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REVIEW

Investigating animal activity patterns and temporal niche partitioning using camera-trap data: challenges and opportunities

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Abstract

Time-stamped camera data are increasingly used to study temporal patterns in species and community ecology, including species' activity patterns and niche partitioning. Given the importance of niche partitioning for facilitating coexistence between sympatric species, understanding how emerging environmental stressors – climate and landscape change, biodiversity loss and concomitant changes to community composition – affect temporal niche partitioning is of immediate importance for advancing ecological theory and informing management decisions. A large variety of analytical approaches have been applied to camera-trap data to ask key questions about species activity patterns and temporal overlap among heterospecifics. Despite the many advances for describing and quantifying these temporal patterns, few studies have explicitly tested how interacting biotic and abiotic variables influence species' activity and capacity to segregate along the temporal niche axis. To address this gap, we suggest coordinated distributed experiments to capture sufficient camera-trap data across a range of anthropogenic stressors and community compositions. This will facilitate a standardized approach to assessing the impacts of multiple variables on species' behaviours and interactions. Ultimately, further integration of spatial and temporal analyses of camera-trap data is critical for improving our understanding of how anthropogenic activities and landscape changes are altering competitive interactions and the dynamics of animal communities.

Introduction

Global biodiversity declines are being driven by the direct and indirect effects of anthropogenic disturbances (Cardinale et al. 2012; Hooper et al. 2012). Although these direct effects manifest in obvious ways through habitat loss and wildlife population declines, more subtle are the myriad indirect and cascading effects of human-driven disturbances, including altered species behaviours and interspecific interactions. A better understanding of these indirect impacts is needed to inform effective conservation planning. Recent technological and statistical advances in the application of camera trapping suggest that this emerging methodology may help provide such understanding.

Camera trapping is widely used in ecology and conservation for investigating species' distributions, estimating population densities and inventorying biodiversity (O'Connell et al. 2011; Burton et al. 2015; Steenweg et al. 2017). While camera-trap studies have typically focused on the spatial and numerical aspects of species and population ecology (e.g. Karanth and Nichols 1998; Linkie et al. 2007; Tobler et al. 2008), they have less often examined species' behaviours and interactions and their associated consequences for community structure.

Only recently have researchers focused attention on the finer scaled temporal data provided by time-stamped camera-trap images (e.g. Ridout and Linkie 2009; Rowcliffe et al. 2014), which detail the timing of wildlife occurrences across points in space. While such temporal data present analytical challenges, they are critical for developing a more complete understanding of population and community dynamics in the face of global change.

Temporal camera-trap data offer the opportunity to address unresolved questions regarding species ecology and community interactions, such as variation in activity patterns and partitioning along the temporal niche axis. These temporal insights are not only valuable from an ecological perspective, but they also provide insight into human-driven changes to species behaviours and interactions, and the resulting impacts on niche partitioning and community structure. The increase in camera-trap studies focused on temporal analyses is beginning to generate new ecological and applied insights, but a synthesis of recent approaches and trends is lacking. In this review, we pursue this synthesis through exploring several principal questions and analytical approaches for investigating temporal data collected by wildlife cameras. These questions reflect common themes we observed in the literature, and associated methods for analysing temporal data in the context of species' behaviour and interactions. Based on an *ad hoc* review, we provide a synthetic overview of frequently cited and more recent papers, building on notable past reviews (Bridges and Noss 2011) by adding more recent advances in approaches and thought. We review the theoretical basis for activity patterns and temporal niche partitioning, summarize current approaches, assess current limitations to more complete analyses and highlight significant advances in gaining a fuller understanding of species and community ecology. Ultimately, species' interactions and community dynamics can only be fully resolved by combining spatial and temporal data, therefore we also discuss new directions where combined spatiotemporal aspects of species niche partitioning and responses to environmental stimuli can be explored.

Exploring Time as a Niche Axis

Temporal dynamics are integral to niche theory (Hutchinson 1957, 1959; MacArthur and Levins 1967), including species autecology and community assembly, diel activity patterns and temporal niche partitioning among sympatric heterospecifics. Animal activity – quantifying how species distribute their activity over the day – is an important dimension of animal behaviour; how species use time as a resource provides valuable information about their ecological niche (Schoener 1974). Extending to the community level, understanding how sympatric species partition time provides insight into the mechanisms facilitating stable coexistence (Carothers and Jaksić 1984; Kronfeld-Schor and Dayan 2003). Numerous studies employing camera-trap data have observed temporal niche partitioning as an important strategy for enabling the coexistence of ecologically similar species (e.g. Di Bitetti et al. 2010; Monterroso et al. 2014; Sunarto et al. 2015).

As diel activities are adapted to local conditions (Halle 2000), the influence of abiotic and biotic variables on activity patterns and temporal niche partitioning is a primary question for both ecological research and biodiversity conservation. Already there is mounting evidence from camera-trap studies that human-driven landscape and community impacts – including land-use change (Ramesh and Downs 2013), human activity (Wang et al. 2015; Ngoprasert et al. 2017), hunting (Di Bitetti et al. 2008), predator control (Brook et al. 2012) and presence of invasive competitors or predators (Gerber et al. 2012; Zapata-Ríos and Branch 2016) – may alter species' activity patterns and competitive or predatory interactions through altered temporal niche partitioning. Therefore, effective conservation decisions must also consider how environmental stressors and shifts in community composition may impact sympatric species' ability to segregate not just spatially, but also temporally.

The circular distribution of temporal data comes with its own set of analytical challenges, and very large sample sizes are required to explore fine-scale temporal responses across spatial gradients. Recent statistical and software developments have made important strides in tackling the challenges of temporal camera-trap data analysis (e.g. Ridout and Linkie 2009; Oliveira-Santos et al. 2013), thereby facilitating characterization of activity patterns and temporal niche overlap. Nevertheless, modelling the degree to which external variables (habitat characteristics, community structure, disturbance variables, etc.) cumulatively influence species' activity patterns and temporal niche partitioning continues to present considerable challenges. To date, few researchers have attempted such multivariate analyses with temporal data (e.g. Norris et al. 2010; Wang et al. 2015). Even more challenging is combining both spatial and temporal species' distributions to gain a fuller resolution of the underlying dynamics structuring interspecific interactions and community-level responses. Tackling this challenge starts with analysing the activity patterns of single species, and builds iteratively towards more complex multispecies and multivariable models.

Current Approaches to the Analysis of Activity Patterns

Activity data reflect an important dimension of animal behaviour and ecology, as they provide relevant information on species' natural history and ecological niche. Temporal data extracted from time-stamped wildlife images have provided some of the first analyses of diel (or circadian) activity of populations and species (e.g. Gerber et al. 2012; Bu et al. 2016).

Early camera-trap studies derived descriptive inferences from tabulated records or graphical displays of activity over discrete time periods of the diel cycle (e.g. van Schaik and Griffiths 1996; Lizcano and Cavelier 2000; Jácomo et al. 2004). This allowed assignment of taxa to general behavioural groups (e.g. diurnal, nocturnal) and better describe the temporal aspects of species' ecological niches. More recently, graphical displays of diel activity patterns use nonparametric kernel density estimates (e.g. Ridout and Linkie 2009; Linkie and Ridout 2011; Farris et al. 2015) to view species' activity as a continuous distribution over the wrapped 24-h cycle. Kernel density functions yield a continuous measure of the density of data points across their scale (Worton 1989), treating the estimates as a random sample from an underlying continuous distribution instead of grouping them into discrete time categories. Meredith and Ridout's (2014) R package 'Overlap' produces kernel density curves of species activity patterns from camera-trap data, with a similar function offered by the R package 'Circular' (Agostinelli and Lund 2013). Such graphical displays of activity patterns reflect aspects of temporal variability in species activity over the diel cycle, including basic behavioural categorizations (e.g. diurnality vs. nocturnality) and periods of peak activity. This approach dramatically improved the level of insight gained without any further investment in data acquisition, and thus represents significantly improved return on investment of camera-trap arrays.

Quantitatively investigating activity patterns comes with various challenges. Time is a wrapped distribution with an arbitrary zero point, thus classical statistical methods cannot be applied (Zar 2010). To solve this, circular statistics use trigonometric functions to derive descriptive statistics of temporal data, including mean time of activity (the mean vector), circular median, standard deviation and variance, as well as other dispersal estimates such as concentration (Batschelet 1981). Various software packages offer functions for deriving the statistical parameters on circular data, including ORIANA (Kovach 2011) and the R packages 'CircStats' (Lund and Agostinelli 2007) and 'Circular' (Agostinelli and Lund 2013). However, multimodal distributions indicating multiple peaks of activity (e.g. a crepuscular species showing activity peaks at dawn and dusk) do not yield intuitive statistical estimates of centrality (Batschelet 1981). As bimodal activity patterns are widespread (Aschoff 1966), the derived mean vector may fall between the two activity modes. Although studies have reported the mean vector to quantify species' mean activity time (e.g. Di Bitetti et al. 2010; Norris et al. 2010; Ramesh et al. 2012), this should be done with great caution to ensure the derived mean vector reflects a biologically accurate and meaningful value.

Oliveira-Santos et al. (2013) proposed conditional circular kernel density functions to characterize 'activity range' and 'activity core' from time of detection camera data. Following an approach similar to telemetry-based home range contours, they created density functions yielding 95% isopleths representing the time interval in which 95% of the animal activity occurs – an ecologically relevant activity range that eliminates outlying periods of activity produced by the statistical smoothing process. More conservatively, the 50% isopleths can be used to determine during which time interval(s) core activity is focused. This approach allows for a more quantitative analysis of temporal data, delimiting hours of peak activity to characterize specific aspects of species' circadian activities. Rowcliffe et al. (2014) also applied kernel density functions to camera data in developing an analysis to quantify the overall proportion of time that an animal spends active (i.e. activity level). The R package 'activity' (Rowcliffe 2016) fits circular distributions to temporal camera-trap data to create activity schedules and calculate species' activity level, thereby facilitating inquiry into animal energetics, predation risk and foraging effort, although key assumptions for deriving this metric may not be met in certain populations (Rowcliffe et al. 2014).

Species' activity patterns may also be characterized according to selection for certain time periods by discretizing the 24-h diel cycle into categories such as dawn, day, dusk and night. Chi-square tests determine if species' activity patterns are non-random (e.g. Bu et al. 2016). Resource selection functions (Manly et al. 2002) have also been used to determine how species distribute activity over various time periods given their availability (e.g. Gerber et al. 2012; Bu et al. 2016), which provides an approach to ascribing behavioural categorizations to species' activity patterns (e.g. diurnal, nocturnal or crepuscular). Species can also be assigned into such categorizations using niche selectivity indices, such as Ivlev's Electivity Index (Ivlev 1961) or its derived Jacobs Selectivity Index (Jacobs 1974). Using a novel approach to investigating how species selectively use different time periods, Farris et al. (2015) used hierarchical Bayesian Poisson analysis by modelling photographic rate (capture events/available hours) for each time category.

Camera-trap studies using such descriptive and quantitative approaches have produced considerable insight into the activity patterns of a wide range of species from diverse systems. These have included carnivore guilds (Di Bitetti et al. 2010; Monterroso et al. 2014), ungulates (Ferreguetti et al. 2015), rodents (Meek et al. 2012), primates (Gerber et al. 2012), birds (Srbek-Araujo et al. 2012) and various other mammals (Oliveira-Santos et al. 2008; Galetti et al. 2015). Interestingly, some conclusions from camera-trap research on species activity patterns have challenged previous conclusions regarding species-specific temporal activity (Bischof et al. 2014), which may arise from past sampling constraints that did not allow non-invasive, 24-h sampling. However, we are aware of no studies that have directly compared animal activity patterns generated via camera-trap data with more complete descriptions of activity derived from high-frequency GPS telemetry relocations. It is possible that activity data collected by camera traps may contain biases related to temporal variability of detectability caused by temperature, humidity or other factors suppressing detectability, but these remain untested to the best of our knowledge.

Despite the potential limitations of sampling species' activity patterns using camera-trap data, many emerging advances in documenting these patterns have been developed. The logical first step is comparing these activity patterns among sympatric species to ask how species divide the temporal niche axis.

Analyses of Temporal Niche Partitioning

Perhaps the ecologically most interesting question asked of species activity data is how sympatric species partition their activities to promote stable coexistence. MacArthur and Levins' (1967) limiting similarity theory predicts that no two species can coexist in time and space; thus, sympatry demands species divide their resources to avoid extinction by competition (Fig. 1). Time can be considered as a resource as it is 'consumed' analogously to other resources with limited availability (Halle 2000). Although not previously emphasized as an important mechanism for reducing competition, partitioning time of activity may be one of the most relevant strategies for the coexistence of species (Schoener 1974). Understanding how ecologically similar species coexist is not just a key question in ecology, but also crucial for understanding community diversity.

Early investigations of temporal niche partitioning relied on qualitative analyses of histograms. Researchers later began using linear frequency statistical procedures with the 24-h cycle categorized in contingency tables (Jácomo et al. 2004; Lucherini et al. 2009; Gerber et al. 2012). Measures of niche similarity and overlap – such as Renkonen's similarity index and Pianka's measure of niche overlap (Krebs 1998) – evaluate differential use and partitioning of time as a resource (e.g. Lucherini et al. 2009; Hofmann et al. 2016), although these require discretization of data into arbitrary bin sizes.

Software packages which fit nonparametric circular density functions to camera-trap data allow researchers to analyse activity through a circular inferential statistical approach. A descriptive measure of the degree of similarity between two kernel density curves can be calculated following Ridout and Linkie's (2009) innovative coefficient of overlap, which fits camera-trap data to a kernel density function and then estimates a symmetrical overlapping coefficient between species using a total variation distance function (Fig. 2). This coefficient of overlap (Δ), whose precision can be estimated via bootstrapping and ranges from 0 (*no overlap*) to 1 (*complete overlap*), has often been used to investigate potential competitive and interaction possibilities between species (e.g. Linkie and Ridout 2011; Farris et al. 2015; Cusack et al. 2017). As Δ is a relative measure, interspecific differences in activity patterns may also be tested for statistical significance. The nonparametric circular Mardia–Watson–Wheeler (MWW) statistical test (Batschelet 1981) and Watson U^2 test (Zar 2010) have both been used to determine if two or more circular distributions vary significantly. Meredith and Ridout's (2014) 'Overlap' package remains a popular tool for presenting the overlap of two activity curves visually and estimating Δ, despite the biases introduced by the smoothing process when applying kernel density functions to temporal data and deriving an estimation of Δ (as discussed by Ridout and Linkie 2009).

Exploring temporal niche partitioning with camera traps has highlighted the prevalence and importance of segregation along the temporal axis for enabling coexistence within diverse assemblages of sympatric species. For example, Bischof et al. (2014) concluded that the elusive Altai mountain weasel *Mustela altaica* compensates for spatial overlap with intraguild predators by adopting an inverse activity pattern to its sympatric dominant predators while still maintaining spatial access to prey. Ferreguetti et al. (2015) concluded that two sympatric deer species may mitigate competition for similar space and food resources through differences in their activity patterns. Di Bitetti et al.'s (2010) analysis of Neotropical felid species activity patterns observed diurnal, nocturnal and cathemeral behaviours among species. Morphologically similar species had the most contrasting activity patterns, suggesting that the ability of species to segregate temporal activities may explain the lack of

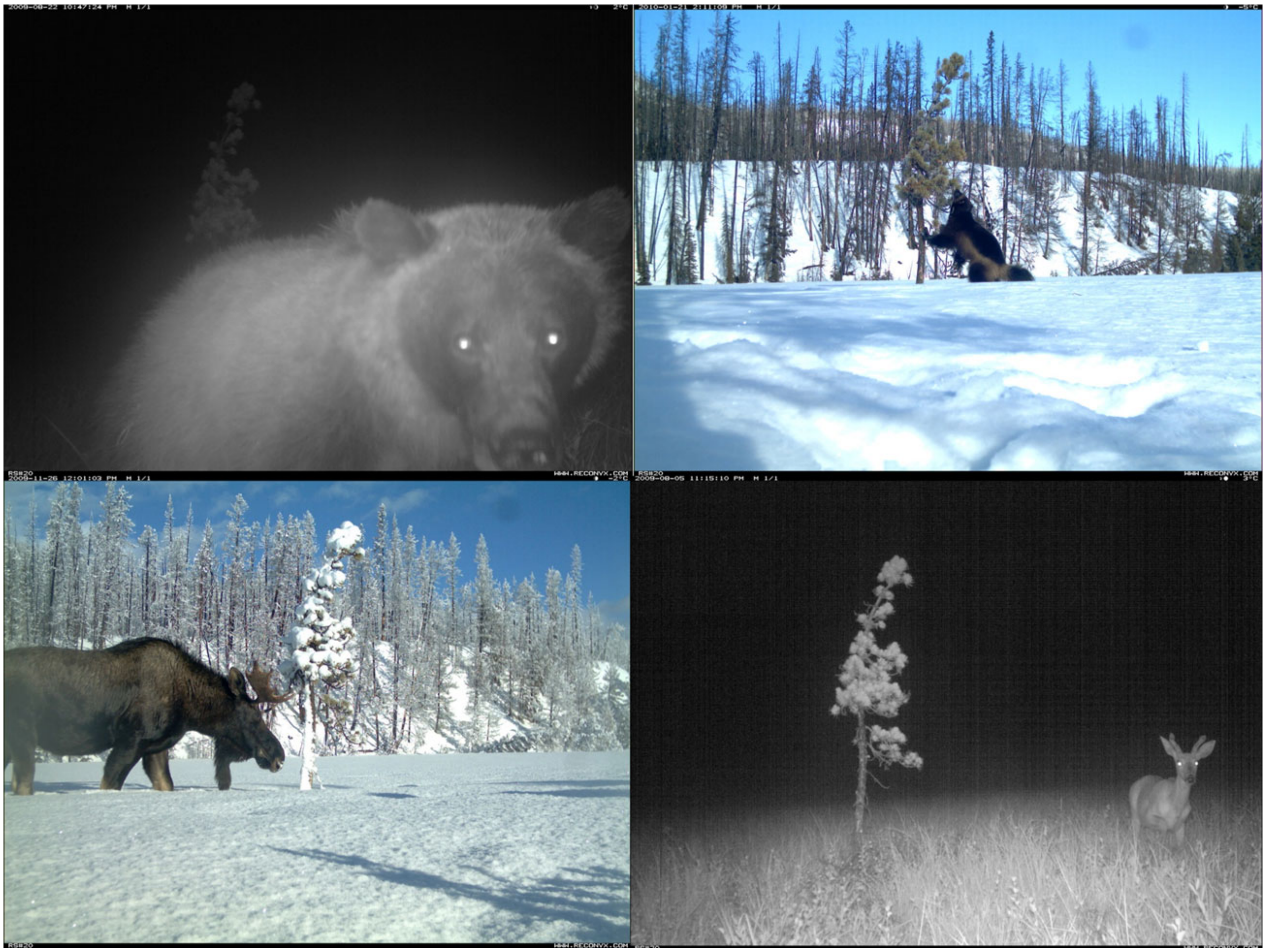

Figure 1. Sympatric species must partition time or space to co-exist. These four species (clockwise: grizzly bear *Ursus arctos*, wolverine *Gulo gulo*, mule deer *Odocoileus hemionus*, moose *Alces alces*) were detected at the same camera-trap location. Spatiotemporal partitioning reduces competition and the potential for agonistic encounters.

character displacement seen in certain assemblages (Di Bitetti et al. 2010). Similarly, Sunarto et al. (2015) observed that within a tropical community of felids, those species with the most similar body size or with similarly sized prey had the lowest temporal overlap. Monterroso et al. (2014) observed a negative correlation between mean pairwise temporal overlap and species richness (number of species with at least 10 detections) across a mesocarnivore community. They suggest that temporal niche partitioning may be influenced by community diversity and likely plays an important role in facilitating stable coexistence in mesocarnivore guilds showing high diversity.

With statistical techniques to quantify temporal niche partitioning using camera data quickly developing, it is increasingly possible to ask questions about the factors that affect partitioning, including anthropogenic pressures induced by landscape and climate change.

Investigating Changes to Species Activity Patterns and Niche Partitioning

Animal activity patterns evolve via processes of natural selection (Kronfeld-Schor and Dayan 2003), such as historic co-evolutionary competitive interactions (‘the ghost of competition past’, Connell 1980), but behavioural plasticity may allow flexible changes to activity patterns in response to environmental stimuli (Halle 2000). Environmental cues such as predation risk, resource availability and the potential for agonistic encounters with dominant competitors influence behavioural decisions that alter a species’ activity (Halle 2000). Activity during suboptimal times of higher predation risk, increased energy demand or lower prey availability may incur fitness costs. Comparing activity patterns in response to external stimuli provides insight into the degree of plasticity in species

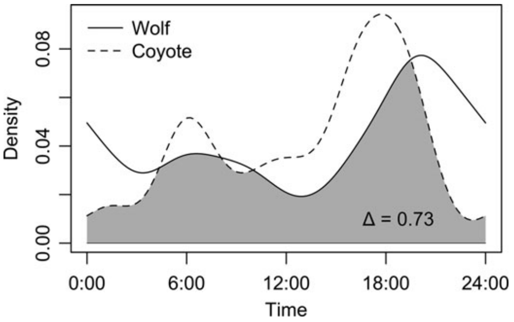

Figure 2. An example of the characterization of diel activity patterns from camera-trap data. Kernel density functions were used to depict grey wolf *Canis lupus* and coyote *Canis latrans* activity sampled via camera trapping during October–March 2006 to 2008, in the Willmore Wilderness Area, Alberta, Canada. The overlap coefficient (Δ) is the area under the minimum of the two density estimates (denoted in grey).

activity schedules and into the extent to which various environmental factors may alter an animal's activity pattern.

Changes to species' activity patterns may lead to altered temporal niche partitioning between species, with potential repercussions to species interactions such as intraguild competition and predator–prey dynamics. Indirect effects of anthropogenic stressors such as climate and landscape change could increase temporal overlap between species, augmenting interspecific conflict and exploitation of prey, or conversely, releasing species from predation or competitive pressure with reduced overlap. However, very few studies have empirically quantified how external factors may influence temporal niche partitioning (but see Wang et al. 2015).

Investigations of altered activity patterns, as with simpler investigations of animal activity, have typically involved descriptive comparisons of activity distributions from graphical displays, but also paired with simple statistical tests to determine whether two or more circular distributions differ significantly. Largely, these data have come from time-stamped wildlife images collected via camera trapping (but see Suselbeek et al. 2014). Generally, authors have divided the camera-trap data into two or three treatment groups based on abiotic or biotic factors such as season, lunar phase, presence/absence of predators or competitors, human activity or landscape change. Significant differences between activity times may be quantified statistically through a chi-squared contingency table of frequency of photographic records (e.g. Jácomo et al. 2004), but again this requires categorization of the temporal data into discrete time bins. The aforementioned MWW and Watson U^2 tests have also both been used to determine if activity distributions between populations vary significantly. For example, Di Bitetti et al. (2009) observed that pampas foxes *Lycalopex gymnocercus* showed significantly different activity patterns in areas where the competitively dominant crab-eating fox occurred. Likewise, statistical comparisons of activity records between two colour morphs of oncilla *Leopardus tigrinus* revealed significant intraspecific differences in diel activity patterns (Graipel et al. 2014).

Intraspecific comparisons between study systems or treatment groups have also been performed using Ridout and Linkie's Δ (e.g. Monterroso et al. 2014; Wang et al. 2015). For example, Monterroso et al. (2014) observed a considerable degree of plasticity in European mesocarnivore nocturnal activity times between seasons and sites based on mean Δ values. By overlaying intraspecific activity curves of predators experiencing high versus low levels of human disturbance, Wang et al. (2015) demonstrated the timing and direction of activity shifts between two treatment groups. Activity overlap may also be quantified at conditional isopleths to determine whether overlap is more concentrated in the activity cores of the species (Oliveira-Santos et al. 2013). Rheingantz et al. (2016) observed very low activity overlap at 95% and 50% conditional isopleths between the two studied otter populations (45.6% and 14.1% respectively), suggesting a high level of plasticity in activity patterns; this was hypothesized to be a product of human activity or shifts in prey availability.

To date, the majority of studies evaluating the impact of external variables on species activity patterns have analysed the effect of a single variable at a time. Comparative tests do not allow for modelling multiple explanatory variables, potentially missing cumulative effects of multiple stressors, and interaction terms. Moreover, differences arising between treatment groups may potentially manifest in response to confounding (or collinear) variables. Alternative options include angular–linear correlations, as done by Hofmann et al. (2016) in comparing peccary activity time in relation to air temperature. Using an information-theoretic analysis of species activity, Norris et al. (2010) used linear mixed effects models to evaluate how abiotic conditions and human disturbance influenced activity pattern of three Amazonian terrestrial mammals. They observed that the time since isolation of forest patches had the strongest influence on agouti activity timing (Norris et al. 2010). However, care should be taken to ensure that the linear (as opposed to circular) scale used to define activity patterns upholds biological relevance; as mentioned, there is little biological difference but marked statistical difference between 2355 h and 0005 h on the linear scale.

A simple test for evaluating the impact of abiotic or biotic variables on temporal niche partitioning between sympatric species could involve directly comparing the bootstrapped mean overlap coefficient and 95% confidence intervals between species pairs across two or more treatment groups. Despite the relative simplicity and potential insights that could be gained from such a comparison, we are aware of no studies that have examined this direct comparison of interspecific temporal overlap across experimental treatments.

One noteworthy study by Wang et al. (2015) evaluated the influence of external variables on temporal niche partitioning in areas of ex-urban development near the Santa Cruz Mountains of California. Using an information-theoretic approach, these authors modelled Δ between mesocarnivore species pairs as a response to landscape development, human activity and forest cover. Wang et al.'s (2015) approach represents one of the few studies that simultaneously models the effect of multiple variables on species' activities and partitioning along the temporal axis. However, such fine-scale inferential analysis requires large amounts of data and a robust sampling design for capturing the effect of multiple explanatory variables across a spatial gradient. Many studies of species activity patterns and temporal niche partitioning are performed as secondary investigations, repurposing camera-trap data collected primarily for analysing spatial patterns or other responses (e.g. Di Bitetti et al. 2006; Sunarto et al. 2015; Ikeda et al. 2016). For all the reasons detailed above, spatially focused study designs with sample sizes only sufficient to confidently yield spatial and numerical responses may not be adequate to extend insight to complex and fine-scale investigation of species' activity patterns and temporal niche partitioning.

In summary, scientists have only begun to delve into discovering how animals spend their days, how species divide up time among them and how our marked impacts on landscapes, climates and biotic communities change these temporal processes. Moreover, although it is tacitly understood that space and time are inextricably linked, their integration in this context remains to be explored.

Future Directions: Analysing Spatiotemporal Species Interactions

With an increasing number of statistical approaches, and emerging studies of species behaviours and partitioning along both the spatial and temporal niche dimensions, our understanding of species interactions across time and space is mounting. However, this subfield is still relatively young, and most studies use opportunistic, not purpose-designed, data. There are many interacting ecological processes and cumulative effects of anthropogenic impacts yet to disentangle. This is a key future area of research, as the indirect effects of environmental stressors on species activity and interactions may be as important as the direct effects (Strauss 1991; Schoener 1993; Abrams 1995).

The opportunity to parse the relative influences of space and time in species sympatric coexistence is an intriguing prospect. The competitive interactions shaping community structure likely manifest as both spatial and temporal patterns, but few studies to date have directly assessed such spatiotemporal interactions (but see Lewis et al. 2015; Swanson et al. 2016; Cusack et al. 2017; Karanth et al. 2017). Based on a comparison of approaches, Cusack et al. (2017) suggested that approaches using the combined spatial and temporal data generated by camera traps yield better insight into the associative patterns between sympatric species.

A second key opportunity is in using environmental stressors as 'treatments' in large-scale experiments designed specifically to understand the factors affecting species activity and interactions. Very little is known about how natural and anthropogenic changes to landscapes and biotic communities influence competitive interactions in animal populations. As it stands, it is difficult to predict how climate change, landscape change and anthropogenic changes to community composition may impact the competitive interactions and behavioural adaptations integral to maintaining biodiversity and ecosystem stability. Altered spatiotemporal interactions between sympatric species in communities could have rippling effects throughout the entire ecosystem (Crooks and Soulé 1999). With anthropogenic landscape changes projected to continue globally (Theobald 2005; Seto et al. 2011; Maxwell et al. 2016), focusing research efforts on understanding species spatiotemporal responses to those impacts is vital to sound conservation and management decisions. However, these questions are exceedingly difficult to answer within a single landscape.

Camera-trap surveys are invaluable for tracking direct effects of anthropogenic change on species distributions and abundances. However, the indirect effects of human influence, mediated by interactions among species in shifting communities, reside at the frontier of our knowledge of wildlife responses in the Anthropocene. With the growth of camera-trap networks deployed across multiple landscapes (Ahumada et al. 2013; Burton et al. 2015; McShea et al. 2016), hopefully growing into a global biodiversity network (Steenweg et al. 2017), network nodes deployed as coordinated distributed experiments (*sensu* Fraser et al. 2013) may help tease apart the effects of landscape and climate change on species interactions in complex environments. This research coordination and accompanying sampling designs remain the greatest opportunity for this emerging field of research. Fully capitalizing on the multi-scale spatial and temporal data produced by these networks may represent one of our best chances of advancing our ecological discoveries and meeting the pressing demands of biodiversity conservation.

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