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Opinion

Daily activity timing in the Anthropocene

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Animals are facing novel 'timescapes' in which the stimuli entraining their daily activity patterns no longer match historical conditions due to anthropogenic disturbance. However, the ecological effects (e.g., altered physiology, species interactions) of novel activity timing are virtually unknown. We reviewed 1328 studies and found relatively few focusing on anthropogenic effects on activity timing. We suggest three hypotheses to stimulate future research: (i) activity-timing mismatches determine ecological effects, (ii) duration and timing of timescape modification influence effects, and (iii) consequences of altered activity timing vary biogeographically due to broad-scale variation in factors compressing timescapes. The continued growth of sampling technologies promises to facilitate the study of the consequences of altered activity timing, with emerging applications for biodiversity conservation.

Highlights

Recent years have seen a growing interest in the role of time in structuring biological patterns and processes.

Among nature's most dramatic and universal temporal patterns are the daily activity patterns shown by organisms. Although the endogenous mechanisms (e.g., circadian rhythms) giving rise to such patterns have been researched extensively, ecological aspects of daily activity patterns are now receiving greater attention.

Plasticity in daily activity patterns may represent an *in situ* adaptation to human-mediated stressors such as climate change and urbanization. However, the effects of novel activity timing, which may emerge at multiple levels of biological organization, are poorly understood.

We offer hypotheses to catalyze future research on the ecological consequences of altered daily activity timing and discuss approaches that may facilitate such investigations.

Novel activity timing in the Anthropocene

Time is an essential currency of life: finding food, avoiding predators, and reproducing requires animals to be active at the right time and in the right place [1,2]. Organisms have evolved **daily activity timing** (see Glossary) in response to **timescapes** [3] (comprising, e.g., resource availability and predation risk; Box 1) that may vary dramatically over the **diel cycle** [4–6]. Daily activity timing may be an example of a **circadian rhythm** [5,7] but typically cannot be confirmed as such in studies of free-living animals. Notably, human activities restructure timescapes and thereby may induce animals to change their activity timing. While mounting research shows that animals may exhibit plasticity in their activity timing in accordance with these altered stimuli [8,9], it is largely unknown whether such behavioral changes are adaptive [10] or whether they represent maladaptive outcomes such as **evolutionary traps** [11]. If novel activity timing carries limited fitness costs, it may buffer organisms from stressors such as climate change or urbanization [3,10,12]. Alternatively, shifted activity timing may incur fitness costs: an experiment in mice (*Mus musculus*) demonstrated strong natural selection against a clock gene mutation that caused animals to be active at atypical times of day [13].

Human activities drive numerous environmental changes that may create novel timescapes and affect the daily activity timing of free-living animals (Figure 1) [14]. Some species perceive humans as predators, leading to fear-motivated shifts in behavior timing; many mammals, for instance, become more nocturnal in human-altered landscapes [8,15–17]. Other species may change their activity timing not in direct response to human disturbance but rather to the human-mediated changes in activity timing of predators, competitors, or introduced species [17,18]. Climate change may also drive novel activity timing; for example, diurnal species may shift to greater **crepuscular** or nocturnal activity to escape rising daytime temperatures [3,12,19]. Finally, **sensory pollution** [20,21] may disrupt or mask the stimuli that organisms use to

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structure their activity timing; for example, artificial light can disturb the sleep of diurnal organisms [22] and cause them to be active later in the evening and earlier in the morning [23,24]. Importantly, these human-altered stimuli often co-occur and may interact to produce complex timescapes that induce changes in activity timing [11,25,26].

The **ecological effects** of novel activity timing might ripple across levels of biological organization, from individuals to ecosystems [27]. At the individual level, shifting activity times can have profound physiological effects, as evidenced by the impaired immunity and other health problems of humans who 'live against the clock' and work night shifts [28,29]. At the population level, altered activity timing might dampen recruitment if an individual's ability to access resources or detect predators is impaired by being active at new times [30]. At the community level, altered activity timing may diminish or amplify competition, predation, or disease transmission [27] by modifying the likelihood of encounter and contact among individuals. Finally, at an ecosystem level, activity-timing shifts could change nutrient flows if altered species interactions disrupt processes such as herbivory [31]. However, these effects are difficult to document, particularly at broader (e.g., ecosystem) scales of organization [8,27].

Opportunities to explore the ecological effects of novel timescapes and altered activity timing are expanding with continued advances in technologies and sampling approaches that allow ecologists to gather behavioral data over ever-expanding spatiotemporal scales. Improving technologies such as Global Positioning System (GPS) tags [32], camera traps [33], trap-based loggers [34], and accelerometers [35], along with citizen science observations, provide researchers with time-stamped behavioral data spanning previously untenable scales. Considering these technological advances and growing interest in understanding behavioral responses to global change, our objectives are to (i) conduct a literature review to summarize the current state of activity-timing research and identify areas for future progress and (ii) present hypotheses regarding the ecological effects of human-mediated activity-timing shifts and discuss the areas for advancement that would facilitate pursuit of such hypotheses.

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Box 1. Timescapes in the Anthropocene

Analogous to the definition of landscapes [95], we define timescapes broadly as durations of time that exhibit fitness-relevant heterogeneity in biotic and/or abiotic factors of interest. This concept differs from existing terminology, such as 'schedules of fear' [6] and 'realized diel light niche' [96], by its emphasis on the cohesive whole of multiple time-varying factors (e.g., temperature, predation risk, resource availability) that influence organism fitness. Timescapes exist at multiple temporal scales (Figure IA). For example, daily timescapes may capture variation in predation risk, seasonal timescapes may capture variation in precipitation, and evolutionary timescapes may reflect variation in allele frequencies. Our review focuses on the daily scale and explores the ecological effects of organismal responses to the novel timescapes of the Anthropocene.

Timescapes by definition vary but often do so predictably. Thus, for individual organisms, timescapes operate as a sort of schedule or calendar dictating behavioral decisions [97]. Importantly, timescapes exist as they are perceived by individual organisms [95] (Figure IB). Consequently, timescapes may differ among species according to functional traits (e.g., body size, generation time, ability to undergo physiological dormancy) and are inherent components of learning, adaptive phenotypic plasticity, and transgenerational effects [98]. Just as animal behavior ultimately provides a means to conceptualize and identify landscapes [95], we posit that behavior and other functional traits are key to conceptualizing timescapes.

Anthropogenic disturbance may modify the actual or perceived timescape or both simultaneously (Figure IB). We expect that organisms should time their activities to coincide with time windows when the net fitness effect of timescape elements is positive; for example, species may time their activity to avoid predation risk (Figure IC). Temporal evolutionary traps may form when anthropogenic disturbance alters timescapes but animals fail to perceive the modified timescape, leading them to be active during costly times (Figure ID). If the fitness costs of these traps are large – or if actual timescapes are simply being modified too rapidly for organisms to respond effectively – novel activity timing may incur far-reaching ecological effects.

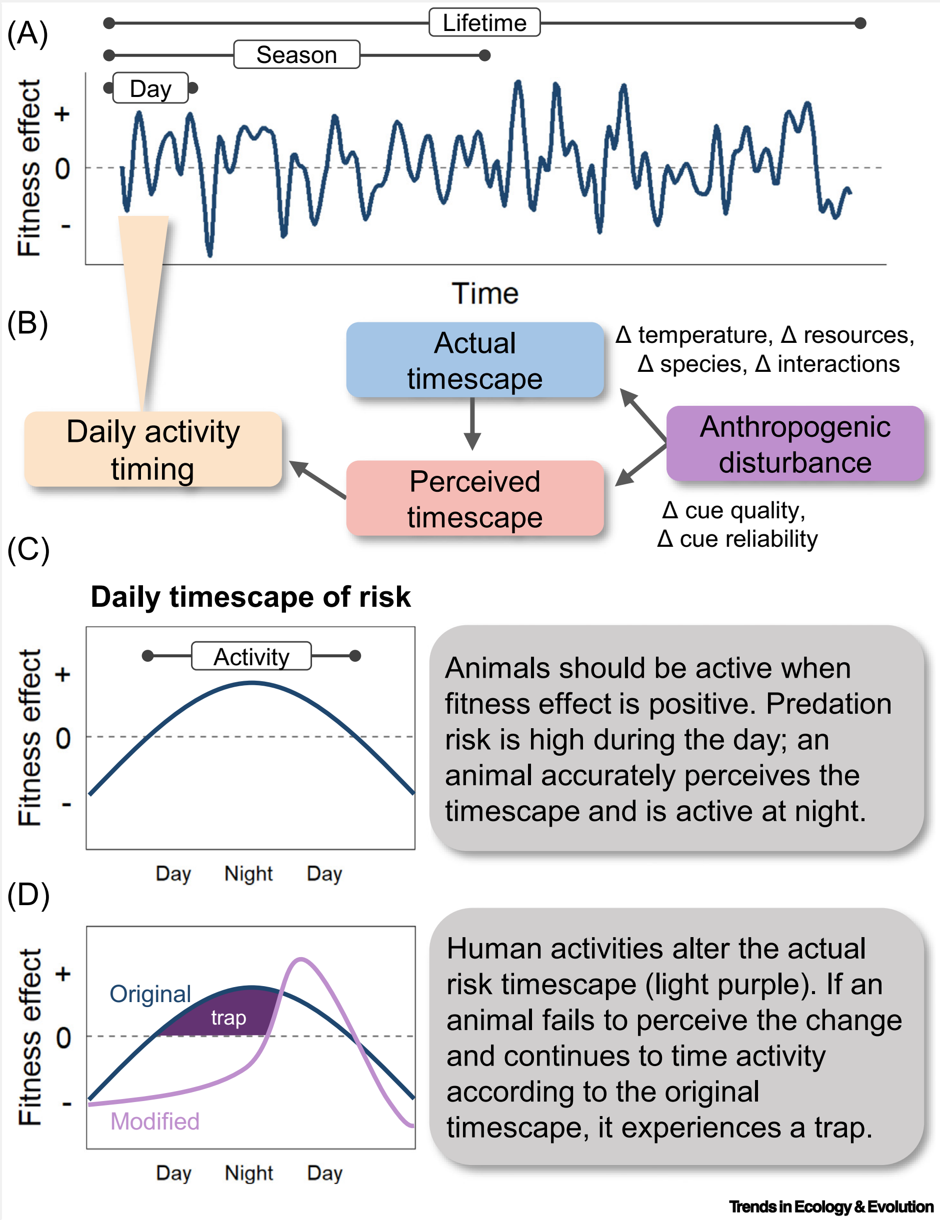

Figure I. The timescape concept. (A) Timescape of some factor's influence on organism fitness, showing that timescapes can be evaluated at multiple temporal scales. (B) Human activities may alter either actual or perceived timescapes (or both) to alter the timing of animal behaviors. (C) Hypothetical daily timescape of risk. (D) Human-mediated timescape modification results in an evolutionary trap.

Glossary

Chronotype: consistent intraspecific variation in biological timing(s).

Circadian rhythm: a biological rhythm that originates from within an organism, has a rhythmicity of approximately 24 h, can be entrained by cues such as light and temperature but persists in the absence of cues (e.g., 24-h darkness in the laboratory), and persists with similar period length under variable environmental settings.

Crepuscular: an organism that is primarily active at dawn and dusk.

Daily activity timing: patterns of behavior and activity that follow a 24-h cycle; note that these may be circadian rhythms but typically cannot be confirmed as such in studies of free-living animals. Common synonyms include 'daily activity patterns', 'diel activity patterns', 'diel activity rhythms', and 'daily activity rhythms'.

Diel cycle: a pattern emerging over 24-h cycles due to Earth's rotation.

Ecological effects/consequences: umbrella term referring to effects of behavioral change at any level of biological organization [e.g., individual (changes in body mass), population (lowered fecundity), community (altered predation rates), or ecosystem (modified nutrient flows)].

Evolutionary trap: a resource that an organism perceives as attractive despite being associated with reduced fitness.

Habitat configuration: how habitat is arranged; in space, this might involve quantifying the connectivity of habitat patches, whereas in a temporal framework, this might refer to the timing of events relative to other events.

Individual-based sensors: data-generating devices that are attached to individual animals (e.g., GPS tags, accelerometers).

Integrated models: statistical models that bring together disparate datasets into a cohesive whole, typically by way of a joint likelihood.

Phenological mismatch: describes situations in which interacting species change the seasonal timing of behaviors or life cycles at different rates and thus become desynchronized with each other.

Photoperiod: day length.

Sensory pollution: anthropogenic emissions of chemical and physical stimuli that interfere with the sensory capacity of organisms.

Review: the state of daily activity timing research in ecology

We reviewed 1328 studies (see the supplemental information online) that measured the daily activity timing of free-living animals. Our goal was to characterize the literature on activity timing and identify areas of future development for the field. Notably, only a small share of studies focused on anthropogenic effects on activity timing (Figure 2A); for example, of 177 studies published in 2021, ~16% fit this

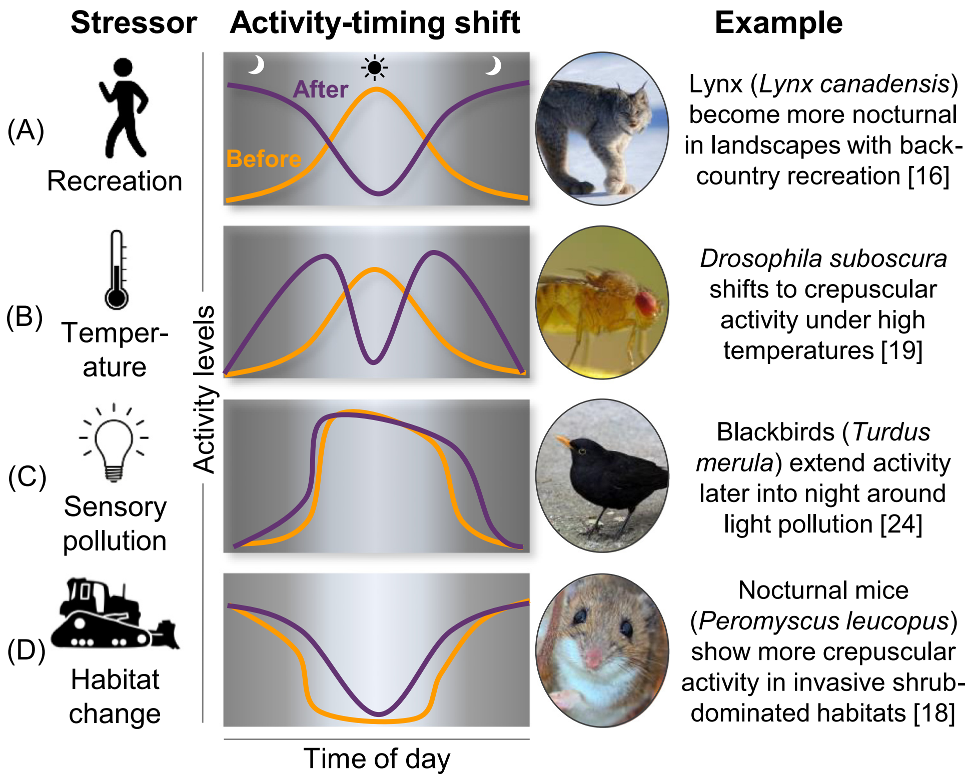

Figure 1. Multiple human-mediated elements of timescapes can induce novel activity timing in free-living animals. (A) Human recreation causes a typically diurnal species (yellow line) to adopt a nocturnal activity pattern (purple line). Photo by Keith Williams. (B) Anomalously warm temperatures cause a typically diurnal ectotherm to become crepuscular to coordinate activity with cooler portions of the diel cycle. Photo by John Tann. (C) Light pollution allows a diurnal species to extend its activity earlier in the morning and later in the evening. Photo by Zeynel Cebeci. (D) Habitat change (invasive shrubs) causes a nocturnal species to be active later in the morning and earlier in the evening, possibly due to habitat-mediated changes in predation risk. Photo by Peter Chen.

Site-based sensors: data-generating devices that are fixed in space and detect animals within some surrounding area (e.g., camera traps, acoustic recording units).

Timescape: a duration of time that exhibits fitness-relevant heterogeneity in biotic and/or abiotic factors of interest (Box 1).

category, whereas ~33% focused on species interactions and ~38% had descriptive objectives. Studies on mammals (41%) and ray-finned fish (26%) predominated (Figure 2B). Aquatic studies were historically dominant, but terrestrial studies rapidly increased around 2010 and became more prevalent than aquatic ones around 2015 such that 70% of studies were in terrestrial systems in 2021 (Figure 2C). Technological advancements likely drove this shift; studies using camera traps (which typically target terrestrial mammals [33]) have increased since roughly 2010, particularly in the last 5 years, such that 54% of studies used camera traps in 2021 (Figure 2D). In parallel, the spatial and temporal extents of studies have expanded. In 2000, ~78% of studies focused on areas roughly 1 km^2 in size. In 2021, only 33% of studies focused on areas ~1 km^2 in size, and 50% and 17% of studies evaluated areas ~100 and ~10 000 km^2 in size, respectively (Figure 2E). Similarly, the temporal extent of studies has grown; in 2000, the average temporal extent of data collection was 3.3 months, but in 2021, it was 17.3 months (Figure 2F). Finally, the temporal resolution of data has also increased; for example, 22% of studies used continuous-time analyses in 2000 compared with 58% in 2021 (Figure 2G). On the basis of our review of the literature, it is clear that advances in animal monitoring and tracking have expanded the spatiotemporal extent and resolution of activity-timing data, allowing researchers to describe even subtle changes in activity timing (e.g., extended activity after sunset in response to artificial light [24]) and compare activity timing among species [36].

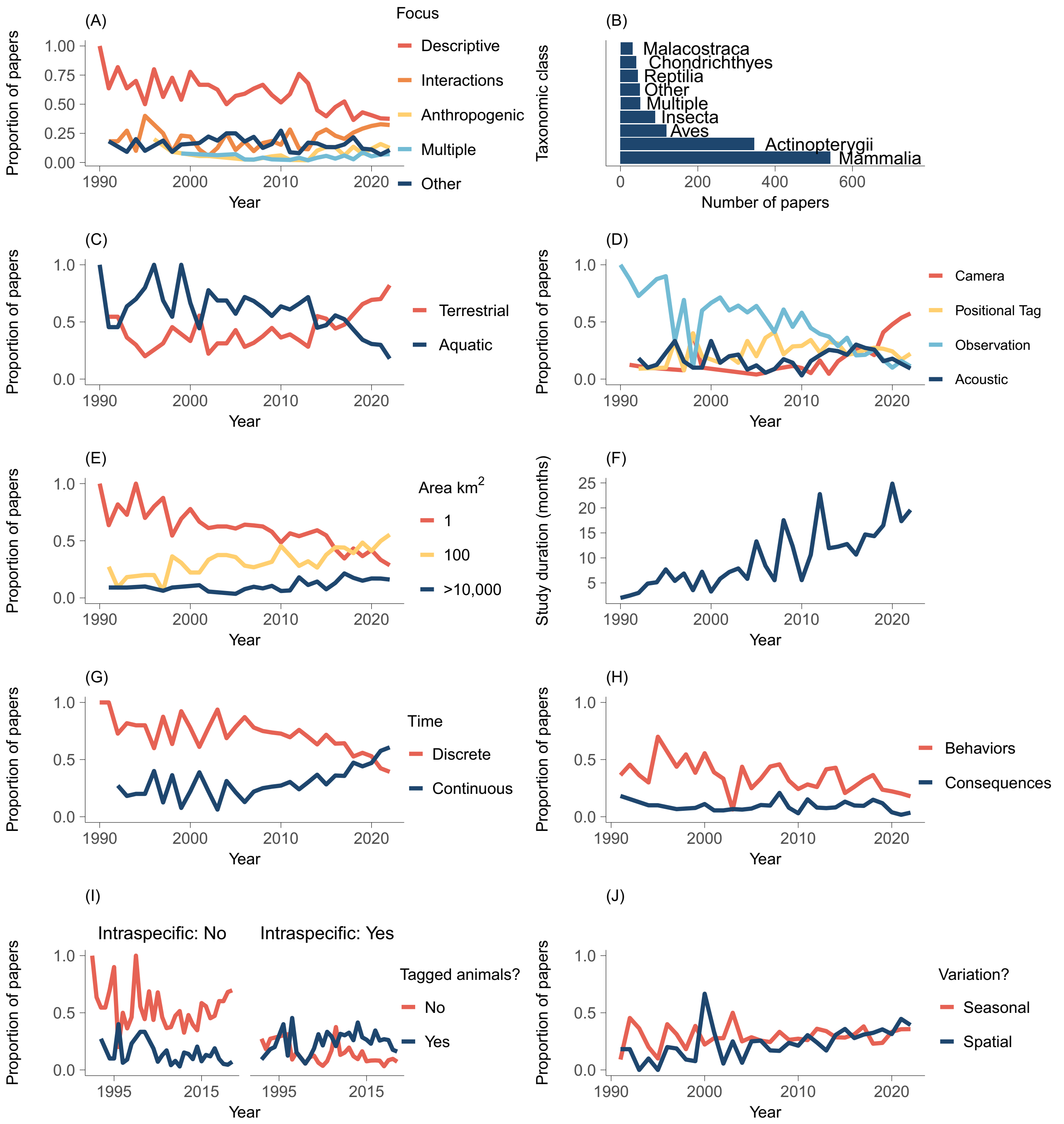

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Figure 2. Trends in activity-timing literature. (A) Relatively few activity-timing studies have an anthropogenic focus. (B) Mammal and fish studies dominate. (C) Terrestrial studies have recently overtaken aquatic ones. (D) The proportion of studies collecting data by direct observation has dropped over the past 30 years; acoustic sensors and cameras are increasing, whereas studies using tagged animals (Positional Tag) have been stable. The spatial (E) and temporal extents (F) of studies are increasing, whereas (G) continuous-time methods are increasingly being applied. (H) Few studies link daily activity timing to other parameters or quantify the timing of specific behaviors. Less than half of studies estimate intraspecific variation in activity timing (I); those that do mostly rely on tagged animals or spatial or seasonal variation in activity timing (J).

Despite recent advancements, we identified four areas primed for future development with regard to understanding the ecological effects of altered activity timing. First, although researchers often describe daily activity timing and even document novel activity timing in response to various forms of anthropogenic disturbance, few studies link activity-timing shifts to other variables; only 7.7% of studies attempted to link activity timing to ecological parameters such as physiology or survival (Figure 2H). Second, although intraspecific behavioral diversity can be vast [37], only 35% of studies measured or accounted for intraspecific variation in activity timing (Figure 2I). Of these, the majority (70%) used **individual-based sensors** such as GPS tags rather than **site-based sensors** such as acoustic recording units (Figure 2I), indicating that site-based sensors may be limited in their capacity to provide information on intraspecific variation because individual animals often cannot be distinguished [38] (although individual-based sensors face their own limitations, e.g., battery life). Third, the activity timing data often recorded by researchers are a general behavioral metric that encompasses many behaviors; only 29% of studies measured the timing of specific behaviors (e.g., foraging, vigilance; Figure 2H). Fourth, researchers often aggregated data from multiple locations or over long temporal scales [39], even though activity timing can be dynamic over space and seasons [8,9]. For example, only 29% of studies evaluated spatial variation in activity timing (e.g., differences between habitats), and only 31% of studies evaluated seasonal variation in activity timing (Figure 2J). We suggest that future research addressing these considerations would be particularly fruitful for understanding the ecological effects of altered activity timing. To stimulate future work, we discuss three hypotheses and further expand on the areas of advancement outlined above (Figure 3).

Mismatch hypothesis: the ecological effects of novel activity timing arise via activity-timing mismatches within and between species

Activity-timing mismatch occurs when individuals or species perceive and respond to timescape modification differently, changing the overlap in daily activity timing within or between species [40]. Drawing an analogy to **phenological mismatch**, such daily activity mismatches may have effects at the individual [41], population [42], community [1], or ecosystem level [43]. For example, we might predict that temporal mismatches of sexually selected behaviors have negative effects on demographic rates [44]. Suppose male birds in urban settings shift the timing of singing to avoid acoustic masking from traffic noise [45]. If female birds structure their activity in response to other stimuli (e.g., light), the decoupled activity timing between males and females may result in fewer pairings and thus reduced recruitment [44,46]. For ecosystems, we expect that activity-timing mismatch between predators and prey [17] can influence processes such as nutrient flows [43]. Imagine a system in which aquatic midges (Insecta: Chironomidae) emerge at dusk and experience predation by diurnal swallows (Aves: Hirundinidae). If warming temperatures cause midges to emerge at night, bird predation may decline (assuming that birds do not exhibit similar activity-timing plasticity, perhaps due to sensory limitations), and there might be increased nitrogen and phosphorus deposition (from midge carcasses) to riparian zones [47,48]. Such mismatches benefit one party but harm the other and thus should not be evolutionarily stable [40]. While they persist, such mismatches may affect nutrient flows if predators switch to new food sources [48] or if the temporal release from predation risk amplifies processes such as herbivory or carcass deposition [43,49].

Evaluating the mismatch hypothesis requires data on the consequences of novel activity timing [27,50]. Thus, we encourage researchers to link activity timing to physiological, demographic, or trophic parameters (Figure 4A). Perhaps the most direct way to evaluate the consequences of activity-timing shifts, though logistically challenging, is to measure individual condition or survival. For example, Lamb *et al.* [10] demonstrated that, in urban areas, more-nocturnal brown bears (*Ursus arctos*) showed reduced mortality risk [10]. Beyond individual-level consequences,

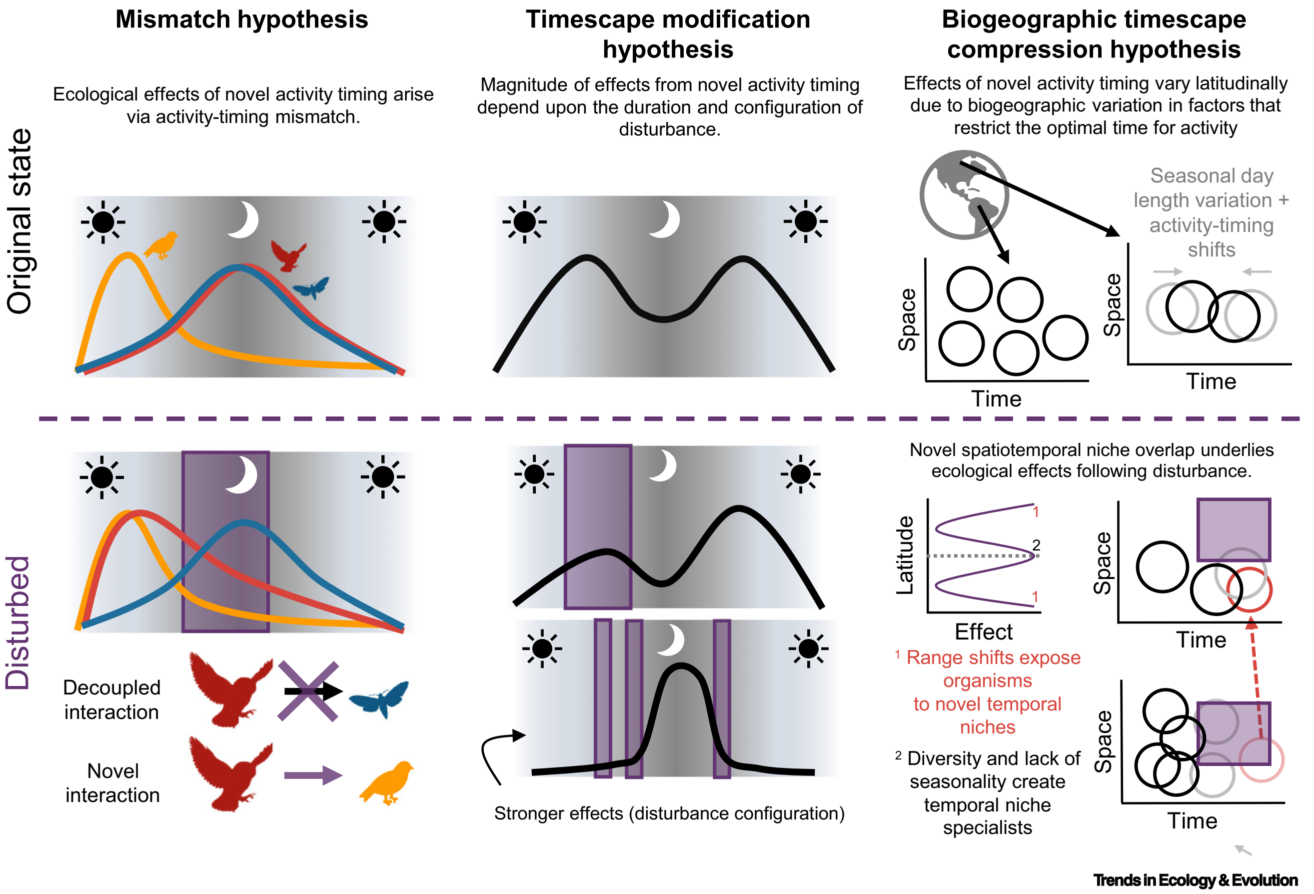

Figure 3. Hypotheses regarding the ecological effects of novel activity timing. In the first column, activity-timing shifts of a predator in response to a disturbance (purple) result in a decoupled predator–prey interaction and a new predator–prey interaction. In the second column, the same amount of disturbance occurs, but the bottom scenario is predicted to precipitate larger effects because disturbance overlaps with two activity peaks. In the third column, the spatiotemporal niches (circles) of species for high- and low-latitude sites shift (semitransparent circles are the original niche) in response to disturbance; we predict that disturbances may precipitate larger effects at low latitudes (greater species diversity and temporal niche specialization due to a lack of seasonality) or at high latitudes (range shifts expose organisms to novel temporal niches).

we encourage researchers to seek ways to link population-, community-, and ecosystem-level parameters to activity timing. Researchers often compare the activity timing of co-occurring species [39,51] but rarely link observed activity timing to parameters such as predation rates to evaluate the consequences of activity-timing overlap on community dynamics. Quantifying predation or competition in free-living animals is a time- and resource-intensive undertaking but is becoming increasingly feasible in the dawning age of high-throughput movement data [32,52].

Evaluating the mismatch hypothesis might also benefit from measuring intraspecific variation in activity timing, or **chronotype** [5] (Figure 4B). Intraspecific factors such as age, sex, body size, or personality [53] may be associated with activity-timing variation, which may confound population-level conclusions if overlooked. Importantly, intraspecific behavioral variation can facilitate adaptation to human-induced global change [54] if certain behavioral phenotypes confer demographic benefits [55]. Moreover, intraspecific differences in activity timing may inform conservation practice by, for example, revealing which individuals or demographic classes may face greater exposure to human disturbance or other time-varying threats [10]. Measuring intraspecific variation in activity timing is most easily accomplished via individual-based sensors such that data correspond to known individuals; however, even for

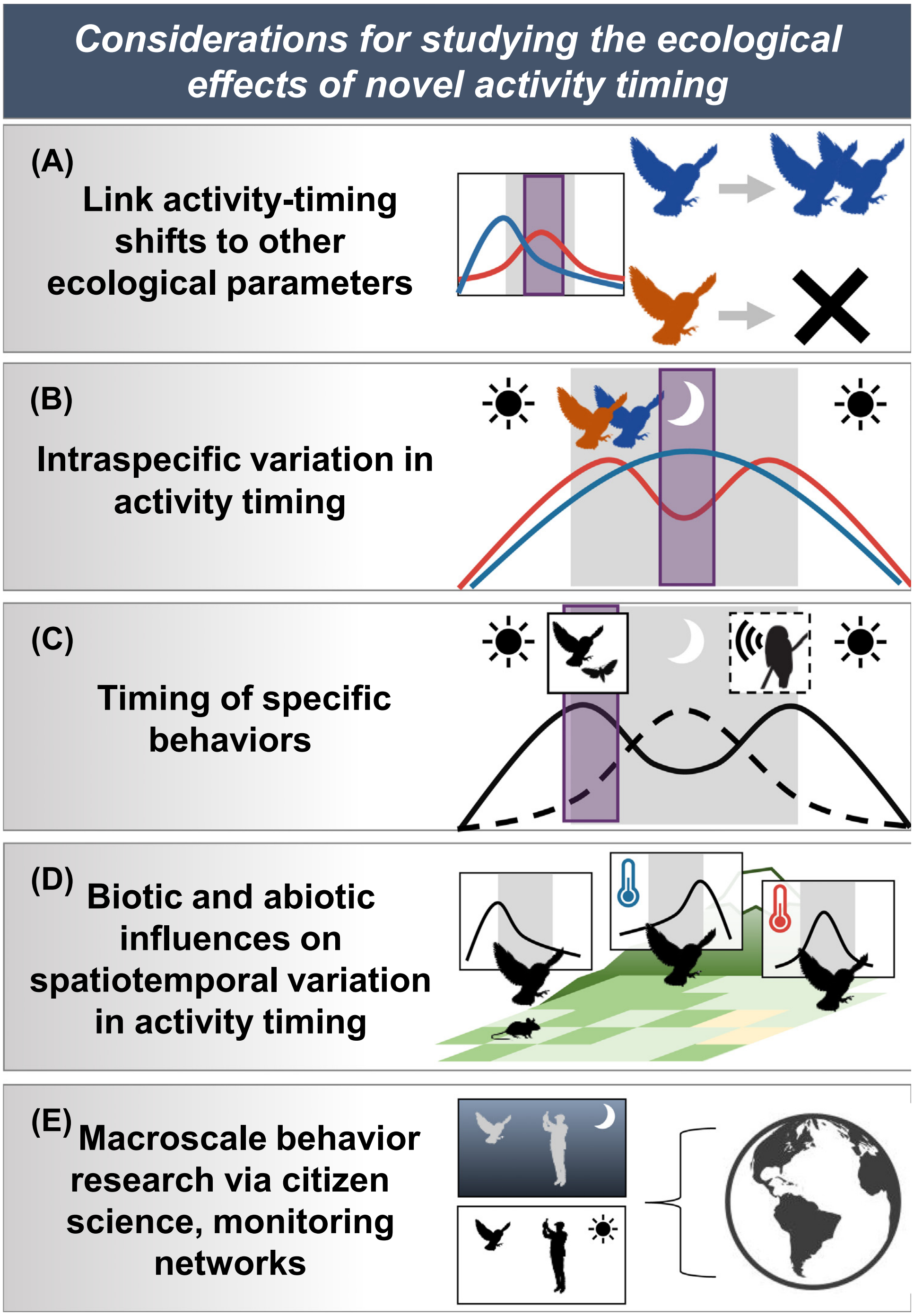

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Figure 4. Considerations for studying the ecological effects of novel activity timing. In order to understand the ecological effects of novel activity timing induced by human disturbance (purple boxes), we encourage researchers to (A) link activity-timing shifts to other ecological (e.g., physiological, demographic) parameters, (B) explore intraspecific variation in activity timing, (C) estimate the timing of specific behaviors rather than general activity, (D) estimate spatiotemporal variation in activity timing due to biotic and abiotic variables, and (E) draw upon emerging broad-scale datastreams to pursue questions at macroscales.

studies using site-based sensors (in which identifying individuals is difficult or impossible), researchers can sometimes classify animals into demographic groups (age, sex, body size) that align with ecologically meaningful differences in activity timing [56,57].

Timescape modification hypothesis: both the duration and temporal configuration of human disturbance influence the ecological effects of novel activity timing

Time can be conceptualized as habitat that is used by organisms [1,2]. Just as anthropogenic modification to spatial habitat can be described as habitat loss (i.e., amount of habitat, agnostic of **habitat configuration** [58]) or habitat fragmentation (i.e., habitat amount with an explicit focus on its configuration [58,59]), it is pertinent to explore the relative influence of timescape loss versus fragmentation on activity-timing responses. Such efforts would require considering the temporal duration of disturbance (timescape loss) as well as the temporal configuration of disturbance (timescape fragmentation). For example, would three consecutive hours of artificial light at the beginning of the night induce a different behavioral response from three 1-h durations of artificial light distributed throughout the night [23,60] (Figure 3)? We predict that timescape fragmentation has outsized ecological effects because organisms may be harder pressed to coordinate activity with undisturbed times (Figure 3). Moreover, we expect that disturbances overlapping with sensitive behaviors precipitate larger ecological effects. We also predict that longer durations of timescape disturbance induce more extreme activity-timing shifts and therefore larger ecological effects. Importantly, the effects of anthropogenic timescape modification may depend upon the nature of the past timescapes experienced by a species (e.g., species that have evolved in highly fragmented timescapes [61]), the relative degree to which historic timescapes differ from contemporary ones, and the existence of phenotypic traits associated with changing environments (e.g., capacity for phenotypic plasticity or learning).

In addition to linking activity timing to other parameters and measuring intraspecific variation in activity timing, pursuing the timescape modification hypothesis might involve measuring the timing of specific behaviors rather than general activity. General activity timing may be uninformative if the timing of specific behaviors is decoupled from general activity peaks. For example, Ditmer *et al.* [62] found that black bears (*Ursus americanus*) preferred to cross roads in the middle of the night, even though bear activity typically peaks around dawn and dusk [63]. We encourage researchers to prioritize measuring the timing of specific behaviors that might confer fitness-related benefits (e.g., foraging, mate signaling) or costs (e.g., crossing roads) over general activity timing (Figure 4C). Such practice might also increase the relevance of activity-timing research to conservation, because conservation objectives are frequently linked to specific behaviors (e.g., reproduction).

Measuring the timing of specific behaviors may require modification of sampling approaches that researchers commonly employ in activity-timing studies (Figure 2D). For example, pairing location tags with other individual-based sensors (e.g., physiological monitors, video cameras, or accelerometers) may permit researchers to better parse the timing of specific behaviors [50,62,64,65]. Alternatively, researchers working with site-based sensors (e.g., camera traps or trap-timing devices [34]) could catalog specific behaviors if they target locations that anchor focal behaviors (e.g., carcasses to monitor the timing of scavenging [66] or underpasses to monitor the timing of road crossing [67]). Finally, **integrated models** that combine data from individual-based and site-based sensors are an appealing prospect [68,69]. Site-based sensors can sample multiple landscapes without capturing animals and can offer behavioral information beyond simple species detections (e.g., particular vocalization types extracted from acoustic recording units [70]). However, individual animals are typically not distinguishable from site-based sensors [38]. Individual-based sensors confidently distinguish individuals, but it can be difficult to assign biological meaning to the behavioral states estimated by statistical models from location data [71]. Integrated models might leverage the strengths of these two datastreams for exploring the consequences of timescape modification (as well as improving inference on quantities of interest such as animal movement and abundance); individual-based sensors could provide information on the individual and its movement behavior, whereas site-based sensors could provide deeper context on behaviors being performed across multiple landscapes [69,72].

Biogeographic timescape compression hypothesis: effects of novel activity timing vary latitudinally due to biogeographic variation in factors that restrict the optimal time for activity

A biogeographic perspective may facilitate prediction of the regions (and constituent taxa) most likely to show strong ecological effects of human-mediated novel activity timing [73]. The biogeographic timescape compression hypothesis predicts that human-mediated changes in activity timing have the largest effects where biotic and/or abiotic factors already strongly limit the optimal time for activity. In particular, this hypothesis makes two alternative (but not mutually exclusive; Figure 3) predictions of how the ecological effects of novel activity timing might vary by latitude.

First, we may predict that human-mediated changes to activity timing induce larger ecological effects at high latitudes because of activity-timing mismatches arising from photic barriers (in turn caused by **photoperiod** seasonality at high latitudes [74–77]). Consider a scenario in which a marine fish species performs diel vertical migrations, feeding near the ocean's surface at night and moving to deep waters during the day to minimize predation risk [75,78]. If this species shifts poleward to escape thermal stress from climate change, it may be faced with fewer nocturnal hours (or none at sufficiently high latitudes) in which to feed and, as a result, greater predation risk [75,78]. Because photoperiod seasonality increases nonlinearly with latitude [76], a 100-km poleward shift is more likely to expose an organism to photic barriers (i.e., temporal niches to which it is not adapted) at high latitudes than a shift of the same distance in more equatorial regions.

Alternatively, we may predict that human-mediated changes to activity timing induce larger ecological effects at low latitudes, a result arising from biogeographic gradients in species diversity and/or photoperiod seasonality. Hyperdiverse low-latitude communities likely partition time in a more granular fashion than depauperate temperate communities; in other words, there is strong biotic pressure limiting the window of optimal activity. As a result, at low latitudes, activity-timing shifts in response to human disturbance may lead to more mismatches among species (relative to comparable shifts in high-latitude communities; Figure 3). In addition, given that low-latitude regions experience less seasonal variation in photoperiod [1,74], tropical species may be adapted to a narrower range of timescape conditions [79,80]. If this is indeed the case, tropical species may encounter relatively more novel conditions [81] if they shift their activity timing, which might lead to stronger effects than similar shifts at high latitudes. Finally, the two predictions need not be mutually exclusive; it is possible that ecological effects of altered activity timing are strongest at latitudinal extremes and comparatively weak at midlatitudes, creating a U-shaped relationship between latitude and the magnitude of the ecological effects of novel activity timing (Figure 3).

Investigating the biogeographic timescape compression hypothesis would require measuring spatial and temporal variation in daily activity timing and furthermore would benefit from parsing the roles of biotic and abiotic variables in structuring activity timing (Figure 4D). Because biotic [82] and abiotic [9,18,74,76,83] factors that constitute the timescape covary across biogeographic gradients, ascribing the ecological effects of human-mediated activity-timing shifts to either biotic or abiotic influences would benefit from a factorial design in which researchers compare human-mediated activity-timing shifts and their consequences from species-rich and species-poor communities across multiple regions (thus controlling for broad gradients in photoperiod and climate). Studies over elevational gradients might also be valuable, because abiotic and biotic factors vary over short geographic distances, thus controlling for photoperiod [84]. Ultimately, the increasing spatiotemporal extent and resolution of activity-timing studies (Figure 2E–G) – and efforts to link activity timing and other parameters (Figure 4A) – will facilitate such investigations, because future sampling will likely cover larger areas, span multiple seasons, draw upon multiple data types, and capture responses to ephemeral human-mediated disturbances such as recreation or extreme weather.

Beyond a factorial investigation across latitudes, pursuing this hypothesis might also benefit from collating macroscale activity-timing datastreams [73] from monitoring networks [85] or citizen science [86] and relating them to remote sensing datastreams on anthropogenic activities (e.g., artificial light or sound; Figure 4E). Such efforts may be particularly helpful for establishing basic biogeographic patterns of daily activity timing [73], an important step in anticipating regional variation in the ecological effects of novel activity timing. For example, Lang *et al.* [86] used eBird data to discover convergent daily hunting strategies among hawk species across continents, with differences according to prey type. Importantly, existing monitoring programs can retrofit their protocols to collect behavioral data [87] or implement experiments [88,89] to gain a mechanistic understanding of species interactions [90]. Finally, macroscale activity-timing data may facilitate forecasts of animal activity [91]. Many anthropogenic threats (e.g., poaching, light pollution) are not static but rather pulsed (and often predictable) through time [92] and, in some cases, can be monitored with remote sensing. Identifying such threats and quantifying animal exposure to them through time may help pinpoint the best locations and times to target for conservation action [93].

Concluding remarks

Although time has long been recognized as an important component of animal behavior, biologists are increasingly exploring ecological aspects of daily activity patterns [5,14,50] and recognizing that activity timing represents a major behavioral response to multiple forms of global change. Thus, it is important to characterize the novel timescapes of the Anthropocene, predict what taxa alter their activity timing in light of these timescapes [75,78], and explore the ecological effects of such behavioral changes (see Outstanding questions). We offer three hypotheses to contextualize future work, namely that (i) ecological effects of novel activity timing arise via activity mismatches within and between species [14,77], (ii) the duration and timing of timescape modification influence the ecological effects of altered activity timing, and (iii) the effects of activity-timing shifts vary latitudinally due to biogeographic variation in factors that restrict the optimal time for activity [74,78]. Measuring the ecological effects of activity-timing shifts remains a challenge (see Outstanding questions), and we synthesize several considerations for researchers seeking to do so [5,14,50,74]. Finally, looking forward, it will be important to understand how changes to daily activity timing may scale to affect processes operating over longer timescales, such as circannual rhythms of physiology or behavior (Box 1, see Outstanding questions) [74,94]. Such work will be crucial to establish the adaptive value of human-mediated behavioral change and devise timescape-informed conservation strategies.

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Outstanding questions

How do sensory and thermoregulatory traits constrain species' ability to respond to human-induced environmental change via activity timing? For example, primarily diurnal taxa with limited night vision and olfactory abilities (e.g., most birds) may be unable to switch to nocturnal behavior, or endotherms may be less sensitive than ectotherms to changing thermal timescapes.

Do species often exhibit both daily and phenological plasticity? Do plasticity in daily activity timing and phenology interact? Can adjustments to daily activity timing compensate for phenological stressors and vice versa?

How do we integrate and apply findings and approaches from chronobiology (typically a lab-based discipline) to investigations of free-living organisms? That is, what questions can be tackled with lab experiments and what questions must be investigated with field experiments or observations?

What are the best ways to design studies or experiments to differentiate the influences of abiotic versus biotic variables on daily activity timing over broad latitudinal gradients?

If ecological consequences of novel activity timing do indeed vary with latitude, what is the form of the relationship? Would it be linear or, alternatively, nonlinear (e.g., a unimodal relationship in which consequences are strongest at extreme latitudes and weakest at midlatitudes)?

Can shifts in activity timing be used to predict changes in the occurrence and magnitude of ecological interactions?

Do human-modified environments tend to show more synchronous timescapes over broader or finer extents than corresponding 'natural' systems? Might increasingly homogeneous timescapes lead to homogenization of daily activity timing, either across space or across species?

How might the study of changes in daily activity timing inform conservation? Are there certain anthropogenic disturbances that can be managed to reduce timescape loss and fragmentation or avoid mismatches?

Declaration of interests

The authors have no interests to declare.

Supplemental information

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