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Abstract

Studies of elusive carnivores often rely on passive sampling when investigating either spatial or temporal interactions. However, inference on behavioral mechanisms are usually lacking. We present an analysis that combines previously published spatial co-occurrence estimates and temporal kernel density estimates to explore spatiotemporal interspecific interactions. We do so by deriving a spatiotemporal value (STV) that is a relative measure of potential interaction in both niche dimensions, across a gradient of degradation, for rainforest carnivore pairs in Madagascar. We also use a conceptual framework to provide insight into the potential behavioral mechanisms of habitat selection. Of the six native and three invasive carnivores, we estimate the spatiotemporal interactions for twelve pairings, which range from no spatial/temporal relationship (n = 5) to spatiotemporal aggregation or segregation (n = 7). We visualized these spatiotemporal interactions along a fragmentation gradient and demonstrate that these interactions are not static, as STV overlap increases with increasing anthropogenic disturbance. Of the three invasive carnivores (free-ranging dogs *Canis familiaris,* cats *Felis species,* and small Indian civets *Viverricula indica*) the latter had the highest number of spatial occurrence (n = 4) and spatiotemporal overlap (n = 4) relationships with native carnivores. Our results highlight the potential for increasing direct and indirect interactions between native and invasive species as forest degradation and invasive predators increase. Our approach allows us to better understand adaptive behaviors, plasticity in temporal activity, community assemblage, and to develop targeted conservation strategies to manage ecological communities in rapidly changing ecosystems.

Keywords

Non-native species, Madagascar, niche dynamics, occupancy, spatial modelling, temporal activity

Introduction

Interspecific interactions are important drivers of population and community dynamics (Hardin 1960; Rosenzweig 1966). Studies of interspecific interactions investigate how species co-occur or avoid each other spatially and/or temporally and, as a result, provide insight into behaviors that contribute to species' survival and reproductive success (i.e., adaptive behavior). Including extrinsic factors (e.g., habitat, landscape, anthropogenic disturbance) into these investigations broadens our understanding of how realized niche dynamics might change across variable environments and result in variable community assemblages. Improving our understanding of interspecific interactions across both space and time is important if we are to develop effective management strategies for wildlife populations and communities, especially as new challenges emerge, resulting from altered landscapes and a changing climate (Rands et al. 2010).

For rare and elusive species, such as carnivores, investigations of interspecific interactions can be challenging and are often lacking for many communities globally (Brooke et al. 2014; Thompson 2013). As a result, attempts to investigate interactions among co-occurring carnivores often include only a spatial or temporal component. Investigations of carnivore communities have revealed that carnivores alter their spatial distribution (Durant 1998; Farris et al. 2015c; Hersteinsson, Macdonald 1992; Linnell, Strand 2000; Mills, Gorman 1997; Mitchell, Banks 2005; Rich et al. 2017; Vanak et al. 2013b) or their daily activity patterns (Farris et al. 2015a; Kitchen et al. 1999; Major, Sherburne 1987; Palomares, Caro 1999; Wang et al. 2015; Wilson et al. 2010) due to interspecific interactions. Investigations of interspecific interactions that combine spatial and temporal analyses simultaneously, however, are exceedingly rare for elusive carnivores (Karanth et al. 2017; Li et al. 2019; Moll et al. 2018; Niedballa et al. 2019; Smith et al. 2019). Yet, such studies may provide heightened insight on the ultimate causes driving co-occurrence of species' populations within communities, since investigations utilizing one dimension alone (spatial or temporal) may fail to elucidate how species alter both spatial and temporal use simultaneously to promote or discourage potential interactions. Additionally, studies combining spatiotemporal components in a carnivore community consisting of native, co-occurring members and non-native, invading species, are particularly important to our understanding of community dynamics and for developing targeted action plans to manage biodiversity conservation.

Invasive species, particularly non-native carnivores, have had adverse effects on biodiversity worldwide (Bonnaud et al. 2011; Loss et al. 2013; Nogales et al. 2013; Weston, Stankowich 2013; Young et al. 2011). Research on interspecific interactions between native and invasive carnivores are limited. However, studying spatial and temporal plasticity of native carnivores in the face of new, unique competitors (i.e., non-native predators) is needed to understand if/how coexistence occurs post invasion. Similarly, investigating adaptive behaviors of native species during these invasion events will provide insight on how fitness may change as resources diminish. Free-ranging dogs and cats are the most ubiquitous introduced, non-native carnivores world-wide (Gompper 2013). Native carnivores are negatively affected by both free-ranging dogs and cats as a result of competition (Vanak et al. 2013a; Vanak, Gompper 2009, 2010; Young et al. 2011), direct aggression and intraguild predation (Hughes, Macdonald 2013; Ralls, White 1995; Young et al. 2011), reduction of prey biomass (Frank et al. 2014; Loss et al. 2013; Wierzbowska et al. 2016), altering of temporal activity and/or spatial distribution (Farris et al. 2015a; Farris et al. 2015c; Gerber et al. 2012a; Hernandez-Santin et al. 2016), and the introduction of diseases and/or pathogens (Knobel et al. 2013; Rasambainarivo et al. 2017). As invasive carnivore populations increase globally, their interactions with native carnivores must be assessed. To better examine these interactions, we require a synthetic framework that incorporates both spatial and temporal scales, and includes landscape and/or habitat variables that may mediate such interspecific spatiotemporal interactions.

Considering patterns across only one niche axis between species', such as temporal use independent of the spatial (or vice-versa), can potentially lead to erroneous conclusions of species interactions. For example, one might conclude that a subordinate species has been temporally displaced due to low temporal overlap, when in actuality the two species do not demonstrate any spatial overlap because they use different local habitats. While there are numerous spatiotemporal modelling approaches (see Cressie, Wikle 2015), few can accommodate typically sparse datasets that are common in carnivore studies. Attempts to model and evaluate spatiotemporal interactions between co-occurring carnivores and carnivore-prey pairings includes investigation via linear models and frequentist statistics (Niedballa et al. 2019), analyses based on radio-tagged animals and step selection functions (Vanak et al. 2013b), as well as analyses combing temporal activity patterns and occupancy modelling (Karanth et al. 2017; Smith et al. 2019). While many of these approaches were designed for non-invasive sampling of carnivore populations, few (if any) provide a combined spatio-temporal interaction estimate that is also allowed to vary across changing landscape and/or habitat variables. Including both spatial and temporal scales simultaneously and investigating how these interactions vary across a landscape provides greater insight into processes that drive competition between native species and between native and invading exotics (Schliep et al. 2018). This is increasingly important as we consider anthropogenic and invasive species effects on native carnivores' spatial habitat use and temporal activity patterns. However, this approach could be applied to other data-poor taxa beyond carnivores.

We are specifically interested in understanding the patterns and drivers of spatiotemporal occurrence and avoidance within a native-invasive carnivore community. We hypothesize that native carnivores will demonstrate spatial segregation (avoidance) with invasive predators, particularly when temporal overlap occurs and that spatiotemporal avoidance will be highest in disturbed and/or anthropogenic landscapes.

Methods

Study site

From 2008 to 2013 we photographically surveyed, via remote cameras, the carnivore community at seven study sites across the Masoala National Park (240,000 ha) and Makira Natural Park (372,470 ha of protected area and 351,037 ha of community management zone) protected area landscape of northern Madagascar. The seven sites varied in levels of degradation and fragmentation, ranging from contiguous, primary rainforest to highly degraded forest patches located approximately five km from the nearest contiguous forest. The Masoala-Makira landscape supports six native species of carnivores, all members of family Eupleridae: fosa (*Cryptoprocta ferox*), falanouc (*Eupleres goudotii*), spotted fanaloka (*Fossa fossana*), ring-tailed vontsira (*Galidia elegans*), broad-striped vontsira (*Galidictis fasciata*), and brown-tailed vontsira (*Salanoia concolor*) (Farris et al. 2015b). Additionally, three invasive carnivores have been documented across the Masoala-Makira landscape: free-ranging dogs (*Canis familiaris*), cats (*Felis sp.*), and small Indian civets (*Viverricula indica*) (Farris et al. 2015c). Not only is the behavioral ecology of these species poorly known (Brooke et al. 2014; Goodman 2012), there is growing evidence from previous work that invasive carnivores adversely affect native and endemic carnivores (Farris et al. 2015a; Farris et al. 2017a; Farris et al. 2017b; Farris et al. 2015c; Gerber et al. 2012b; Rasambainarivo et al. 2018; Rasambainarivo et al. 2017). For details on each native and local carnivore body size, diet, IUCN classification, activity pattern, and habitat preference see Table 1 in Farris et al. (2015a). Local bushmeat hunting of all nine carnivore species exists across this region and within the seven survey sites (Farris et al. 2015b; Golden 2009).

Photographic sampling

We established a camera grid at each of the seven sites, consisting of 20-25 camera stations spaced at approximately 500 m between stations (based on the estimated home range of five of the six native carnivore species, excluding the wide-ranging fosa). Each camera grid was operational for an average of 63.4 days (± 2.4 SE) and we moved the 20-25 camera stations to a new grid. We did not establish and survey at multiple camera grids simultaneously. Each camera station consisted of two cameras placed on opposing sides of human (> 0.5 m in width) or animal (< 0.5 m in width) trails to capture both flanks of passing wildlife. We used both film (DeerCam DC300) and digital (Reconyx PC85 & HC500, Wisconsin, USA, Moultrie D50 & D55, Alabama, USA, Cuddeback IR, Wisconsin, USA) cameras that we set to high sensitivity, three photos per trigger (when available, not all cameras had this option), 0 to 30 second time delay between triggers, and placed 20-30 cm off the ground. We did not use bait or lure at any camera station and we checked cameras every 5-10 days to change memory cards and ensure proper functioning. We photographically sampled each site an average (± SD) of 67 ± 8 days (Farris 2014).

Habitat sampling and landscape metrics

We sampled habitat around each camera station at all seven sites across the landscape. At each camera station we walked a 50 m transect in three directions (0, 120, and 240 degrees; Davis et al. 2011) and sampled canopy height and percent cover at 10 m intervals along each transect (totalling five samples per transect and 15 per camera station; Online Resource 1). We used the point-quarter method (Pollard 1971) to estimate tree density and basal area at 25 m and 50 m intervals along each transect. We estimated understory cover at 20 m and 40 m intervals along each transect by establishing a 20 m transect running perpendicular to the 50 m transect. We measured cover at three levels (0–0.50 m, 0.5–1.0 m, and 1.0–2.0 m) by holding a 2 m pole at 1 m intervals along the transect and recording presence (1) or absence (0) of vegetation (Farris 2014).

We measured landscape features at each of the seven sites using Landsat satellite imagery from 2004, 2006, and 2009 (WGS 84 datum, pixel size 29 m x 29 m) to classify land cover types (rainforest, degraded forest, and matrix or non-forest) in Erdas Imagine (Intergraph Corporation, Madison, AL, USA). For analysis in the program FragStats (McGarigal et al. 2012), we placed a 500 m buffer around individual camera stations (based on estimated home range of native carnivores using ranging data and body size from camera traps) and clipped the classified imagery for each of the resulting seven camera grid buffers (each providing an approximately 10–15 km^2 area). We calculated the following landscape metrics from FragStats: 1) number of habitat patches: total number of rainforest, degraded forest, and matrix patches (based on habitat classifications from satellite imagery) within the buffer, where a patch is an area of habitat type separated from similar habitat by ≥50 m, 2) largest patch index: the percentage of total buffered area comprised by the largest rainforest patch, 3) landscape shape index (LSI) or the standardized measure of total edge adjusted for the size of the buffered area (McGarigal et al. 2012), 4) percent rainforest within the buffered area, 5) percent matrix or non-forest, cultivated area within the buffered area, 6) total rainforest core area: the sum of the core areas (accounting for edge of depth of 500 m) of each rainforest patch within the buffer, and 7) total edge (in m/ha) (McGarigal et al. 2012). Finally, we calculated the distance of each camera station to the nearest forest edge (Dist. to Edge) and to the nearest village (Dist to Village, Farris 2014). Previous research on Madagascar's carnivores (Gerber et al. 2010; Gerber 2011; Gerber et al. 2012b; Goodman 2012; Hawkins 1998; Hawkins, Racey 2005) explored how landscape and habitat variables influence native carnivore spatial distribution. However, we still lack an understanding of exactly which habitat and landscape variables best explain space use for each individual carnivore species (both native and invasive), including how anthropogenic changes to these landscapes affect native carnivore spatial distribution. For spatiotemporal analyses, we included this wide range of variables to better understand which factor(s) explains the space use of each individual carnivore and whether these native-invasive interactions might be habitat- or behaviorally-mediated effects.

Spatial co-occurrence analysis

In a previous analysis (Farris et al. 2015c), we examined spatial co-occurrence between native and invasive carnivores across the landscape with two-species, single-season occupancy using the conditional probability parameterization (psiBa parameterization, Richmond et al. 2010) and included habitat and landscape covariates. We used the same data set described in the methods here (sampled seven sites, each using 20-25 camera stations from 2008-2013). We used Akaike Information Criterion [corrected for small sample sizes (AICc)] for model selection (Burnham, Anderson 2002) and reported all top-ranking models (ΔAICc < 2.0). This conditional modelling approach accounts for imperfect detection (MacKenzie et al. 2004) and estimates the probability of occurrence for the native (N) carnivore when the invasive (I) carnivore is present (psiNI) and when the invasive is absent (psiNi, Farris et al. 2015c). This approach requires designation of a dominant and subordinate species and in this study, we designated native carnivores to be the subordinate to invasive species. While it is possible for a subordinate species to influence an invasive species' spatial and temporal activity, thus influencing exploitative competition between the two species, we used these designations as our goal was to explore the effects that invasive species have on native species, given that all three invasive species are of larger body size than all native species (excluding cat-fosa pairing, Farris et al. 2015a). We derived the species interaction factor (SIF) to provide a measure of co-occurrence between target species. The SIF value is used to determine if two species occur independently (SIF = 1.0), or have a higher (SIF > 1.0) or lower (SIF <1.0) probability of co-occurrence than random chance (MacKenzie 2006).

Using results from Farris et al. (2015c) we had 12 native-invasive carnivore pairings with sufficient captures to provide spatial co-occurrence estimates (Table 1). In this previous research, one carnivore pairing demonstrated spatial aggregation (SIF > 1.0) and six demonstrated spatial segregation (SIF < 1.0) relationships. The remaining five pairings demonstrated no spatial relationship (SIF = 1.0; spatial distribution is independent of the other species). The six spatial segregation relationships (SIF < 1.0) indicated that six native carnivores have lower probability of occupancy when an invasive carnivore is present (psiNI) compared to when the invasive is absent (psiNi). Small Indian civets had the highest number of spatial interactions for invasive carnivores. The number of habitat patches (#Patches, n = 5) and distance to the nearest village (Village, n = 3) were the most common variables to explain relationships of co-occurrence (Online Resource 2).

Temporal analysis

In a previous analysis of each carnivore (Farris et al. 2015a), we modelled captures (capture events/available hours), where a capture event is all photos of distinct individuals of a given species within a 30 min period (to ensure independence in photo captures) using a nonparametric kernel density analysis to estimate the probability density of temporal activity distribution for each species (Ridout, Linkie 2009). We conducted model selection, making inference from the most simple, parsimonious model. Finally, for each native- invasive carnivore pairing, we estimated the coefficient of overlap of the probability densities throughout the entire diel period using an estimator supported for small sample size [denoted Δ_1] (Ridout, Linkie 2009). This coefficient is bounded by 0 and 1 such that $\Delta_1 = 0$ indicates no overlap and $\Delta_1 = 1.0$ indicates complete overlap in daily activity pattern. High temporal overlap does not mean the carnivores occur together during the same 24 h period, but indicates they overlap in their use of diel cycle periods (i.e., dawn, dusk, day, night).

Using results from Farris et al. (2015a), we estimated temporal overlap for 16 of the 18 potential native- invasive carnivore pairings (Table 1). In this previous research, the estimates of temporal overlap ranged from a low of 0.23 (nocturnal small Indian civet and diurnal ring-tailed vontsira) to a high of 0.88 (diurnal dog and diurnal brown-tailed vontsira). The coefficient of overlap (proportional overlap, 0 – 1.0) across the entire diel cycle from this previously published kernel density analysis (Farris et al. 2015a) revealed a high degree of overlap (e.g. temporal aggregation) among temporal activity patterns for native and invasive carnivore pairings (average $\Delta_1 = 0.59 \pm \text{SD } 0.23$, Table 1).

Relative species interaction

Here, we focus on providing a theoretical framework to investigate carnivore interactions from passive spatial sampling (e.g., camera-traps) and we derive a measure of spatiotemporal overlap that incorporates landscape and/or micro-habitat variables. We do so by combining results of the two-species, spatial co-occurrence model (Farris et al. 2015c) and the temporal, non-parametric circular kernel density estimator (Farris et al. 2015a). We combine these two approaches because 1) the co-occurrence models can account for a major source of bias: that sites may be used by one or both species, yet species can go undetected (MacKenzie 2006) and 2) the circular density estimator is a flexible approach to estimate highly variable diel activity patterns that are common for many species (Gerber et al. 2012a).

This approach, combining the two-species interaction factor (SIF, spatial) and the kernel density analysis ($\Delta_{1,}$ temporal), allowed us to calculate a spatiotemporal value (STV), or measure of spatiotemporal overlap, for each native- invasive carnivore pairing across important landscape features. Specifically, we calculated the STV by multiplying the SIF value, which varied across the landscape or habitat covariate included in each co-occurrence model, by the normalized interaction of the two species' temporal activity density, $\Delta_{1,}$ within 30 minute periods across the diel cycle from our kernel density analysis (i.e., STV = SIF * Δ_1). The STV value provides a measure of overlap for each carnivore pairing such that a value of 0 indicates no overlap and as the STV value increases this indicates increasing spatial *and* temporal overlap, and thus increasing potential for direct interaction. Because the temporal activity analyses do not distinguish between sites where both species occurred or otherwise, we estimate a population-level (across all sites) temporal profile. This was a necessity for sparse data reasons that are typical of carnivore data.

Conceptual framework for interpreting spatiotemporal overlap

There are four potential states when considering spatiotemporal overlap between species (Figure. 1). High spatial or temporal overlap by itself does not indicate costly species interactions, nor does low spatial or temporal overlap by itself indicate the displacement of the subordinate species. Inferring the consequences of low or high overlap depends on understanding the mechanisms that led to the observed pattern (Figure 2), which necessitates knowledge of each species' ecology. Or alternatively, a study design that allows inference to compare the spatial and temporal activity of the subordinate species in areas with and without the potential competitor. The ecological mechanisms and likely costs that could cause low spatial and/or temporal overlap between species are: i) a separation in niche, which could be an evolutionary outcome of reduced competition between native species (no fitness costs), ii) a separation in niche, due to the subordinate species switching their preferred habitat, resource(s), or temporal activity (likely inducing fitness consequences due to using fewer or lower quality resources or marginal habitat that could increase mortality risks or reduce reproductive success), iii) no interactions because two species do not occupy the same space (no fitness costs), iv) no interactions because the species do not overlap along any niche axes despite sharing the same space (no fitness costs), or v) species overlap in space and have high indirect interactions through interference or exploitative competition of shared resources that are temporally available to both species (likely inducing fitness costs due to competition). To identify the likely process that led to the observed pattern of low temporal overlap, and thus the consequence and importance of low overlap, several additional pieces of evidence are needed: i) degree of spatial overlap, ii) potential for direct or indirect competition, and iii) whether the subordinate species is altering its temporal activity pattern due to the potential for direct or indirect interactions with the dominant species.

We outline the possible types of interactions (i.e., direct, indirect, no interaction) for each combination of spatial and temporal overlap in Figure 3. Direct interactions between carnivore species include aggression/harassment, intraguild predation, kleptoparasitism, and disease transmission. High spatial overlap (i.e., SIF) indicates that two carnivores are using the same space more than expected at random, while high temporal overlap indicates the chance of interacting at the same place and time is high, it does not necessarily mean the two carnivores are active during the same 24 hr period. Rather, it indicates the two overlap in their use of the diel cycle. As a result, if there is high overlap in both space and time, any combination of direct, indirect, and no interactions may occur. Otherwise, when there is either low spatial or temporal overlap (but not both), it is more likely that indirect or no interactions occur, and when there is both low spatial and temporal overlap, no interactions are most likely (Figure 3). Interpreting the lack of interaction is perhaps the most challenging. To do so requires one to consider the fundamental and realized niche of both species. The lack of interaction may result from two species simply coexisting in fundamentally separate niche spaces, or that one species may have altered its spatiotemporal activity in response to the dominant species (Figure 2).

Results

Over this six year period, we conducted 13 photographic surveys across seven sites surveying for a total of 824 days, providing 15,253 trap nights (defined as a 24 hr period that an individual camera station surveyed with no malfunctions occurring). We collected approximately 120,000 photographic captures. Of these photographic captures, 2,991 were of a carnivore species with 1,639 captures of the six native carnivores and 1,352 captures of the three invasive carnivores.

Spatiotemporal interactions

Using estimates from our spatial co-occurrence modelling and temporal overlap, we were able to estimate spatiotemporal values for eight native-invasive carnivore pairings. Small Indian civets had the highest number of spatiotemporal overlap relationships (n = 4), followed by dogs (n = 3), and cats (n = 1, Figure 4). The highest likelihood of spatiotemporal overlap occurred between small Indian civets and broad-striped vontsiras (STV = 23.20, Figure 4 h) occurring between the hours of 23:00-24:00 in habitat primarily made up of patchy, non-forest matrix. Dogs had a high likelihood of spatiotemporal overlap with fosa and falanouc between the hours of 06:00 – 08:00, particularly in patchy degraded habitat (Figure 4 a-b). Feral cats had a high likelihood of spatiotemporal overlap with falanouc, which increased moving away from villages, during the hours of 05:00 – 07:00 (Figure 4 d). The small Indian civet had a high likelihood of spatiotemporal overlap with three native, nocturnal carnivores (falanouc, fanaloka, and broad-striped vontsira) occurring between the hours of 20:00 – 06:00 (Figure 4 e-h). Two native-invasive carnivore pairings showed highly variable spatiotemporal overlap across the diel cycle: the diurnal dog and nocturnal broad-striped vontsira (Figure 4 c), and the nocturnal small Indian civet and diurnal ring-tailed vontsira (Figure 4 g). Six of the eight spatiotemporal relationships revealed increasing overlap as anthropogenic disturbance (measured in distance to village, percent rainforest/matrix, and patchiness) increased (Figure 4).

Our conceptual framework (Figure 1) provided four potential scenarios: 1) spatial and temporal segregation (Figure 1, Top-left), 2) spatial segregation and temporal aggregation (Figure 1, Top-right), 3) spatial aggregation and temporal segregation (Figure 1, Bottom-left), and 4) spatial aggregation and temporal aggregation (Figure 1, Bottom-right). Three of the native-invasive carnivore pairings (dog-falanouc, dog-broad-striped vontsira, and Indian civet-ring-tailed vontsira) fall under scenario one above, by demonstrating low spatial overlap/segregation (spatial segregation, SIF < 1.0) and low temporal overlap (temporal segregation). Three of the native-invasive carnivore pairings (Indian civet with fanaloka, with falanouc, and with broad-stripe vontsira) fall under scenario two above by demonstrating low spatial overlap (spatial segregation), but high temporal overlap (temporal aggregation, Figure 1 Top-right). We did not observe any scenario three examples (spatial aggregation, temporal segregation, Figure 1, Bottom-left). Finally, the cat and falanouc was the only native-invasive carnivore pairing to fall under scenario four (spatial aggregation, temporal aggregation, Figure 1, Bottom-left) given the high spatial and temporal overlap.

Discussion

We demonstrate the effectiveness of a spatiotemporal model that combines methods in co-occurrence modelling (spatial) and kernel density analysis (temporal) to explore interactions between native and invasive carnivores. We demonstrate how anthropogenic disturbance influences these spatiotemporal interactions between native and invasive carnivores by showing that species interaction factors (SIF) and spatiotemporal values (STV) are not static, but change across a variable landscape. We found evidence of spatiotemporal interspecific interactions between multiple native and invasive carnivore pairings, we provide interpretation of each carnivore pairing, and we highlight the effectiveness of this modelling approach for informing managers of wild carnivore community ecology or other elusive or data-poor species.

For scenario one relationships (low spatial overlap/segregation), we observed three native-invasive pairings (dog-falanouc, dog-broad-striped vontsira, and Indian civet-ring-tailed vontsira). Free-ranging dogs in Madagascar are widespread and their diets diverse (Farris et al. 2015b; Goodman 2012); however, their diet has not been shown to overlap with the falanouc, which feeds primarily on earthworms and invertebrates (Goodman 2012). However, we did demonstrate a strong potential increase in interaction in this pairing as habitat becomes more patchy and degraded. As forest degradation and fragmentation increases throughout Madagascar, the potential interactions between dogs and falanoucs, particularly during crepuscular periods, should be monitored. The diurnal activity of dogs and their extensive use of degraded, forest edge (Farris et al. 2017a), contrasts with the nocturnal activity and preference for contiguous forest of the broad-striped vontsira (Farris et al. 2015b; Goodman 2012), which likely contributes to the high variability in Figure 4 c and adds further support to our interpretation of little to no interaction. Small Indian civets diverge greatly with ring-tail vontsira in temporal activity (Farris et al. 2015a; Gerber et al. 2012a) and Indian civets are found almost exclusively in edge, open, and matrix habitat (Gerber et al. 2012b; Goodman 2012), adding support to our interpretation of little to no interaction between small Indian civet and ring-tailed vontsira.

For scenario two relationships (low spatial overlap, high temporal overlap), we observed three native-invasive carnivore pairings (Indian civet with fanaloka, with falanouc, and with broad-stripe vontsira). The small Indian civet is known to consume a wide-range of resources, including prey items with wide spatial distributions that are used by all three of these native carnivores (i.e. rodents, small vertebrates, and invertebrates, Goodman 2012). We suggest the potential for indirect interactions with Indian civets is highest for the fanaloka and the broad-stripe vontsira as the overlap in shared resources is greatest, given the apparent specialization in diet by the falanouc. Our STVs demonstrate that these potential interspecific interactions with Indian civets are likely to increase for fanaloka (Figure 4 e) and broad-striped vontsira (Figure 4 h) as degradation and fragmentation increase.

We observed no scenario three relationships (high spatial overlap, low temporal overlap). Spatial aggregation between invasive and native carnivores was rare, as would be expected for most habitats where non-native predators invade. This scenario of spatial aggregation presents a serious risk to native species as it would threaten any potential shared resources (e.g. indirect interaction) and possibly result in disease transmission to native carnivores (e.g. potential for direct interaction; Rasambainarivo et al. 2018; Rasambainarivo et al. 2017).

For scenario four (high spatial and temporal overlap), we observed only one native-invasive relationship (cat and falanouc). The type of interaction between cats and falanoucs is likely to vary depending on habitat. Occupancy estimates (Farris et al. 2015b) revealed that the falanouc had similar occupancy across the entire landscape (from non-degraded to degraded), but cats show considerably higher occupancy in degraded forest. In degraded forest, these two carnivores had very high spatial overlap (SIF = 2.0) and that was explained by distance to village (psiNI≠psiNi[Village], Farris et al. 2015c). This reveals that within non-degraded forests, where cats are more rare, direct and indirect interactions are unlikely to occur. However, as degradation increases these two carnivores are highly likely to come into direct contact (Figure 4 d). We suggest this presents a serious threat to falanoucs potentially in the form of aggression, harassment, and disease transmission from cats, which are of similar body size (Goodman 2012).

Five carnivore pairings resulted in no spatial relationship (SIF = 1.0) and, as a result, failed to fit into the four interaction scenarios above. We interpret these relationships as two carnivores occurring together within a study area but with no spatial interaction (Figure 1). However, we highlight the relationship occurring between dogs and brown-tailed vontsiras, and cats and fosas, as both reveal no spatial overlap, but high temporal overlap. Despite the finding of no spatial overlap, we suggest there is strong potential for these invasive species to negatively affect these natives as the result of the rapid changes in rainforest habitat, the plasticity in habitat selection and resource use for these two invasive species, and the expansive ranges of dogs, cats, and fosas.

The ultimate goal of spatial, temporal, and/or spatiotemporal analyses is to accurately interpret behavior, spatial distribution, and/or activity patterns of co-occurring species with the aim of deciphering between habitat and behaviorally mediated effects. While this is a fundamental goal for behavioral and community ecologists alike, interpretation remains challenging despite the development of a diverse set of novel sampling and modelling approaches in recent years. Our 3-dimensional figures visually demonstrate the challenge in interpretation. For example, Figure 2 demonstrates how a species may alter or change spatial or temporal (or both) states depending on the presence and amount of overlap with a dominant species. However, to understand if this alteration in spatial/temporal state results from the presence of the dominant requires a study design in which the target species is studied in both the presence and absence of the dominant. Figure 3, however, demonstrates that each possible spatiotemporal overlap scenario could include a no interaction scenario between the co-occurring species. To interpret these scenarios and infer interaction, we require detailed natural history, movement (home range), and behavioral information on both co-occurring species. Given that we have not studied these native carnivores in both the presence and absence of invasive carnivores, and the fact that much natural history and behavioral information is lacking for each of the native carnivores, we are currently unable to differentiate between behavioral and habitat mediated effects.

Detailed information on resource and habitat use for both native and invasive species would improve our ability to make more accurate predictions of species interactions. Karanth et al. (2017) used similar sampling and modelling approaches to explore carnivore spatiotemporal interactions and compared these interspecific interactions across sites with varying resource availability. This approach allowed researchers to demonstrate carnivore plasticity in spatial and temporal activity as resource and co-occurring carnivore density varied across the landscape, highlighting mechanisms contributing to carnivore sympatry. Carnivores in our study may demonstrate similar variability in spatial and temporal activity across the landscape. However, the Karanth et al. (2017) study investigated three native, sympatric carnivore species. The same variation in spatial and temporal patterns that permitted sympatry in that carnivore community, may not alleviate negative interactions for Madagascar's native-invasive community as invasive predators present a novel threat and native carnivores may not yet have developed behavioral adaptations to avoid conflict with invasive species. Vanak et al. (2013b) conducted a similar investigation of intraguild interactions and found similar plasticity in carnivore spatial and temporal activity in response to variation in season, resource availability, and potential threats. Their investigation was conducted in a closed system (85 km^2 fenced conservation area), allowing researchers to examine fine-scale, avoidance behaviors with variations in resource availability.

Using our spatiotemporal model in this type of closed system where resource availability is well known, would provide more detailed insight and allow researchers to identify which type of interspecific interaction is occurring. Few systems, however, allow for the type of investigation carried out by Karanth et al. (2017) and Vanak et al. (2013b). Our survey and modelling approaches can provide researchers a useful approach to investigate and interpret potential interspecific interactions or possible outcomes for co-occurring species in open systems where important data on resource availability may not be available.

Our modelling approach is useful for identifying precise locations in space and time where species are likely to co-occur. For example, we demonstrate that dogs and fosas are most likely to co-occur between the hours of 05:00 and 09:00 with potential interactions increasing as the habitat becomes more patchy. Similarly, in multi-year carnivore surveys across Ranomafana National Park (RNP), Madagascar (Farris et al. 2017a) we found dogs and fosas had high probabilities of spatial co-occurrence (SIF > 1.0), resulting in strong potential for indirect and direct interactions. These results could provide valuable insight for managers working across RNP to address this burgeoning conservation issue. For example, these findings could be used to develop targeted education programs that inform people living near forest habitat or traveling with their dogs to forested areas of the negative impacts their dogs may have on fosas and co-occurring wildlife. Policies that instruct, or encourage, people to leave their dogs at home when traveling into the forest during this time period, or change the time of day they take dogs to the forest, could greatly decrease the probability of direct and indirect interactions between these two carnivores and result in increased spatial habitat and resource use of fosa across these forested areas. Additionally, the results of this study highlight potential interactions between multiple native carnivores and free-ranging cats and dogs. These findings on where interactions are likely to occur on the landscape are being used to inform veterinarian clinics and disease ecology research currently on going throughout Madagascar’s eastern rainforest region. These potential interspecific interactions between native and invasive carnivores also are being used to inform managers and researchers on where to establish vet clinics and where disease transmission may be occurring. Additional studies of native and invasive carnivores across Madagascar’s rainforest ecosystem are needed to better understand these interspecific interactions. In particular, we need information on resource use by Madagascar’s native carnivores to determine if they have the same plasticity in resource use and activity, as has been observed in other studies (Karanth et al. 2017; Kronfeld-Schor, Dayan 2003; Vanak et al. 2013b). Investigations of fine scale behaviors will allow us to understand the severity of threat posed to native carnivores by invading invasive carnivores.

The theoretical and statistical modelling approach discussed herein provides a synthetic framework to explore the potential for interspecific interactions between invading, non-native carnivores and rare, elusive native carnivores. Also, this approach allows researchers to collect data non-invasively while exploring potential interactions across multiple dimensions, which is ideal for investigations of wild carnivores. We encourage future carnivore spatiotemporal activity studies to frame questions in terms of theoretical considerations (i.e., Table 1) and appropriate study designs to identify potential behavioral mechanisms driving carnivore species interactions.

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Figure Legends

Fig. 1 Conceptual framework for types of potential spatial and temporal overlap between a dominant (e.g., *C. familiaris*) and subdominant carnivore (e.g., *C. ferox*). Top left, species significantly differ in space use and temporal activity; top right species share temporal patterns but do not significantly overlap in space use; bottom left, species overlap in space use but differ significantly in temporal activity; bottom right, species significantly overlap in space use and temporal activity.

Fig. 2 Conceptual framework for potential spatiotemporal shifts by a subdominant species (e.g., *C. ferox*) in response to an invading dominant species (e.g., *C. familiaris*) with varying levels of spatiotemporal overlap. The subdominant can respond by, 1) staying in the current state (no response), 2) transitioning states and thus shifting their spatial and/or temporal activity (altering interaction strength), or 3) transitioning states independent of the dominant species' invasion. Arrows represent directional shifts with associated potential change in interaction consequence at the new state (e.g., Green→ Orange = moving from a neutral state to intermediate negative state). The subdominant species should stay at the current state if the consequences of the interaction (Figure 3) are neutral or less negative than moving to an alternative state (e.g., *C. ferox* would not transition from a green state if all alternative states lead to orange or red). Conversely the subdominant should transition if the current state had a higher negative interaction potential than an alternative state. For example, if *C. ferox* initially had low temporal and spatial overlap with *C. familiaris* (upper left), however, due to reduction in habitat availability was forced to respond by increasing spatial overlap with *C. familiaris* (lower left), where in the new state *C. ferox* may experience fitness costs via indirect interactions with *C. familiaris*, or none if fundamental niches are divergent (Figure 3)

Fig. 3 Conceptual framework for potential interactions given four possible interspecific spatiotemporal patterns of a subdominant (e.g., *C. ferox*) and dominant carnivore (*C. familiaris*). Each state has 1-3 possible interaction categories (no interaction, indirect interaction or direct interaction) that give rise to probable interaction outcomes between species with either no (green), possible (blue), or direct (orange) fitness cost for the subdominant

Fig. 4 Likelihood of spatiotemporal interactions for native and invasive carnivore pairings occupying the Masoala-Makira landascape, NE Madagascar. Each pairing reveals the estimated spatiotemporal value (STV, Y-axis), which varies based on time of day (X-axis) and landscape or habitat variable (Z-axis). Increases in height and color gradient reveal higher likelihoods of potential interspecific interaction for each carnivore pairing. Carnivore pairings include, a) dog *Canis familiaris* and fosa *Cryptoprocta ferox*, b) dog and falanouc *Eupleres goudotii*, c) dog and broad-striped vontsira *Galidictis fasciata*, d) cat *Felis species* and falanouc, e) small Indian civet *Viverricula indica* and spotted fanaloka *Fossa fossana*, f) small Indian civet and falanouc, g) small Indian civet and ring-tailed vontsira *Galidia elegans*, h) small Indian civet and broad-striped vontsira.

Table 1. Summarized estimates (SE) from Farris et al. (2015c) for spatial co-occurrence among native- invasive species pairings, including occupancy of native (N) when invasive (I) is present (psiNI) and when absent (psiNi), species interaction factor (SIF), coefficient of temporal overlap (Δ^1) estimates from Farris et al. (2015a), and average spatiotemporal value (STV). SIF estimates in bold indicate value with error do not overlap zero.

Farris ZJ, Kelly MJ, Karpanty SM, Ratelolahy F (2015c) Patterns of spatial co-occurrence among native and invasive carnivores in NE Madagascar. Animal Conservation 19:189-198.

Farris ZJ, Gerber B, Karpanty SM, Murphy A, Ratelolahy F, Kelly MJ (2015a) When carnivores roam: temporal patterns and partitioning among Madagascar's native and invasive carnivores. Journal of Zoology (London) 296:45-57.

Species	psiNE (SE)	psi Ne (SE)	SIF	Δ^1	Avg. STV
C.familiaris & *C.ferox*	0.51 (0.06)	0.51 (0.06)	0.95 (0.09)	0.44	1.84
C.familiaris & *F.fossana*	0.43 (0.05)	0.43 (0.05)	1	-	-
C.familiaris & *E.goudotii*	0.23 (0.05)	0.69 (0.11)	**0.51 (0.11)**	0.39	0.99
C.familaris & *G.elegans*	-	-	-	0.87	-
C.familaris & *G.fasciata*	0.24 (0.06)	0.90 (0.15)	**0.59 (0.09)**	0.23	0.93
C.familaris & *S.concolor*	0.31 (0.05)	0.31 (0.05)	**0.91 (0.002)**	0.88	-
F.species & *C.ferox*	0.85 (0.03)	0.85 (0.03)	0.98 (0.05)	0.65	-
F.species & *F.fossana*	-	-	-	-	-
F.species & *E.goudotii*	0.43 (0.03)	0.07 (0.03)	**1.90 (0.21)**	0.63	4.21
F.species & *G.elegans*	-	-	-	0.56	-
F.species & *G.fasciata*	-	-	-	0.42	-
F.species & *S.concolor*	0.13 (0.04)	0.13 (0.04)	1	0.61	-
V.indica & C.ferox	-	-	-	0.82	-
V.indica & *F.fossana*	0.33 (0.11)	0.72 (0.31)	**0.50 (0.26)**	0.80	0.57
V.indica & *E.goudotii*	0.11 (0.05)	0.64 (0.19)	**0.22 (0.06)**	0.74	0.97
V.indica & *G.elegans*	0.14 (0.06)	0.86 (0.27)	**0.26 (0.01)**	0.23	1.22
V.indica & *G.fasciata*	0.11 (0.08)	0.89 (0.22)	**0.21 (0.01)**	0.83	4.45
V.indica & *S.concolor*	-	-	-	0.29	-

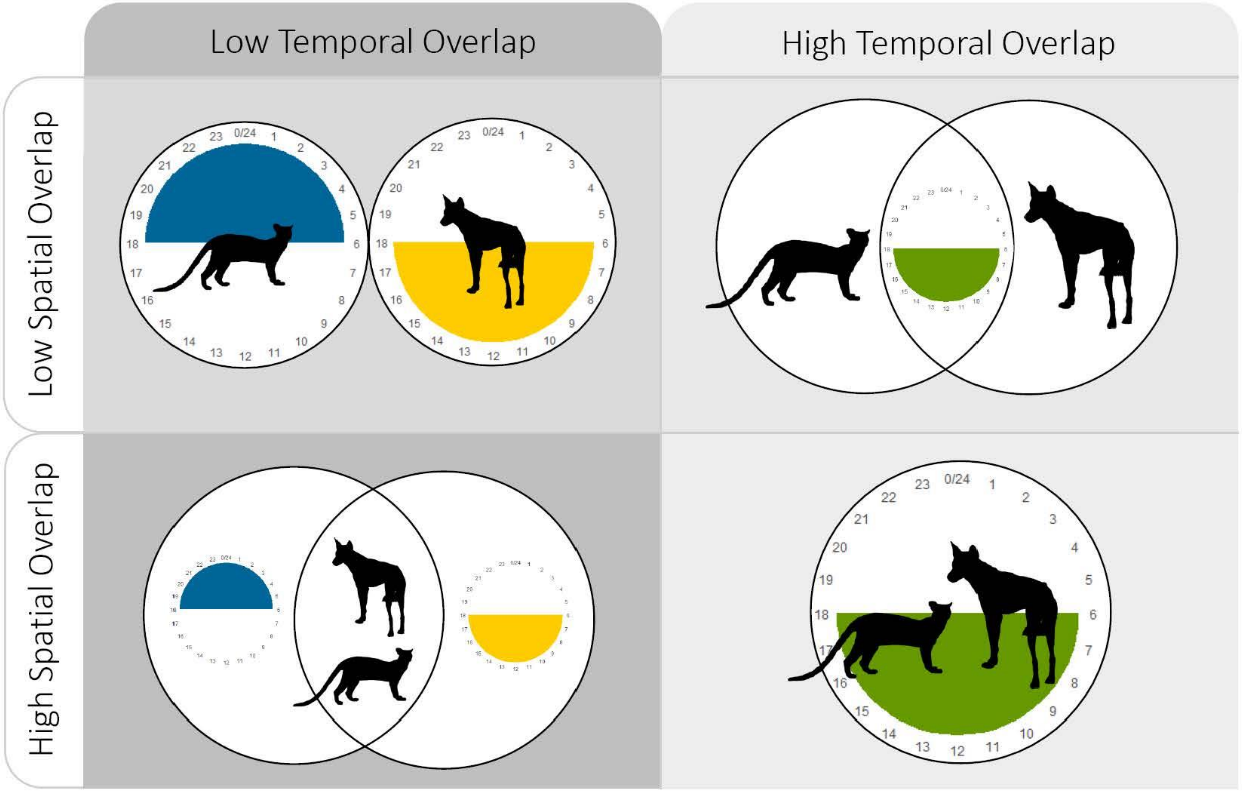

Low Temporal Overlap
High Temporal Overlap
Low Spatial Overlap
High Spatial Overlap

Figure 1.

688

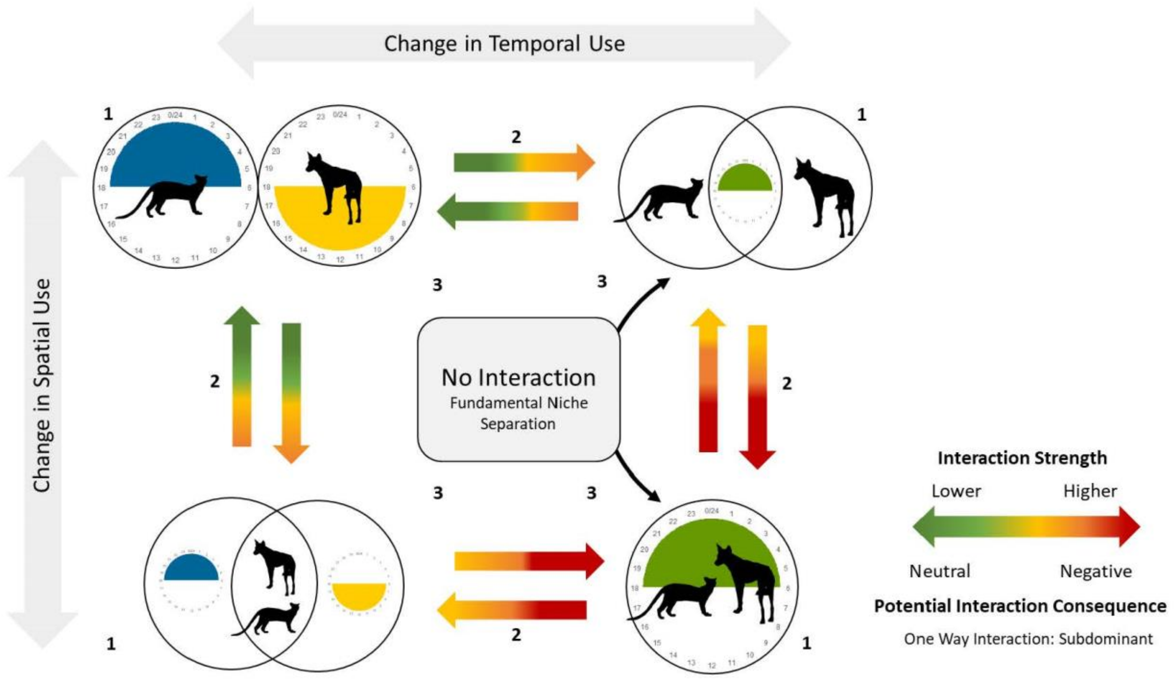

Change in Temporal Use
Change in Spatial Use
1
2
3
No Interaction
Fundamental Niche Separation
Interaction Strength
Lower
Higher
Neutral
Negative
Potential Interaction Consequence
One Way Interaction: Subdominant

Figure 2.

689

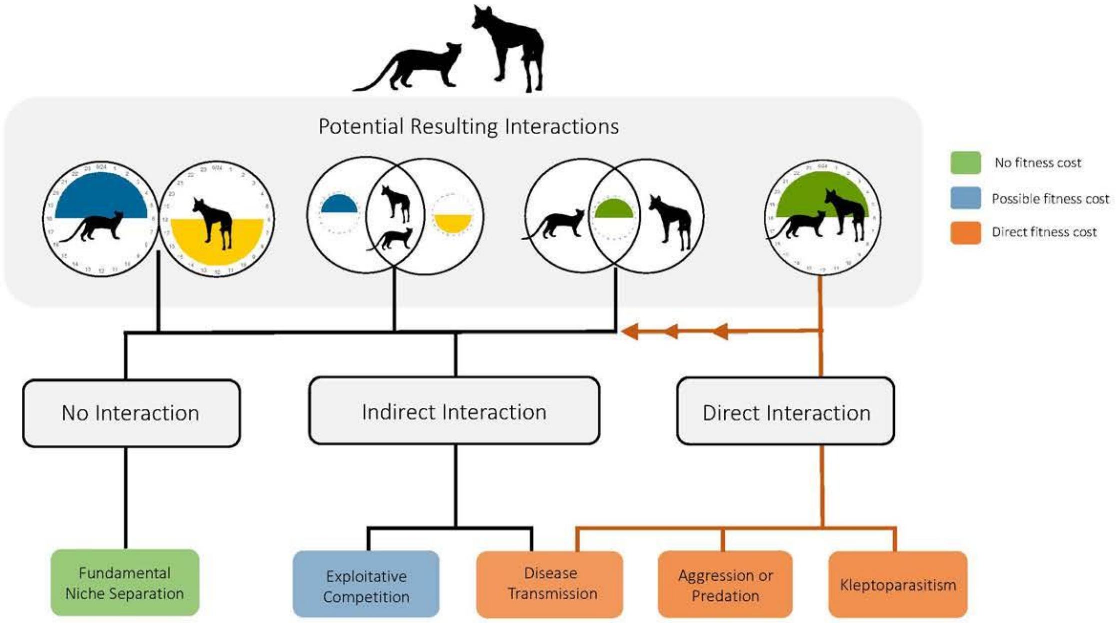
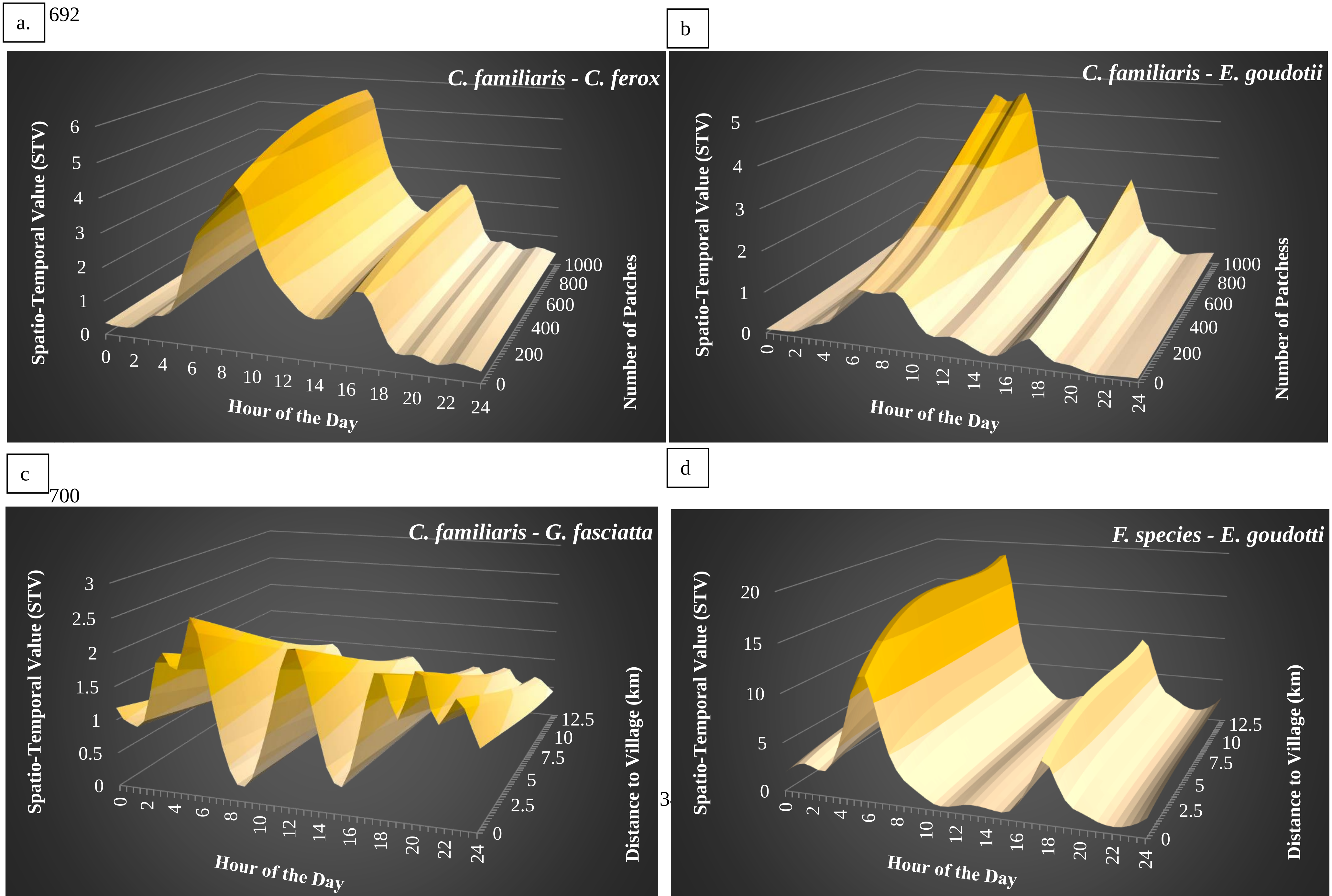
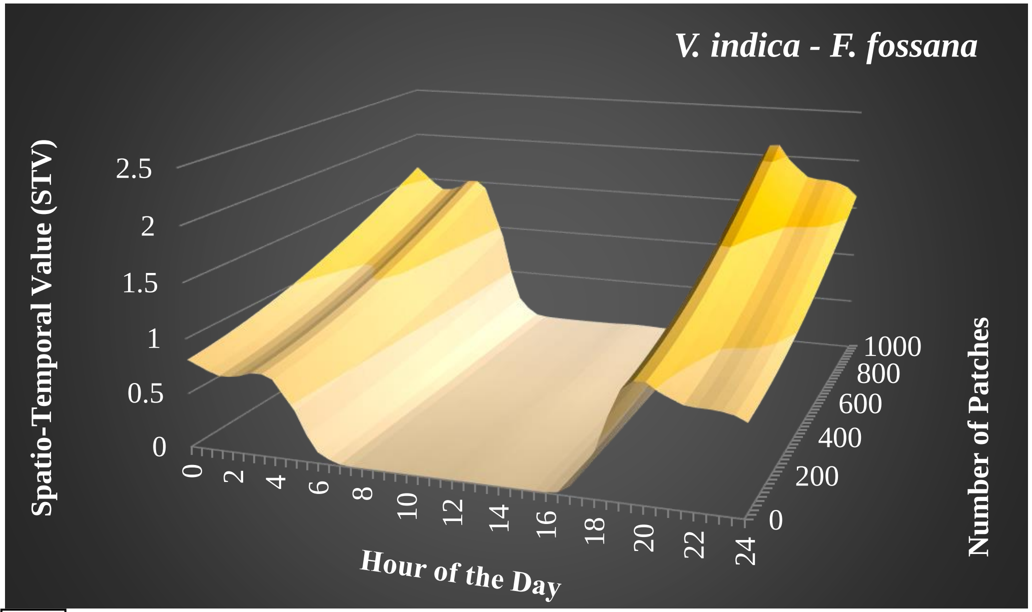

Potential Resulting Interactions
No fitness cost
Possible fitness cost
Direct fitness cost
No Interaction
Indirect Interaction
Direct Interaction
Fundamental Niche Separation
Exploitative Competition
Disease Transmission
Aggression or Predation
Kleptoparasitism

Figure 3.

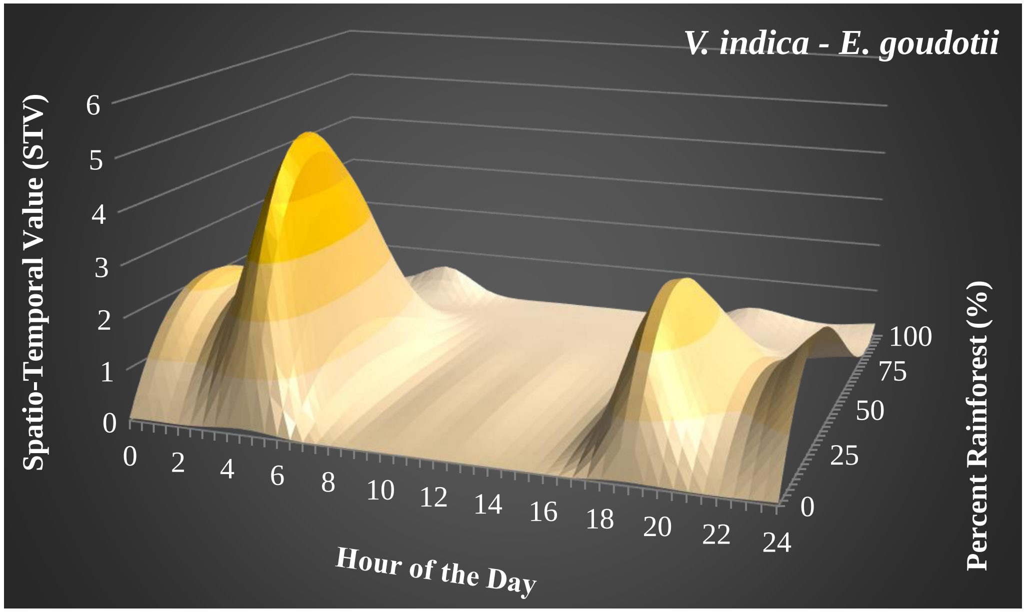
Figure 4.


a.
C. familiaris - C. ferox
Spatio-Temporal Value (STV)
0
1
2
3
4
5
6
Hour of the Day
0 2 4 6 8 10 12 14 16 18 20 22 24
Number of Patches
0
200
400
600
800
1000
b
C. familiaris - E. goudotii
Spatio-Temporal Value (STV)
0
1
2
3
4
5
Hour of the Day
0 2 4 6 8 10 12 14 16 18 20 22 24
Number of Patchess
0
200
400
600
800
1000
c
C. familiaris - G. fasciatta
Spatio-Temporal Value (STV)
0
0.5
1
1.5
2
2.5
3
Hour of the Day
0 2 4 6 8 10 12 14 16 18 20 22 24
Distance to Village (km)
0
2.5
5
7.5
10
12.5
d
F. species - E. goudotti
Spatio-Temporal Value (STV)
0
5
10
15
20
Hour of the Day
0 2 4 6 8 10 12 14 16 18 20 22 24
Distance to Village (km)
0
2.5
5
7.5
10
12.5

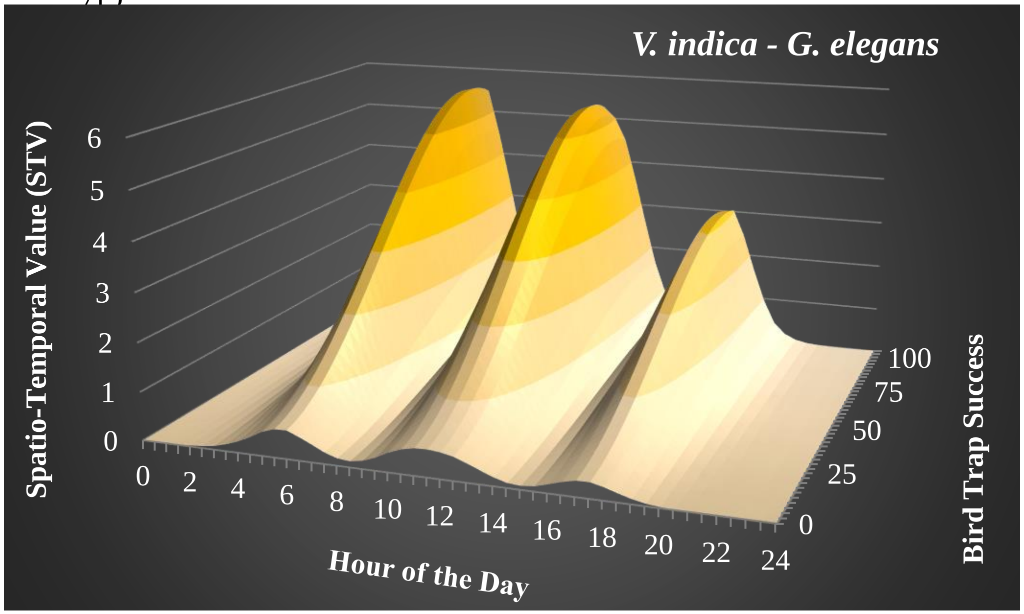
e


V. indica - F. fossana
Spatio-Temporal Value (STV)
0
0.5
1
1.5
2
2.5
Hour of the Day
0
2
4
6
8
10
12
14
16
18
20
22
24
Number of Patches
0
200
400
600
800
1000

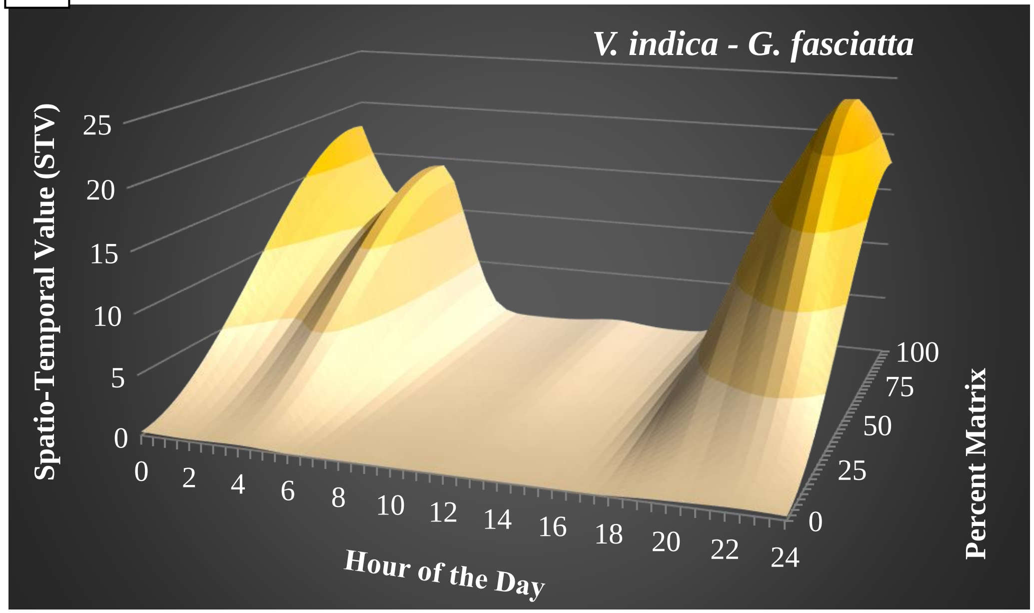
f


V. indica - E. goudotii
Spatio-Temporal Value (STV)
0
1
2
3
4
5
6
Hour of the Day
0
2
4
6
8
10
12
14
16
18
20
22
24
Percent Rainforest (%)
0
25
50
75
100

g


V. indica - G. elegans
Spatio-Temporal Value (STV)
0
1
2
3
4
5
6
Hour of the Day
0
2
4
6
8
10
12
14
16
18
20
22
24
Bird Trap Success
0
25
50
75
100

h


V. indica - G. fasciatta
Spatio-Temporal Value (STV)
0
5
10
15
20
25
Hour of the Day
0
2
4
6
8
10
12
14
16
18
20
22
24
Percent Matrix
0
25
50
75
100