survive in new locations may tend towards particular traits or greater plasticity [48]. At present, we know little about whether this is actually the case, or if dispersal distance is more strongly linked with environmental and morphological/physiological factors. Researchers, wildlife managers, and the public, are also quick to label problem individuals as bold [48], despite often lacking the evidence to do so. Yet, plastic individuals may opportunistically feed on domestic animals or anthropogenic foods, while others may overcome their personality traits (e.g., risk averse or human intolerant) to avoid starvation. Incorrectly labeling these individuals could therefore misguide management plans (e.g., targeted culling) (see Outstanding questions).

When apex predators decline due to anthropogenic pressures [6], generalists (e.g., coyotes, *Canis latrans*) that typically occupy middle trophic positions may take larger prey [49], becoming apex predators *sensu lato*. As human tolerance as a personality trait may also exist on an independent axis, tolerant individuals subject to human habituation (e.g., suburban dwellers) may adopt an apex role as intolerants are filtered out (Box 2). Thus, even where humans and predators coexist, filtering for specific traits (via habitat selection and/or biased mortality) may be an unappreciated way in which we are redistributing community interactions (Box 2). Limiting these effects within more sparsely populated areas may be possible by allowing wildlife enough

Outstanding questions

How are the survival and reproductive success of individuals with varying personality traits affected by global change and how do these diverse individuals use varying strategies to cope with landscape change, habitat fragmentation, or human recreation in protected areas?

To what extent are different traits inherited, learned, or developed/reinforced during life experiences? Can this information be used to inform preemptive management strategies (e.g., aversive conditioning) to mitigate human–wildlife conflict?

How does the composition of traits found in a predator population affect the strength of community interactions? Is the composition of traits important for indirect effects – such as with inducing fear effects and altering prey behavior?

Do individuals with specific personality traits have differential risks from disease transmission, conspecific aggression, or intraguild predation?

In social carnivores, does the composition of personality traits within a group help to shape interactions with other predators (or rival groups/packs) or affect prey selection? Do individuals with specific personality traits exert greater control over prey selection?

space to roam (e.g., periodically shutting down sections of protected areas from tourists [50]) and minimizing human activities within corridors between larger protected areas, allowing a greater diversity of phenotypes to move across large landscapes.

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Declaration of interests

No interests are declared.

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