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What can mixed-species flock movement tell us about the value of Amazonian secondary forests? Insights from spatial behavior

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What can mixed-species flock movement tell us about the value of Amazonian secondary forests? Insights from spatial behavior

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ABSTRACT

The value of secondary forest for rain forest species remains an important question for conservation in the 21st century. Here, we describe the spatial behavior of understory mixed-species flocks in a heterogeneous landscape in central Amazonia. Understory mixed-species flocks represent a diverse, highly organized component of the rich Amazonian avifauna. We recorded movements within 26 flock home ranges in primary forest, secondary forest, interfaces between forest types, and forest fragments. We describe frequency and movement orientation in relation to forest edges, movement patterns and proportion of use between secondary and primary forest, the relation between home range sizes and vegetation height, and home range configuration. Flocks visited only a small portion of forest edges, and showed a tendency for moving parallel to edges next to less-developed secondary forest. Movement patterns in secondary forests did not show significant differences compared to primary forests. Time spent in secondary forests increased in proportion to mean canopy height. Flocks were consistently present in secondary forests where vegetation height averaged over 15 m, but home ranges were nearly twice as large compared to primary forest. Home range limits tended to be aligned with disturbed vegetation, essentially rearranging a territorial configuration normally adjusted by topography. The spatial behavior of this important subset of the Amazonian avifauna shows that secondary forests are tolerated above a certain development threshold, but perceived as sub optimal habitat until canopy height closely matches primary forests.

RESUMO

O valor de florestas secundárias para espécies florestais continua sendo uma importante questão na conservação de ecossistemas tropicais no século XXI. Aqui, descrevemos o comportamento espacial de bandos mistos de sub-bosque em uma paisagem heterogênea na Amazônia central. Registramos os movimentos em 26 áreas de vidas de bandos em floresta primária, floresta secundária, interfaces entre ambas e fragmentos florestais. Descrevemos a frequência de uso e orientação em relação a bordas florestais, e padrões predominantes de movimento, proporções de uso entre floresta primaria e secundaria, relação entre tamanho de áreas de vida em relação à altura da vegetação, e configuração territorial em paisagens heterogêneas. Resultados mostram uma pequenos trechos de bordas florestais sendo visitadas e uma tendência de movimento paralelo a borda quando próximas a capoeiras pouco desenvolvidas. Não foram detectadas diferenças significativas em padrões de movimento entre florestas primarias e secundárias. Tempo passado em florestas secundárias aumentou proporcionalmente com a altura média da vegetação. Bandos foram detectados consistentemente em florestas secundárias após estas atingirem alturas medias maiores que 15 m, mas áreas de vida eram quase o dobro da área de bandos em floresta primária. Houve uma correlação negativa entre altura média da vegetação e tamanho da área de vida. Limites de áreas de vida tendiam estar alinhados a vegetação degradada, essencialmente reorganizando configuração territorial normalmente ajustada por topografia. O comportamento espacial deste importante subconjunto da avifauna amazônica mostra que florestas secundárias são toleradas acima de um certo limite de desenvolvimento, mas são percebidas como habitat subótimo até que a altura média da vegetação alcance estatura próxima de florestas primárias.

Key words: Amazon; animal movement; BDFFP; forest fragmentation; heterogeneous landscapes; mixed-species flocks; secondary forests.

HOW VALUABLE ARE SECONDARY FORESTS AND WHAT ROLE WILL THEY PLAY IN 21ST CENTURY CONSERVATION? Recent paradigm shifts in conservation biology have prompted an increase in the perceived value of secondary forests (Chazdon *et al.* 2009, Marris 2009, Didham 2011). Nonetheless, it is challenging to objectively quantify their contribution to species conservation. Understanding how species interact with disturbed or regenerating environments requires detailed behavioral information, a remarkable challenge in species-rich ecosystems. A general framework for determining the conservation value of secondary forests derives from species counts and the proportions of species unique to primary forests (Barlow *et al.* 2010). These assessments usually implement stationary-sampling inventories (Barlow *et al.* 2007, Gardner *et al.* 2009, Dent & Wright 2009), and have provided important advancements to our understanding of altered habitats. Yet, these methodologies provide no information on habitat use, establishment of stable home ranges or territorial configuration. For example, highly mobile species with large home ranges, as seen in a considerable number of forest bird species (Terborgh *et al.* 1990, Stouffer 2007, Johnson *et al.* 2011) may move between adjacent habitats. Thus, despite being detected in secondary forests, some species still depend on primary forest (Jirinec *et al.* 2011).

It is estimated that 70% of today's forests are within 1 km of forests edges (Haddad *et al.* 2015) and secondary forests are usually embedded within heterogeneous landscapes (Neeff *et al.* 2006). Much insight may be gained from understanding how individuals perceive and deal with these altered landscape features. Habitat use patterns emerge from decision-making processes at fine temporospatial scales (Jones 2001, Moorcroft & Barnett 2008, Potts *et al.* 2014[a]), and behavioral data in landscape ecology has been proposed as a promising way to refine predictive models (Lima & Zollner 1996, Grimm *et al.* 2006, Moorcroft *et al.* 2006, Carter *et al.* 2015).

Birds compose a significant portion of the highly mobile species in tropical forests, and understory insectivores are known to be particularly sensitive to habitat changes (Stouffer & Bierregaard 1995). Among this vulnerable guild, mixed-species flocks may provide a representative study case. Mixed-species flocking behavior is a worldwide occurrence. It exists within an ecological margin of advantages provided by foraging enhancement and predator avoidance (Goodale & Kotagama 2005, Martinez & Zenil 2012, Dolby & Grubb 1999, Sullivan 1984), and penalties due to competition, kleptoparasitism, and higher demands in movement rate (Darrah & Smith 2013, Munn 1986).

Understory flocks in Amazonian *terra firme* forests are recognized as a system led by the cinereous antshrike, *Thamnomanes caesius* (or its sister species *T. schystogynus* in parts of Bolivia and Peru). There is a core of about eight species with overlapping territories, represented by one territorial reproductive pair per flock (Munn & Terborgh 1979). Outside this core, about 20 species join these flocks frequently, and a much higher number of species have been recorded joining these aggregations sporadically (Jullien & Thiollay 1998, Powell 1985). Up to 65 species may be detected in a single flock over the course of a day (Martínez *et al.* 2013). Flocking species are known to be heavily forest-dependent, are reluctant to cross roads (Develey & Stouffer 2001) and disappear in selectively logged forests and small fragments (Thiollay 1997, Barlow *et al.* 2006). Some core species have been detected in secondary forest (Borges & Stouffer 1999), but it is not known if they participate in aggregations or form stable territories. Territory area usually averages 8 ha which may remain quite stable over decades in pristine areas (Martínez *et al.* 2013, Jullien & Thiollay 1998). Core species gather in the same location every day at dawn and actively forage throughout their territory, eventually returning to the vicinity of the gathering point, where individuals roost within about 50 m from each other (Potts *et al.* 2014[a]).

Approaches to spatial behavior are mainly based on utilization distributions generated from animal location records (Seaman & Powell 1996) and are useful for a depiction of spatial activity within home ranges and their boundaries. For example, some forest-dependent species avoid proximity to forest edges, limiting home ranges to forest interior (Hansbauer *et al.* 2010). Yet, in the absence of edge avoidance, it is still possible that more refined spatial behaviors, such as path direction, are affected. Trajectory patterns may reflect a species' decision-making process and how it perceives certain landscape features (Giuggioli & Bartumeus 2010).

In this study, we assess the spatial behavior of mixed-species flocks in a heterogeneous landscape in central Amazonia asking the following: (1) what types of vegetation are avoided by flocks? We measure trajectory orientation in relation to forest borders, and we use a Bayesian partitioning of Markov models to classify trajectories in primary forest, forest edges, and secondary forest. And (2), how do flocks apportion their activity in primary and secondary forest when both are available? We examine how home range shape and size are related to vegetation height.

METHODS

STUDY SITE.—The study was conducted at the Biological Dynamics of Forest Fragments Project (BDFFP), located about 80 km north of the city of Manaus, Brazil. It is a structurally heterogeneous patchwork of continuous primary forest, forest fragments of different sizes, and adjoining secondary forests of varying ages and structure (Mesquita *et al.* 2001) (Fig.1). For practical reporting, we define well-developed secondary forest as having a canopy cover with mean height >15m and less-developed secondary growth as a thin canopy cover ≤ 15m, typically dominated by trees of the genus *Vismia* (Borges & Stouffer 1999), with little developed understory. These thresholds have been determined from field observations at the study site. Details on the history of this landscape can be found in (Bierregaard *et al.* 2001).

DATA COLLECTION.—We collected data between June 2009 and August 2011. Mixed-species flock territories were located in five habitat configuration types: primary forest (interior and edge); 100-ha fragments (interior and edge); 10-ha fragments; secondary forest, and primary-secondary forest mix, which are areas consisting of strips of primary forest not wide enough to fully accommodate a flock home range (Table 1 & Fig.1). Flock activity is conspicuous, enabling them to be followed on foot (Mokross & Ryder *et al.* 2014). The observer (KM) maintained a distance of 15–20 m from the core of activities. As flocks moved, the observer's positions were recorded at 30-second intervals with a hand-held GPS unit (Garmin Vista HCX), but for these analyses, we used data at 2 min intervals to reduce noise on turning angle values.

TRAJECTORY ANALYSIS.—We quantified duration and distance of forays into secondary forest in each habitat configuration type. Due to significant effects of forest edges on water vapor deficit, temperature, and foliage density within approximately 20 m from the border (Kapos 1989, Laurance 2002), we defined a 40-m-wide zone which included 20 m on each side of the forest border and is henceforth called the *edge buffer*. To test if flocks align their movement steps to forest edges, we gathered the absolute angles of all relocations inside edge buffers and compared them to forest edge angles through a Rayleigh test of uniformity (V0 test) in the *CircStats* R package (Lund & Agostinelli 2001, Batschelet 1981).

Trajectory partition and classification were performed with the *modpartltraj* function in the AdehabitatLT library (Calenge *et al.* 2008). We defined three movement behaviors from parameters based on field observations (Table S1): (1) area-restricted behavior (*ARB*), *i.e.* when flocks foraged at speeds of about 3 m/min with tight turning angles (*i.e.*, >90^o); (2) *normal* behavior, *i.e.* when flocks foraged at about 9 m/min, noticeably dislocating forward, but turning with constant frequency; and (3) *fast* behavior, *i.e.,* when flock speed was about 17 m/min with similar turning patterns to *normal* behavior. We only used trajectories with more than 50 relocations and analyzed the proportions of these movement modes in the three main landscape elements: primary forest (PF), secondary forest (SF), and edge buffers (ED). To probe flock behavior in more detail, we created a finer classification within these landscape elements: primary continuous forest (CF), primary-secondary forest mix (MIX), 100-ha fragments (100ha) and 10-ha fragments (10ha). Edges were subdivided into soft edges (S), where forest edges transition to well-developed secondary forests, usually a gradient within 5–20 m; and hard edges (H), where primary forest meets less-developed secondary forest, usually within 5 m or less. Secondary forest was subdivided in well-developed secondary forest (Wd) and less-developed secondary forest (Ld) (Table S2). We obtained the proportion of movement modes and tested the differences in each landscape feature using multinomial regression through the *mlogit* package in R.

HOME RANGES NEXT TO SECONDARY FORESTS.—To map the proportions of home ranges that were in secondary forest, which parts were used more frequently, and the total area, we recorded flock positions and created quadratic kernels via Geospatial Modeling Environment (GME) software (Beyer 2012) (kernel parameters in SM). The standard descriptors of home ranges are isopleths derived from kernels, we used intervals ranging from 99% (entire home range area) to 10% (areas of highest location densities) for these analyses (Fig. 2).

To quantify the proportion of time spent in second growth, we counted the number of positions in primary and secondary forest. To quantify the percentage of area in secondary forest we used the 99% isopleth. To test if there was a relationship between secondary forest use and vegetation height, we used a linear model (*lm*) in R software (R Development Core Team 2016) (Fig. 2).

To measure mean vegetation height, we used a Light Detection and Ranging (Lidar) canopy height model (CHM) (Specifications in SM), and generated the zonal statistics for the vegetation located inside each isopleth (Table S3).

To test if vegetation height influences the shapes of home range kernels (*i.e.,* if there is a correlation between vegetation height and areas where flocks concentrate activities), we averaged canopy height values in 10 × 10 m squares due to the high small-scale variance and constructed a model of space use. The probability of using a particular square $\mathbf{x}$ is modelled to be proportional to $f(\mathbf{x}|\alpha)=\exp[\alpha C(\mathbf{x})]$, where $C(\mathbf{x})$ is the canopy height and α is a model parameter. The null model is $\alpha=0$, meaning that any square is as equally likely to be used as any other. We tested this against the alternative hypothesis that there is some $\alpha>0$ that significantly improves the fit of the model to the data. We used a maximum likelihood approach, seeking to find the alpha that minimizes the sum of $\ln[f(\mathbf{x}_n|\alpha)]$ over a set of independent fixes $\mathbf{x}_n$. This sum is the log-likelihood function $l(\mathbf{x}_1 ,\ldots, \mathbf{x}_N |\alpha)$ where $\mathbf{x}_1 ,\ldots, \mathbf{x}_N$ is the set of independent fixes being used for the test. For this analysis we used the Lidar set that encompasses the Dimona flocks (Table

1), which was the best-sampled area. Because each flock gathers at the same point at the start of each day, each day's path of motion within the territory is independent of the previous days'. This daily resetting allows us to assume that a recorded flock position one day is independent from a position recorded on another day, so we let each $\mathbf{x}_n$ be a randomly selected position from a single flock on a single day. To avoid bias from the random selection, we considered all possible sets of such positions $\mathbf{x}_1 ,\ldots, \mathbf{x}_N$ and took the average of the various values of $l(\mathbf{x}_1 ,\ldots, \mathbf{x}_N|\alpha)$. We denoted this average by $L(\mathbf{x}_1 ,\ldots, \mathbf{x}_N|\alpha)$.

Additionally, we also tested if home range area was correlated to mean vegetation height by using the same approach, but using entire home ranges for flocks located entirely in primary forest or secondary forest.

RESULTS

A total of 26 flocks were recorded, compiling 941 hours of observation in six different landscape compositions (min.= 0.05 h, max.= 10.4 h, mn = 3.9 h, se = 2.6 h) (Table 1, Table S7). Three flocks were recorded in three 10-ha fragments. Nine flocks in two 100-ha fragments, of which six were in contact with an edge. Two flocks in primary-secondary forest mix and three flocks entirely within secondary forest. Finally, nine flocks were entirely located in primary forest, of which four had contact to forest edge. No flocks were found in 1-ha fragments (Table 1). Each 10-ha fragment held one flock home range, while 100-ha fragments held about 10 (Fig.1, Fig. S3). Flocks in primary-secondary forest mix centered their home ranges in primary forest and extended their margins into secondary forest (Fig. S4).

TRAJECTORY ANALYSES.—Flocks tended to avoid, or quickly cross areas with clear understory, such as temporary ponds, even after water subsided (Fig. S1) and usually circled around large forest gaps (Figs. S2A, S2C, S3A, S4 & S5). On rare occasions, they quickly crossed open areas of up to 25 m. Overall, flocks generally did not enter vegetation below 5 m in height. Four out of ten flocks showed significant Rayleigh test values for tests on perpendicularity along forest edges, all of them being hard forest edges (Fig. 3) (Table S4). In such cases, flocks foraged along forest edges for lengths up to 30 m, with individuals moving up to 10 m into secondary forest. Forest edges were not used uniformly. Some sections were frequently used, while others were not visited at all (Figs. S2, S3 and S5). Flocks adjacent to well-developed second growth did not move parallel to forest edges, but concentrated their foraging at edge buffers.

Flock activity in secondary forests consisted mainly of forays. Average times and distances in secondary forest are listed in the online Supporting Information (Table S5). Flocks in 10-ha fragments showed little activity in secondary forests regardless of development stage while flocks in 100-ha fragments showed higher activity, and spent more time in better developed secondary forests. Flocks in primary-secondary forest mix showed a much higher activity and exhibited large maximum foray distances in secondary forest. Lastly, primary forest flocks next to well-developed secondary forests spent a high percentage of time in forays, but did not cover distances as great as in primary-secondary forest mix.

To assess the movement patterns inside landscape features, 121 different trajectories were analyzed (Fig. 4). The multinomial model was statistically significant (Likelihood ratio test: chi square 2138.7, $p<0.001$); but magnitude range was small, mostly between -0.5 and 1, with the exception of *fast* movements in 10-ha forests and along hard edges (Fig. 5, Table S6). Fast movements increased slightly in young secondary forests compared to older second growth, but their overall proportions were not consistently higher than what is predicted for primary forest and edges.

HOME RANGE ANALYSES.—All flocks located near edges entered secondary forest, and time spent there was correlated to the mean vegetation height in secondary forest ($R^2 = 0.519$, $F_{1,8} = 8.64$, $P = 0.0187$) (Fig. 6A, Fig. S6A). Despite higher use in well-developed secondary forests, flock home range cores remained in primary forest (Table 2 & Fig. 2). The only exception was recorded next to the best-developed area of secondary forest, where the home range core for one flock was located on the forest edge (Table 2, Fig. S5). Despite this, the area used in secondary forest was not correlated to mean vegetation height ($R^2 = 0.221$, $F_{1,8} = 2.274$, $P = 0.17$).

There were also flocks inhabiting secondary forest, but the one found in the least developed area of secondary forest was not consistently present throughout the sampling period. It was found in June 2010 led by one female *Thamnomanes caesius*. The same individual alongside a male was seen in October 2010, but neither were found in May 2011 after several visits to their former gathering area.

Total home range area showed a negative correlation to mean vegetation height ($R^2 = 0.31$, $F_{1,8} = 7.638$, $P = 0.013$) (Fig. 6B, Fig. S6B). The smallest home range was 6.7 ha in an area of primary forest with an average canopy height of 23.4 m, while the largest home range was 17.1 ha, in an area of secondary forest with an average canopy height of 13.1 m.

Flock kernel shapes responded to the layout of anthropogenic features (Fig. S7). The response of home range shapes and layout to vegetation, the value of α that maximizes $L(\mathbf{x}_1, \ldots, \mathbf{x}_N|\alpha)$, is α=0.065. Using the likelihood ratio test, the P-value associated with rejecting the null hypothesis in favor of the hypothesis that canopy height is a predictor of space use is P =

0.0000033. Regarding edge effects on home range shapes, this value of alpha means that if an area of primary forest of 30 m height is next to a 10 m tall secondary forest, flocks near the boundary between the two will be 3.7 times more likely to be found in the primary forest (*i.e.:* exp[0.065*(30-10)]).

DISCUSSION

Fine-scale spatial behavior has provided an unprecedented view of how secondary forests are perceived by an important set of the understory avifauna in central Amazonia. Despite being found using secondary forests, there is strong evidence that it is a sub optimal habitat for flocking species until forest structure approaches primary forests.

Trajectories revealed that flocks avoided short vegetation. Occasionally, flocks remained stationary or skirted edges before quickly crossing open areas. This indicates that less-developed secondary forests may be perceived as unfavorable, either due to fewer resources, higher depredation risk, or a combination of the two. Areas that are occasionally flooded, even when dry, were also bypassed, possibly due to the sparser understory. In fact, these temporary lagoons, a common feature in *terra firme* forests, have a noticeable effect on flock space use and should be taken into account when considering their spatial behavior.

The fact that flocking species could move and forage so close to forest edges indicates some tolerance to edge habitat. This finding was not surprising given results from previous studies in the same area (Develey & Stouffer 2001); however, the fact that few flocks visited edges and only small sections were frequently used suggests that it is not optimal habitat and may only offer resources under specific conditions. It has been shown that flocks are more likely to move into lower terrain such as stream valleys (Potts *et al.* 2014[a]) and edge segments that overlapped with these topographical features were frequently visited (Fig. S2, S3). The behavior of moving short distances between primary and secondary forest along forest edges may be due to arthropod spillover from primary forest (Lucey & Hill 2011). While movement parallel to edges tended to disappear near well-developed secondary forest, flock activity was still concentrated within primary forest limits (Fig. S5). This suggests that while trajectories normalize with secondary forest development, overall space use is still affected.

Flocks near edges showed reluctance to cross over to secondary forests. Some species like *Thamnomanes caesius*, *Xiphorhynchus pardalotus* and *Xenops minutus* were more prone to enter less-developed secondary forest than other species, such as *Myrmotherula longipennis*, *M. menetriesii* and *Thamnomanes ardesiacus,* which tended to avoid less-developed secondary forests. Occasionally, *T. caesius* entered secondary forests, while individuals from other species would remain inside primary forest near the edge. If the majority of the aggregation remained in primary forest, it would return. If the majority of the flock entered secondary forest, some species would still remain behind and would re-join the flock only when it returned to primary forest. During this process, individuals usually maintained some degree of movement, traveling along the forest edge. These processes partially explain the parallel, rectilinear movements near hard edges and suggest some form of collective decision-making for habitat use even when *T. caesius*, which typically leads flock movements, tries to lead the flock into secondary forest. Flock composition influence on space use; however, remains to be properly quantified.

We expected flocks to move faster and in more rectilinear fashion in secondary forests with more sinuous trajectories and slower movements in primary forests. Differences in movement mode proportions were not stark, but some movement patterns appeared to be associated with particular landscape elements. For example, fast and rectilinear bouts were recorded in secondary forests and inside 10-ha fragments, whereas the same behavior was not observed in primary forest. The mechanisms determining different movement behaviors, however, may not be effectively explained by forest height variables alone, and may be influenced by finer variables such as understory vegetation structure, flock composition and the presence of potential predators. It is also important to note that the number of flocks in certain habitat types, such as well-developed secondary forests, soft forest edges is relatively small. Therefore, more information should be gathered to increase certainty about drawn inferences.

Flock use of secondary forest responded strongly to development stage. It is important to note that flocks still anchored their territory cores in primary forest until vegetation reached an average height of 23 m, which is close to the mean height of primary forest (~25 m). While we acknowledge that mean vegetation height may not be the proximal cause determining space use, this metric seems to efficiently summarize vegetation structure and other properties relevant to birds (Hinsley *et al.* 2002, Hyde *et al.* 2006, Clawges *et al.* 2008). A possible explanation lies in prey density, which may respond to vegetation density due to microclimatic conditions buffering and available substrate (Kapos 1989, Laurance & Gomez 2005, Ewers & Banks-Leite 2013, Potts *et al* 2014[a]). Considering its importance to a significant number species, invertebrate density and its relation to structural conditions in the landscape remains a poorly studied and necessary line of inquiry.

Our results suggest that during forest regeneration, flocks incorporate secondary forest beyond previous vegetation borders, as hypothesized by Powell *et al.* (2016). Our results partially corroborate this model, but with one important difference: while time spent in secondary forests increases with its development, there is no clear relation between vegetation height and area of secondary forest that is used. Area seems to be largely influenced by terrain and territorial interactions. It is likely that pressure from neighbors inside large fragments pushes flocks near borders to secondary forests, while flocks eventually establishing in secondary forest contain territorial boundary expansion. Our previous work modeling flock spatial behavior suggests that these interactions are an important aspect on flock space use (Potts *et al.* 2014[b]).

Adding further evidence to the scarcity of resources in secondary forests, flocks located in secondary forests occupy much larger areas, effectively reducing densities by half when compared to pristine areas. The inverse relationship between territory size and resource, as well as habitat structure and resource density has been explored and described in this system as well as with other species (Huxley 1934, Litvaitis *et al.* 1986, Jullien & Thiollay 1998), but the possibility of other factors influencing territory size, such as predation risk and intruder pressure (Adams 2001, Willems & Hill 2009) should also be considered.

Flock home range layout was strongly affected by the layout of disturbed areas. Flock home range layout in primary forests seems to be mainly set by topography, but in altered areas, vegetation takes precedence. This is an important consideration, given that certain flocks may eventually be pushed into sub-optimal habitat under certain habitat configurations. This is reinforced by the observation of depauperate and unstable flocks in poorly-developed secondary forests. The mechanisms underlying the intermittent occupation of these areas remain to be investigated, and may be related to a lack of resources, predation, or both. Lastly, even large and nearly equilateral fragments (100 ha) are bound to have up to 70% of flocks in contact with an edge, which may have impacts on demographic processes and territorial dynamics.

In summary, Amazonian mixed-species flocks tolerate secondary forests, but they seem to comprise sub-optimal habitat resulting in a rearrangement of territories in the landscape. Spatial behavior only becomes roughly equivalent to primary forest after mean vegetation height reaches 23 meters or more with a well-preserved understory. It is important to highlight that composition data from the same study area show flocks to be less cohesive even in well-developed secondary forests, implying that flock composition and participation may take much longer to recover than spatial behavior (Mokross & Ryder *et al.* 2014).

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.8vn80rv (Mokross *et al*. 2018).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

APPENDIX S1. Lidar specifications and kernel parameters.

TABLE S1. *Parameters used in the partlmod function to define the three movement modes*.

TABLE S2. *Flocks and the respective habitat features inside each landscape element*.

TABLE S3. *Mean vegetation height in each kernel isopleth for each flock territory analyzed.*

TABLE S4. *V test results of trajectory step absolute angles in relation to forest edge angle.*

TABLE S5. *Forays into secondary forest by mixed-species flocks.*

TABLE S6. *Results of the multinomial model.*

TABLE S7. *Sampling effort for each flock ordinated by date.*

FIGURE S1. Mixed-species flock trajectories near temporary puddles.

FIGURE S2. Trajetories displayed by flocks in 10-ha fragments.

FIGURE S3. Trajectories displayed by flocks in 100-ha fragments.

FIGURE S4. Trajectories displayed by flocks in primary-secondary forest mix.

FIGURE S5. Trajectories displayed by flocks next to soft borders.

FIGURE S6. Home range analysis.

FIGURE S7. Flock territorial configuration.

LITERATURE CITED

ADAMS, E. S. 2001. Approaches to the study of territory size and shape. Annu. Rev. Ecol. Syst. 32: 277–303.

BARLOW, J. ET AL. 2007. Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. Proc. Natl. Acad. Sci. U. S. A. 104: 18555–60.

BARLOW, J., T. A. GARDNER, J. LOUZADA, and C. A. PERES. 2010. Measuring the Conservation Value of Tropical Primary Forests: The Effect of Occasional Species on Estimates of Biodiversity Uniqueness. PLoS One 5: 1–8.

BARLOW, J., C. A. PERES, L. M. P. HENRIQUES, P. C. STOUFFER, and J. M. WUNDERLE. 2006. The responses of understorey birds to forest fragmentation, logging and wildfires: An Amazonian synthesis. Biol. Conserv. 128: 182–192.

BATSCHELET, E. 1981. Circular Statistics in Biology C. Sibson R. J. (Ed.). Academic Press, New York.

BEYER, H. L. 2012. Geospatial Modelling Environment.

BIERREGAARD, R., S. LAURANCE, C. GASCON, and R. MESQUITA. 2001. Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest.

BORGES, S. H., and P. C. STOUFFER. 1999. Bird communities in two types of anthropogenic successional vegetation in central Amazonia. Condor 101: 529–536.

CALENGE, C., S. DRAY, and M. ROYER-CARENZI. 2008. The concept of animals â€TM trajectories from a data analysis perspective. Ecol. Inform. 4: 34–41.

CARTER, N., S. LEVIN, A. BARLOW, and V. GRIMM. 2015. Modeling tiger population and territory dynamics using an agent-based approach. Ecol. Modell. 312: 347–362.

CHAZDON, R. L., C. A. PERES, D. DENT, D. SHEIL, A. E. LUGO, D. LAMB, N. E. STORK, and S. E. MILLER. 2009. The Potential for Species Conservation in Tropical Secondary Forests. Conserv. Biol. 23: 1406–1417.

CLAWGES, R., K. VIERLING, L. VIERLING, and E. ROWELL. 2008. The use of airborne lidar to assess avian species diversity, density, and occurrence in a pine/aspen forest. Remote Sens. Environ. 112: 2064–2073.

DARRAH, A. J., and K. G. SMITH. 2013. Comparison of foraging behaviors and movement patterns of the wedge-billed woodcreeper (*Glyphorynchus spirururs*) traveling alone and in mixed-species flocks in Amazonian Ecuador. Auk 130: 629–636.

DENT, D. H., and J. S. WRIGHT. 2009. The future of tropical species in secondary forests: A quantitative review. Biol. Conserv. 142: 2833–2843.

DEVELEY, P. F., and P. C. STOUFFER. 2001. Effects of roads on movements by understory birds in mixed-species flocks in central Amazonian Brazil. Conserv. Biol. 15: 1416–1422.

DIDHAM, R. K. 2011. Life After Logging: Strategic Withdrawal from the Garden of Eden or Tactical Error for Wilderness Conservation? Biotropica 43: 393–395.

DOLBY, A. S., and T. C. GRUBB. 1999. Functional roles in mixed-species foraging flocks: A field manipulation. Auk 116: 557–559.

EWERS, R. M., and C. BANKS-LEITE. 2013. Fragmentation impairs the microclimate buffering effect of tropical forests. PLoS One 8: e58093.

GARDNER, T. A., J. BARLOW, R. CHAZDON, R. M. EWERS, C. A. HARVEY, C. A. PERES, and N. S. SODHI. 2009. Prospects for tropical forest biodiversity in a human-modified world. Ecol. Lett. 12: 561–582.

GIUGGIOLI, L., and F. BARTUMEUS. 2010. Animal movement, search strategies and behavioural ecology: A cross-disciplinary way forward. J. Anim. Ecol. 79: 906–909.

GOODALE, E., and S. W. KOTAGAMA. 2005. Testing the roles of species in mixed-species bird flocks of a Sri Lankan rain forest. J. Trop. Ecol. 21: 669–676.

GRIMM, V. ET AL. 2006. A standard protocol for describing individual-based and agent-based models. Ecol. Modell. 198: 115–126.

HADDAD, N. M. ET AL. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci. Adv. 1.

HANSBAUER, M. M., I. STORCH, F. KNAUER, S. PILZ, H. KUECHENHOFF, Z. VEGVARI, R. G. PIMENTEL, and J. P. METZGER. 2010. Landscape perception by forest understory birds in the Atlantic Rainforest: black-and-white versus shades of grey. Landsc. Ecol. 25: 407–417.

HINSLEY, S. A., R. A. HILL, D. L. A. GAVEAU, and P. E. BELLAMY. 2002. Quantifying woodland structure and habitat quality for birds using airborne laser scanning. Funct. Ecol. 16: 851–857.

HUXLEY, J. S. 1934. A natural experiment on the territorial instinct. Brit. Birds 27: 270–277.

HYDE, P., R. DUBAYAH, W. WALKER, J. B. BLAIR, M. HOFTON, and C. HUNSAKER. 2006. Mapping forest structure for wildlife habitat analysis using multi-sensor (LiDAR, SAR/InSAR, ETM plus , Quickbird) synergy. Remote Sens. Environ. 102: 63–73.

JIRINEC, V., B. R. CAMPOS, and M. D. JOHNSON. 2011. Roosting behaviour of a migratory songbird on Jamaican coffee farms: landscape composition may affect delivery of an ecosystem service. Bird Conserv. Int. 21: 353–361.

JOHNSON, E. I., P. C. STOUFFER, and C. F. VARGAS. 2011. Diversity, biomass, and trophic structure of a central amazonian rainforest bird community. Rev. Bras. Ornitol. 19: 1–16.

JONES, J. 2001. Habitat selection studies in avian ecology: A critical review. Auk 118: 557–562.

JULLIEN, M., and J. M. THIOLLAY. 1998. Multi-species territoriality and dynamic of neotropical forest understorey bird flocks. J. Anim. Ecol. 67: 227–252.

KAPOS, V. 1989. Effects Of Isolation On The Water Status Of Forest Patches In The Brazilian Amazon. J. Trop. Ecol. 5: 173–185.

LAURANCE, S. G. W., and M. S. GOMEZ. 2005. Clearing width and movements of understory rainforest birds. Biotropica 37: 149–152.

LAURANCE, W. F. 2002. Hyperdynamism in fragmented habitats. J. Veg. Sci. 13: 595–602.

LIMA, S. L., and P. A. ZOLLNER. 1996. Towards a behavioral ecology of ecological landscapes. Trends Ecol. Evol. 11: 131–135.

LITVAITIS, J. A., J. A. SHERBURNE, and J. A. BISSONETTE. 1986. Bobcat Habitat Use and Home Range Size in Relation to Prey Density. J. Wildl. Manage. 50: 110–117.

LUCEY, J. M., and J. K. HILL. 2011. Spillover of Insects from Rain Forest into Adjacent Oil Palm Plantations. Biotropica 44: 368–377.

LUND, U., and C. AGOSTINELLI. 2001. CircStats: Circular Statistics, from “Topics in circular Statistics.”

MARRIS, E. 2009. Ecology: Ragamuffin Earth. Nature 460: 450–453.

MARTÍNEZ, A. E., J. P. GOMEZ, and A. E. MARTI. 2013. Are Mixed-Species Bird Flocks Stable through Two Decades ? 181.

MARTINEZ, A. E., and R. T. ZENIL. 2012. Foraging guild influences dependence on heterospecific alarm calls in Amazonian bird flocks. Behav. Ecol. 23: 544–550.

MESQUITA, R., K. ICKES, G. GANADE, and G. B. WILLIAMSON. 2001. Alternative successional pathways in the Amazon Basin. J. Ecol. 89: 528–537.

MOKROSS, K., T. B. RYDER, M. C. CÔRTES, J. D. WOLFE, and P. C. STOUFFER. 2014.

Decay of interspecific avian flock networks along a disturbance gradient in Amazonia. Proc. R. Soc. B Biol. Sci. 281: 01–10.

MOKROSS, K., J. POTTS, C. L. RUTT, AND P. C. STOUFFER. 2018. Data from: What can mixed-species flock movement tell us about the value of Amazonian secondary forests? Insights from spatial behavior. Dryad Digital Repository. doi:10.5061/dryad.8vn80rv

MOORCROFT, P. R., and A. BARNETT. 2008. Mechanistic home range models and resource selection analysis: A reconciliation and unification. Ecology 89: 1112–1119.

MOORCROFT, P. R., M. A. LEWIS, and R. L. CRABTREE. 2006. Mechanistic home range models capture spatial patterns and dynamics of coyote territories in Yellowstone. Proc. R. Soc. B-Biological Sci. 273: 1651–1659.

MUNN, C. A. 1986. Birds that cry wolf. Nature 319: 143–145.

MUNN, C. A., and J. W. TERBORGH. 1979. Multi-species territoriality in Neotropical foraging flocks. Condor 81: 338–347.

NEEFF, T., R. M. LUCAS, J. R. DOS SANTOS, E. S. BRONDIZIO, and C. C. FREITAS. 2006. Area and Age of Secondary Forests in Brazilian Amazonia 1978--2002: An Empirical Estimate. Ecosystems 9: 609–623.

POTTS, J. R., K. MOKROSS, P. C. STOUFFER, and M. A. LEWIS. 2014[a]. Step selection techniques uncover the environmental predictors of space use patterns in flocks of Amazonian birds. Ecol. Evol. 4:4578-4588.

POTTS., J. R., K. MOKROSS, and M. A. LEWIS. 2014[b]. A unifying framework for quantifying the nature of animal interactions. J. R. Soc. Interface 11:20140333.

POWELL, G. V. N. 1985. Sociobiology and Adaptive Significance of Interspecific Foraging Flocks in the Neotropics. Ornithol. Monogr. 36: 713–732.

POWELL, L. L., J. D. WOLFE, E. I. JOHNSON, and P. C. STOUFFER. 2016. Forest recovery in post-pasture Amazonia: Testing a conceptual model of space use by insectivorous understory birds. Biol. Conserv. 194: 22–30.

R DEVELOPMENT CORE TEAM. 2016. R: A language and environment for statistical computing.

SEAMAN, D. E., and R. A. POWELL. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77: 2075–2085.

STOUFFER, P. C. 2007. Density, territory size, and long-term spatial dynamics of a guild of terrestrial insectivorous birds near Manaus, Brazil. Auk 124: 291–306.

STOUFFER, P. C., and R. O. BIERREGAARD. 1995. Use of Amazonian Forest Fragments by Understory Insectivorous Birds. Ecology 76: 2429–2445.

SULLIVAN, K. A. 1984. The advantages of social foraging in Downy Woodpeckers. Anim. Behav. 32: 16–22.

TERBORGH, J., S. K. ROBINSON, T. A. PARKER, C. A. MUNN, and N. PIERPONT. 1990. Structure and Organization of an Amazonian Forest Bird Community. Ecol. Monogr. 60: 213–238.

THIOLLAY, J. M. 1997. Disturbance, selective logging and bird diversity: A Neotropical forest study. Biodivers. Conserv. 6: 1155–1173.

WILLEMS, E. P., and R. A. HILL. 2009. Predator-specific landscapes of fear and resource distribution: effects on spatial range use. Ecology 90: 546–555.

FIGURES

FIGURE 1. (A) Map of the BDFFP. White boxes represent areas where flocks were sampled. (B) LIDAR coverage of one of these areas (Dimona ranch) and examples of home ranges of flocks in different landscape elements. From left to right: 10-ha fragment (yellow), secondary forest (red), primary-secondary forest mix (white) and 100-ha fragment (lime green), other studied flocks are shown lighter shades than the examples. Flocks are generally absent in areas of scrubby vegetation (light grey), such as the buffers around fragments. The flock with a red asterisk was considered unstable as it was not detected in subsequent sampling periods. Darker colors represent areas of taller vegetation based on Lidar data.

FIGURE 2. Depiction of a flock home range (FL_IB) adjacent to secondary forest. Home range is represented by isopleths ranging from 10% (areas of highest use density) to 99% (edges of home range). Black dots are locations taken at 30-second intervals. The section of home range occupying secondary forest is shaded in dark gray. Red line shows the edge between primary and secondary forest. Height of individual trees appears in green, with darker green representing taller trees. Notice that flock home range cores (>50%) are located in primary forest.

FIGURE 3. Trajectory angles in relation to forest edges for a 10-ha fragment flock (Dimona). North and south edges are highlighted in blue, while east and west facing edges are highlighted in red. The rose diagrams indicate the distribution of directions for each edge set, highlighted in the same color code.

FIGURE 4. (A) Example of a trajectory that was partitioned using the *partmodltraj* function. The blue triangle represents the beginning of the trajectory and the red square the end. The flock enters secondary forest, eventually returning to primary forest while changing its movement patterns. Vegetation is shown by a Lidar-derived canopy height model, where darker shades represent taller vegetation. Movement models are color coded: *Area restricted behavior* (ARB) in blue, *normal* movement modes in yellow, *fast* movements are in red. This frame is a subset of the trajectories in the following panel. (B) Primary-secondary forest mix (Ig. Cmp. Flk). (C) Primary-secondary forest mix (FLIA). (D) 10 ha-fragment (Dimona).

FIGURE 5. Prediction from the multinomial model on the proportions (represented as percentages) of movement modes inside each landscape element. **PF**: Primary forest, **ED**: Edge (20 m at each side of forest-secondary forest interface), **SF**: Secondary forest. Under PF, the types are **CF**: Continuous forest, **10ha**: 10ha-forest fragment, **100ha**: 100ha-forest fragment, **MIX**: primary-secondary forest mix. ED types are **S**: soft edges and **H**: hard edges. SF types are **Wd**: Well-developed secondary forest and **Ld**: Less-developed secondary forest. Blue color represent partitions categorized as *Area Restricted Behavior*, red Colors indicate *Fast* movement behavior and Yellow is *Normal* movement behavior. The bars with black outlines represent the averaged proportions of movement modes in each landscape element.

FIGURE 6. (A) Flocks adjacent to secondary forest: relation between time spent in secondary forest and mean vegetation height of second-growth. (B) Relationship between total home range area and mean canopy height.

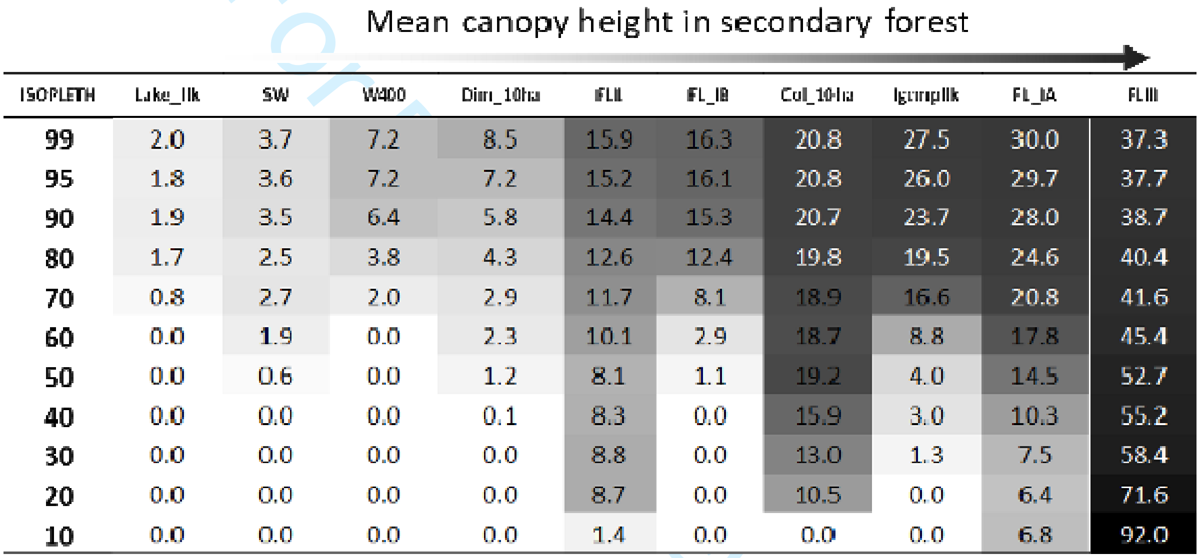
TABLES

TABLE 1. Understory mixed-species flocks sampled in the study. Habitat types are: 100-ha/edge: flocks located in 100-ha fragments with contact to edge; 100-ha/interior: flocks located in 100-ha fragments located at the center of the fragment, surrounded by neighboring flocks and having with no contact with forest edge; 10-ha: flocks located in 10-ha fragments, their home ranges are surrounded by forest edges; prim./sec.: flocks located in areas with a patches of primary and secondary forest; primary edge: flocks located in areas of primary forest that interface with secondary forest; primary interior: flocks in primary forest with no contact to forest edge; secondary forest: flocks in which the entire home range occupies secondary forest. Total hours sampled, and total hours sampled in the dry season. * Unstable flock - see text . ** Flocks in *Cecropia* secondary forest without Lidar coverage for which we could analyze vegetation height.

Area	**Flock**	**Habitat type**	**Total Hours**	**Total Hours (dry)**
Dimona	Cap_II	second growth	23	23
	Cap_N	second growth	20	20
	Central	100-ha /interior	101	61
	Dim_10ha	10-ha	121	81
	Ig_cmp_flk	prim. /sec.	83	43
	Lake_flk	100-ha /border	20	20
	South_Central	100-ha /interior	20	20
	Southwest	100-ha /border	20	20
	W400	100-ha /border	39	39
Colosso	Col_10ha	10-ha	95	55
	Col_cabfrioI	primary border	20	20
	Col_Cap1ha	second growth	86	46
Florestal	Fl_a	prim. /sec.	21	21
	Fl_I_b	primary border	20	20
	Fl_II	primary border	74	34
	Fl_III	primary border	21	21
Gavião	Gav_10_ha	primary interior	20	20

	Gavião_I	primary interior	22	22
	Gavião_II	primary interior	20	20
Km37	Km37_III	primary interior	20	20
	Km37_V	primary interior	17	17
Porto Alegre	PA_10ha**	10-ha	23	23
	PA1**	100-ha /border	12	12
	PA2**	100-ha /border	7	7
	PA3**	100-ha /border	10	10
	PA4**	100-ha /interior	5	5
Total			**941**	**700**

TABLE 2. Percentage of time mixed-species flocks spent in secondary forest. First column shows kernel isopleths from complete home ranges (99%) to areas of most intense use, or home range core areas (10%). Cells are color-coded: higher percentages of time in secondary forest are darker. Flock IDs ordered from lowest to highest percentage of total home range area in second growth.



Mean canopy height in secondary forest

ISOPLETH	Lake_llk	SW	W400	Dim_10ha	FLII	FL_IB	Col_10-ha	Igarapllk	FL_IA	FLIII
99	2.0	3.7	7.2	8.5	15.9	16.3	20.8	27.5	30.0	37.3
95	1.8	3.6	7.2	7.2	15.2	16.1	20.8	26.0	29.7	37.7
90	1.9	3.5	6.4	5.8	14.4	15.3	20.7	23.7	28.0	38.7
80	1.7	2.5	3.8	4.3	12.6	12.4	19.8	19.5	24.6	40.4
70	0.8	2.7	2.0	2.9	11.7	8.1	18.9	16.6	20.8	41.6
60	0.0	1.9	0.0	2.3	10.1	2.9	18.7	8.8	17.8	45.4
50	0.0	0.6	0.0	1.2	8.1	1.1	19.2	4.0	14.5	52.7
40	0.0	0.0	0.0	0.1	8.3	0.0	15.9	3.0	10.3	55.2
30	0.0	0.0	0.0	0.0	8.8	0.0	13.0	1.3	7.5	58.4
20	0.0	0.0	0.0	0.0	8.7	0.0	10.5	0.0	6.4	71.6
10	0.0	0.0	0.0	0.0	1.4	0.0	0.0	0.0	6.8	92.0

SUPPORTING INFORMATION

What can mixed-species flock movement tell us about the value of Amazonian secondary forests? Insights from spatial behavior

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APPENDIX S1.

Lidar specifications

Vegetation was measured using LIDAR (Light Detection and Ranging) canopy height models (CHM) provided by Scott Saleska (University of Arizona) and Michael Lefsky (Colorado State University). Similarly, topography (Digital Elevation Models DEM) was acquired using small footprint airborne LIDAR. The derived (post-processed) images from the LIDAR data are 1m/pixel resolution, which we transformed into 10m lattices by bilinear interpolation. LIDAR data were collected by airborne laser scanning using a Hexagon-LEICA ALS50 PHASE II MPiA sensor of 150 kHz, at 800 m altitude, with 24 degrees opening, 118 MHz pulse rate, 58 Hz scan rate, 3,7 points/m2 density. Swaths were of 340 meters wide, spaced at 240 meters. Postprocessing used a Forest Service methodology to generate DEM and CHM at 1 m2/pixel [see Stark et al. (2012) for more details on LIDAR data collection and analysis].

Kernel Parameters

Kernels were created using the Geospatial modelling environment at 1m resolution, 275 bandwidth (*i.e.*, radius of a circle in which points are counted around each pixel) at default scaling factor (*i.e.*, a value that the point density values are multiplied for scaling). We chose these settings because the kernels were more conservative when considering total home range extent.

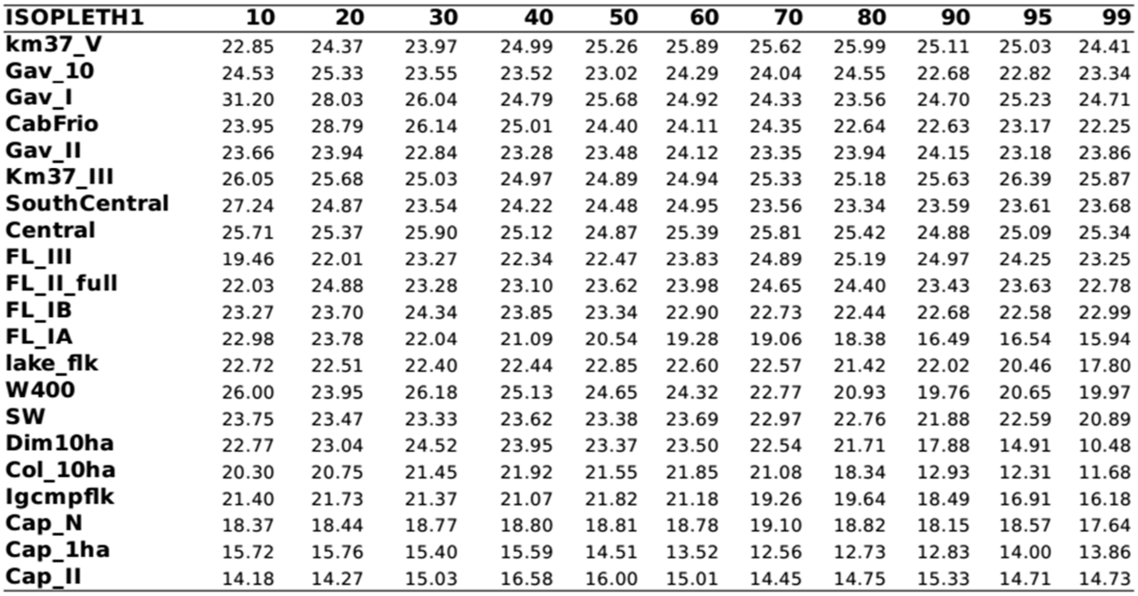
TABLE S1. Parameters used in the partlmod function to define the three movement modes. Step length distributions are normal, while I used a Von Mises distribution for turning angles.

	Angle		**Step length**	
Distribution	**Wrapped cauchy**		**Normal distr.**	
Parameter	**μ**	**P**	**mean**	**SD**
Fast	0	0,5	17	7
Normal	0	0,5	9	3
ABR	180	0,5	3	3

TABLE S2. Flocks and the respective habitat features inside each landscape element. **PF**: Primary forest, **SF**: Secondary forest, **ED**: Edge (20 m at each side of forest-secondary forest interface). Under PF, the types are **100ha**: 100ha-forest fragment, **MIX**: primary-secondary forest mix, **CF**: Continuous forest, **10ha**: 10ha-forest fragment. ED types are **S**: soft edges and **H**: hard edges. SF types are **Wd**: Well-developed secondary forest and **Ld**: Less-developed secondary forest.

Flock	**PF**	**SF**	**ED**
w400	100ha	Ld	H
SW	100ha	Ld	H
Lake	100ha	Ld	H
igcmp	MIX	Ld	S
FLIII	CF	Wd	S
FL_II	CF	Wd	S
FL_IB	CF	Wd	S
FL_IA	MIX	Ld	H
Dim10	10ha	Ld	H
Col10	10ha	Ld	H

TABLE S3. Mean vegetation height (in meters) in each kernel isopleth for each flock territory analyzed. This data includes entire isopleths, without separation between primary and secondary forest. 99% isopleths represent entire home ranges, while 10% isolpleths represent areas of higher use density.



ISOPLETH1	10	20	30	40	50	60	70	80	90	95	99
km37_V	22.85	24.37	23.97	24.99	25.26	25.89	25.62	25.99	25.11	25.03	24.41
Gav_10	24.53	25.33	23.55	23.52	23.02	24.29	24.04	24.55	22.68	22.82	23.34
Gav_I	31.20	28.03	26.04	24.79	25.68	24.92	24.33	23.56	24.70	25.23	24.71
CabFrio	23.95	28.79	26.14	25.01	24.40	24.11	24.35	22.64	22.63	23.17	22.25
Gav_II	23.66	23.94	22.84	23.28	23.48	24.12	23.35	23.94	24.15	23.18	23.86
Km37_III	26.05	25.68	25.03	24.97	24.89	24.94	25.33	25.18	25.63	26.39	25.87
SouthCentral	27.24	24.87	23.54	24.22	24.48	24.95	23.56	23.34	23.59	23.61	23.68
Central	25.71	25.37	25.90	25.12	24.87	25.39	25.81	25.42	24.88	25.09	25.34
FL_III	19.46	22.01	23.27	22.34	22.47	23.83	24.89	25.19	24.97	24.25	23.25
FL_II_full	22.03	24.88	23.28	23.10	23.62	23.98	24.65	24.40	23.43	23.63	22.78
FL_IB	23.27	23.70	24.34	23.85	23.34	22.90	22.73	22.44	22.68	22.58	22.99
FL_IA	22.98	23.78	22.04	21.09	20.54	19.28	19.06	18.38	16.49	16.54	15.94
lake_flk	22.72	22.51	22.40	22.44	22.85	22.60	22.57	21.42	22.02	20.46	17.80
W400	26.00	23.95	26.18	25.13	24.65	24.32	22.77	20.93	19.76	20.65	19.97
SW	23.75	23.47	23.33	23.62	23.38	23.69	22.97	22.76	21.88	22.59	20.89
Dim10ha	22.77	23.04	24.52	23.95	23.37	23.50	22.54	21.71	17.88	14.91	10.48
Col_10ha	20.30	20.75	21.45	21.92	21.55	21.85	21.08	18.34	12.93	12.31	11.68
lgcmpflk	21.40	21.73	21.37	21.07	21.82	21.18	19.26	19.64	18.49	16.91	16.18
Cap_N	18.37	18.44	18.77	18.80	18.81	18.78	19.10	18.82	18.15	18.57	17.64
Cap_1ha	15.72	15.76	15.40	15.59	14.51	13.52	12.56	12.73	12.83	14.00	13.86
Cap_II	14.18	14.27	15.03	16.58	16.00	15.01	14.45	14.75	15.33	14.71	14.73

TABLE S4. V test results of trajectory step absolute angles in relation to forest edge angle. All steps are within 20 m from forest edge. **Rbar** is the mean resultant length, **MuO** the axial angle of the border that flock absolute angles at each step are being compared to, Total sampled column indicates the number of steps that were used in the analysis, **% in EDGE** indicates the amount of time spent within 20 m of primary-secondary forest interface. Bold characters indicate significant results.

Flock	Rbar	P value	MuO	Total sampled	% in edge
Col10ha	0.093	**0.000**	328	2828	25.7
Dim10ha	0.064	**0.007**	36	3508	19.4
FLIA	0.104	**0.019**	298	643	31.4
FLIB	0.220	**0.033**	334	610	5.9
Igcmpflk	0.025	0.175	310	3004	23.5
Lake	0.069	0.263	216	614	10.6
FLIII	0.024	0.341	334	641	22.8
SW	0.027	0.393	282	619	8.1
FLII	-0.019	0.672	334	2587	11.4
w400	-0.128	0.957	36	1228	7.6

TABLE S5. Forays into secondary forest by mixed-species flocks. **Mean:** mean time spent in secondary forest, **st.err** : standart error, **min:** minimum foray distance, **max:** maximum foray distance, **MIX.avg:** primary-secondary forest mix average values; **CF.avg:** continuous forest flocks near edges average values; **100ha.LD:** Flocks in 100-ha fragments surrounded by less-developed forest average values **100ha.WD:** Flocks in 100-ha fragments surrounded by well-developed forest average values; **10ha.avg:** Flocks surrounded by less developed secondary forest. The flock that was sampled surrounded by well-developed secondary forest did not exit fragment after 18 hours of observation.

Flock	Mean	st.err	min	max
Igcmpflk	17,20	3,50	1,50	230,00
FLIA	23,34	8,90	1,50	127,00
MIX.avg	**20,27**	**6,20**	**1,50**	**178,50**
FLIB	27,79	23,80	2,00	171,00
FLII	15,31	4,97	1,50	102,50
FLIII	22,70	7,60	1,50	128,50
CF.avg	**21,93**	**12,12**	**1,67**	**134,00**
Lake	4,70	2,06	1,50	10,50
W400	25,42	11,93	1,50	62,00
SW	4,30	1,40	1,50	6,50
100ha.LD	**11,47**	**5,13**	**1,50**	**26,33**
PA_sw	14,05	6,57	1,5	68,5
PA_nw	12	6,63	1,5	43
PA_fl1	5,06	0,93	2	9
100ha.WD	**10,37**	**4,71**	**1,67**	**40,17**
Dim10	6,70	2,05	1,50	46,00
Col10	11,72	2,08	2,00	82,00
10ha.avg	**9,21**	**2,07**	**1,75**	**64,00**

TABLE S6. Results of the multinomial model.

The dependent variable was defined as the movement mode chosen at each step and the landscape features as individual-specific variables, each flock grouped as an individual (*id.var*) and within flock, each step as the choice ID (*chid.var*).

```
mlogit(formula = model ~ 1 | type, data = xml, reflevel="norm",
method="nr", print.level = 0)

Frequencies of movement modes in the dataset:
   norm    fast    slow
0.45641 0.23562 0.30798
```

TABLE S6A. Output from the multinomial model for landscape elements (PF:Primary forest, ED: Edge, SF: Secondary Forest) and landscape types (CF: Continuous Forest, 10ha: 10-ha Fragment, 100ha: 100-ha Fragment, MIX: Primary-secondary forest mix, S: soft forest edge, H: Hard forest edge, Wd: Well-developed secondary forest, Ld: Less developed secondary forest).

```
:
                   Estimate Std. Error  t-value  Pr(>|t|)
fast:(intercept) -1.608452   0.076891 -20.9185 < 2.2e-16 ***
slow:(intercept) -0.471188   0.050655  -9.3018 < 2.2e-16 ***
fast:type10ha     1.648418   0.084988  19.3958 < 2.2e-16 ***
slow:type10ha    -0.780239   0.074638 -10.4536 < 2.2e-16 ***
fast:typeH        1.449560   0.097666  14.8420 < 2.2e-16 ***
slow:typeH       -0.155753   0.085793  -1.8155   0.06945 .
fast:typeMIX     -0.260317   0.122480  -2.1254   0.03355 *
slow:typeMIX      0.483265   0.070580   6.8471 7.538e-12 ***
fast:typeWd       -0.173155   0.203267  -0.8519   0.39429
slow:typeWd       0.075875   0.123466   0.6145   0.53886
fast:typePF       0.569317   0.106029   5.3695 7.897e-08 ***
slow:typePF       0.389984   0.073955   5.2733 1.340e-07 ***
fast:typeS        0.171627   0.144934   1.1842   0.23635
slow:typeS        0.714418   0.087962   8.1219 4.441e-16 ***
fast:typeLd        0.505603   0.119983   4.2140 2.509e-05 ***
slow:typeLd        0.236348   0.085755   2.7561   0.00585 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Log-Likelihood: -12101
McFadden R^2:  0.081193
Likelihood ratio test : chisq = 2138.7 (p.value = < 2.22e-16)
```

TABLE S6B. Predicted values on proportion of movement modes in different landscape elements (PF:Primary forest, ED: Edge, SF: Secondary Forest) and landscape types (CF: Continuous Forest, 10ha: 10-ha Fragment, 100ha: 100-ha Fragment, MIX: Primary-secondary forest mix, S: soft forest edge, H: Hard forest edge, Wd: Well-developed secondary forest, Ld: Less developed secondary forest) from the multinomial model. These values are the same shown in Fig. 5.

Element	type	Normal	Fast	ARB
PF	**CF**	0.439	0.155	0.405
PF	**10ha**	0.430	0.447	0.123
PF	**100ha**	0.548	0.110	0.342
PF	**MIX**	0.462	0.071	0.467
PF average		**0.470**	**0.196**	**0.334**
ED	**S**	0.398	0.095	0.507
ED	**H**	0.419	0.357	0.224
ED average		**0.408**	**0.226**	**0.366**
SF	**Y**	0.471	0.156	0.373
SF	**O**	0.543	0.091	0.366
SF average		**0.507**	**0.124**	**0.369**

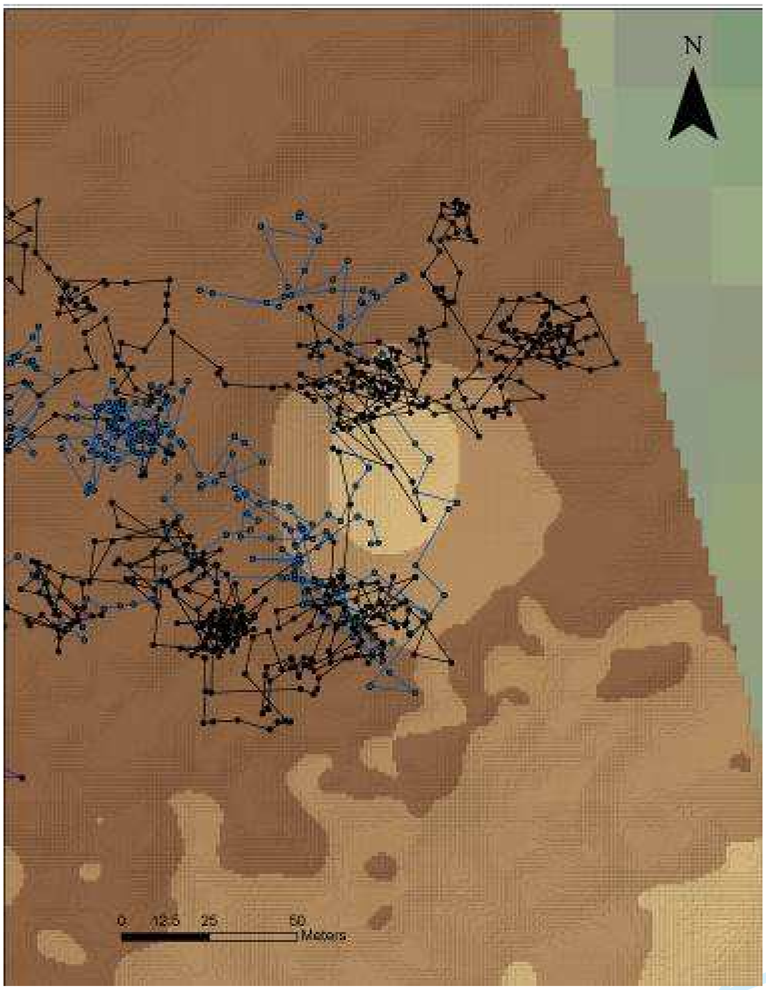


FIGURE S1. Mixed-species flock trajectories near temporary puddles. Flocks are able to cross these areas, but move considerably faster across these features, tending to concentrate activity at its fringes. Track colors correspond to sampling events two days apart for a continuous forest flock (Km37_V). Each step corresponds to 30 seconds. Darker colors in the topographic map correspond to higher ground. The puddle was dry at the time of sampling.

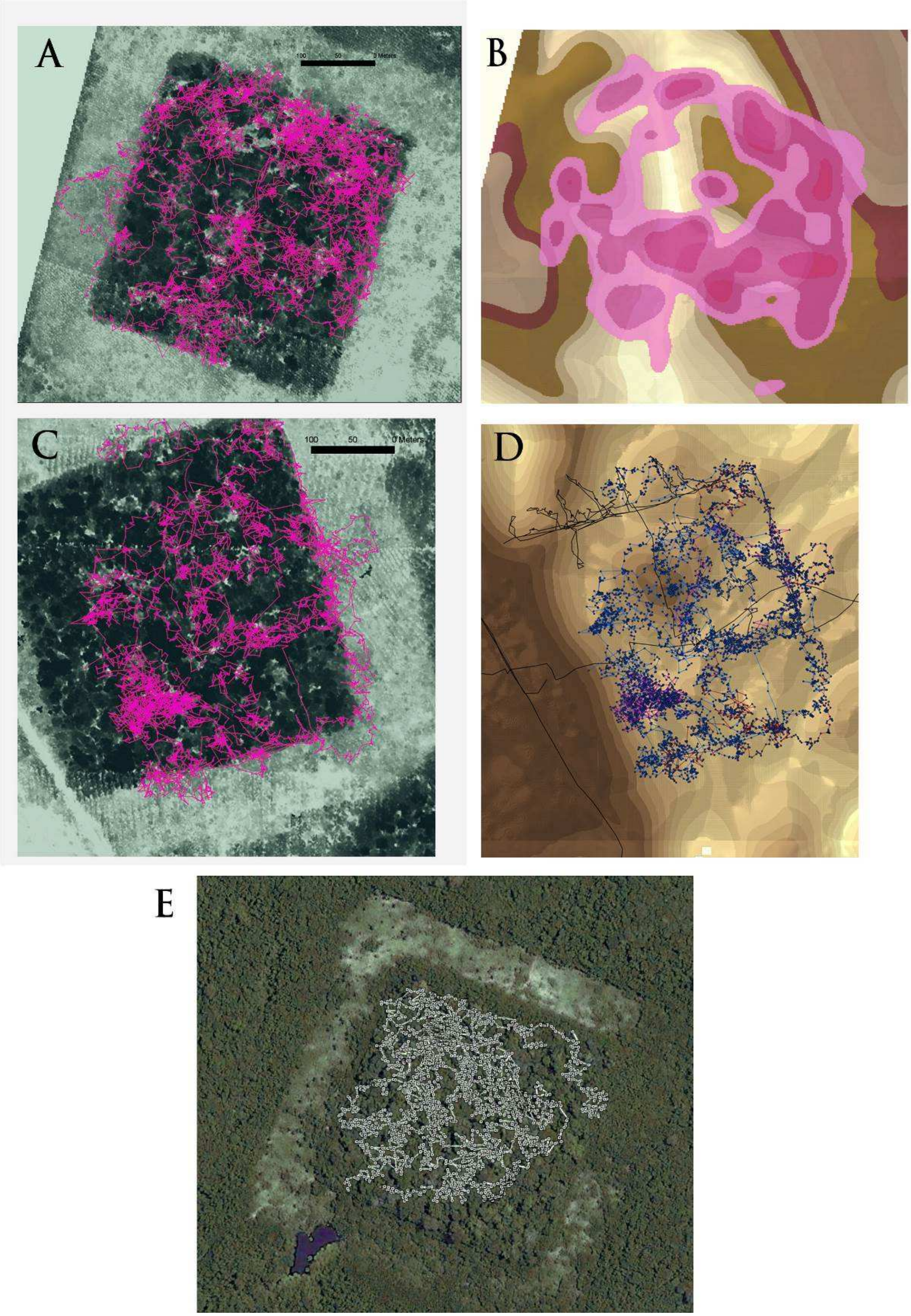


FIGURE S2. Trajetories displayed by flocks in 10-ha fragments. **A:** Dimona 10 ha, canopy height model (CHM) and trajectories. **B:** Dimona 10 ha digital elevation model (DEM) and kernel. **C:** Colosso 10 ha and CHM. **D:** Colosso 10 ha and DEM. **E:** Porto Alegre trajectories over Google Earth image.

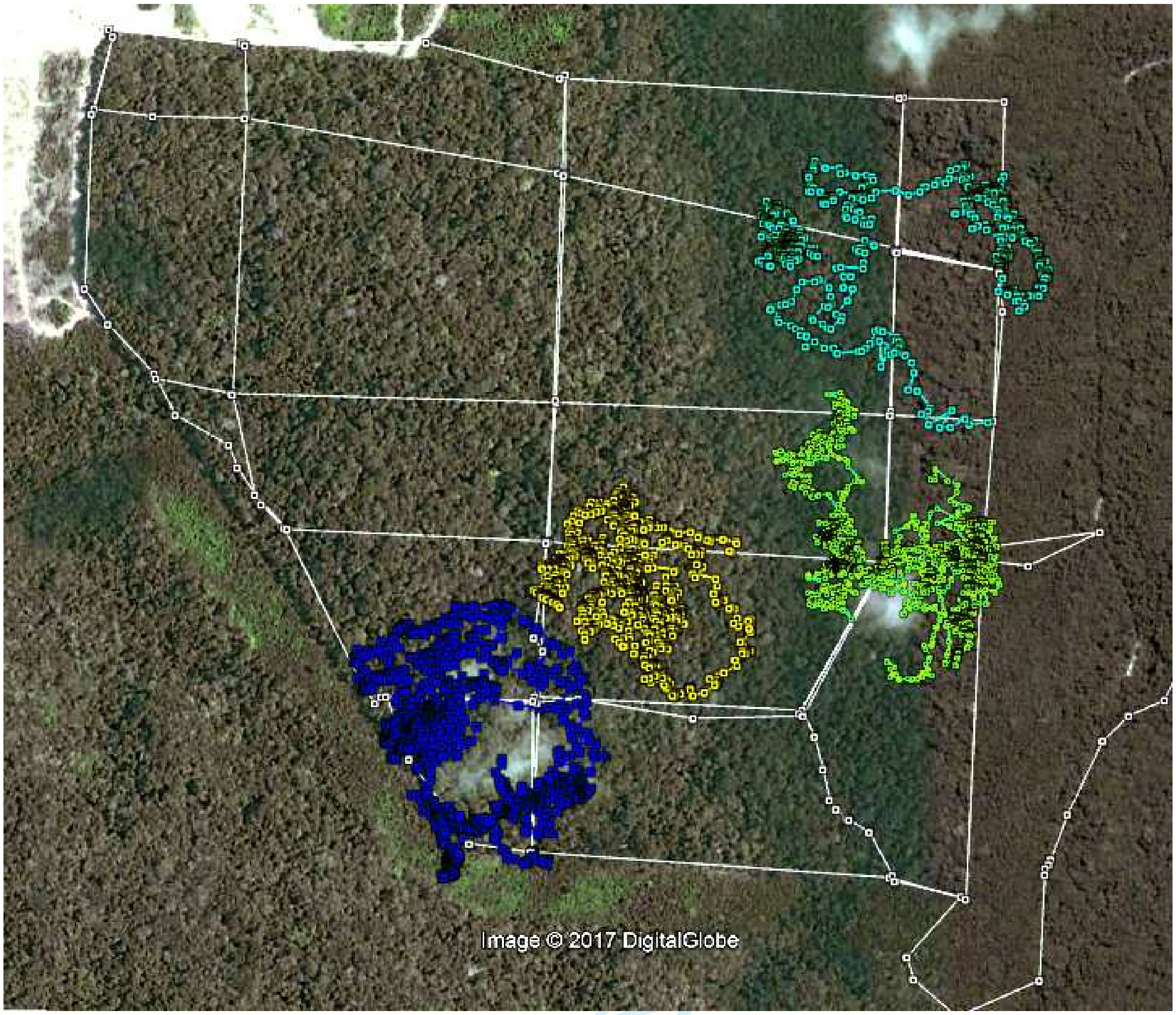


Image © 2017 DigitalGlobe

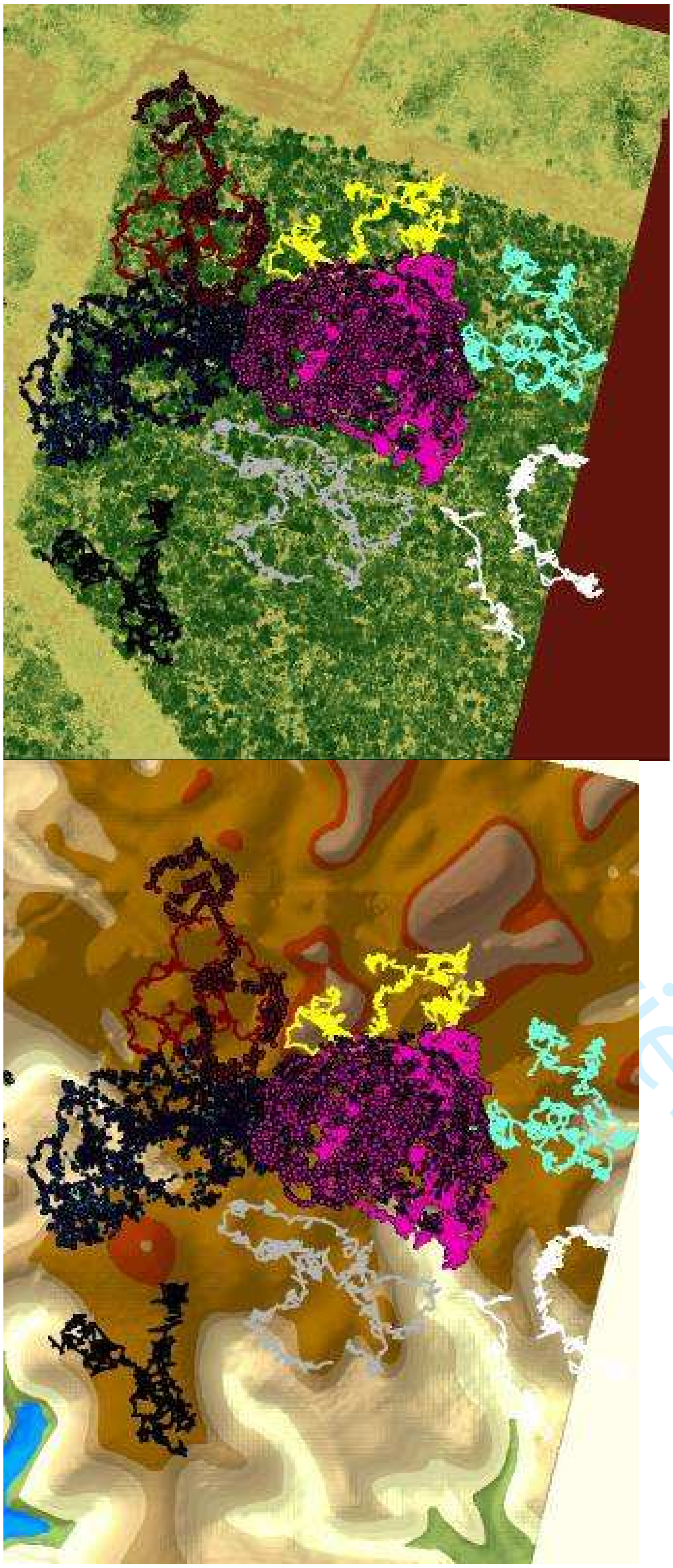


FIGURE S3. Trajectories displayed by flocks in 100-ha fragments. Each color represents one flock territory.**A.** Flocks in 100-ha fragment surrounded by well-developed secondary forest. Darker areas represent secondary forest. **B.** Flocks in a 100-ha fragment surrounded by less-developed secondary forest. **C.** Topographical map of flocks in a 100-ha fragment surrounded by less-developed secondary forest.

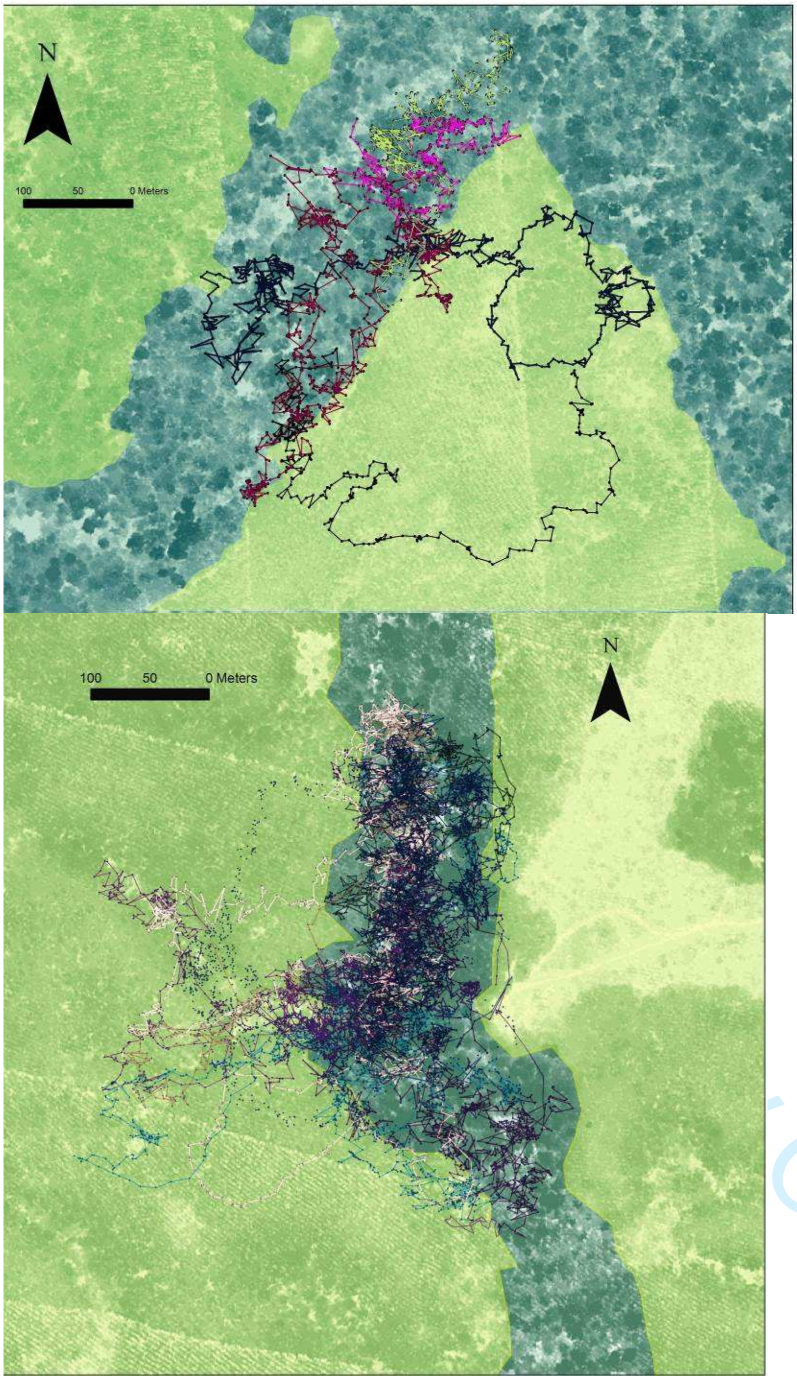


FIGURE S4. Trajectories displayed by flocks in primary-secondary forest mix. Secondary forests are highlighted in yellow. These flocks display deep forays in secondary forests compared to flocks in other landscape compositions. Top picture: Igcmp_flk, bottom: FLIA

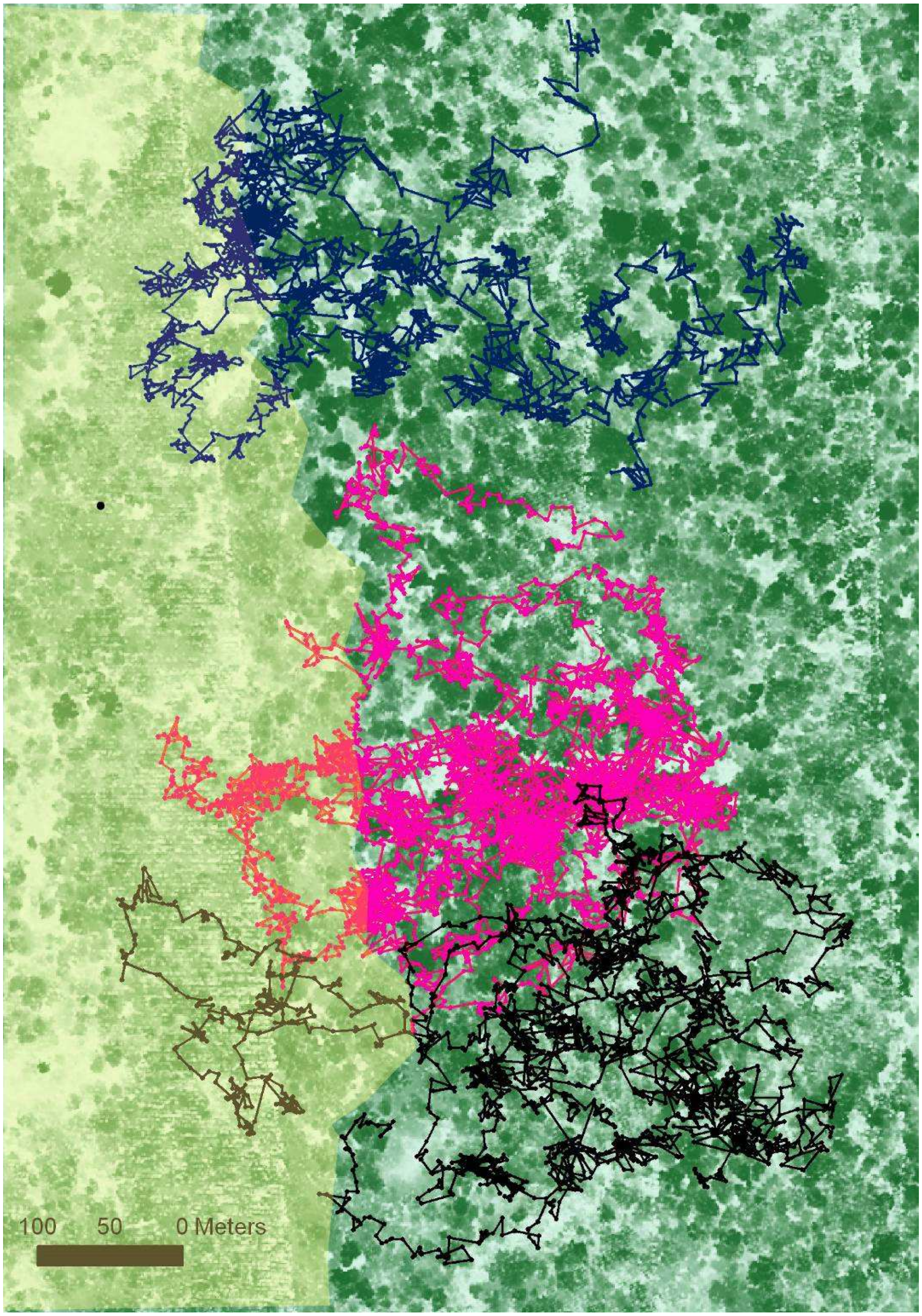


FIGURE S5. Trajectories displayed by flocks next to soft borders. Each color corresponds to a distinct flock territory. Top, in blue: FLIII. Middle, in red: FLII. Bottom, in black: FLIB.

FIGURE S6. **Home range analysis:** Quartile-quartile plot and Shapiro-Wilk normality test for A.time in secondary forest and B.home range area.

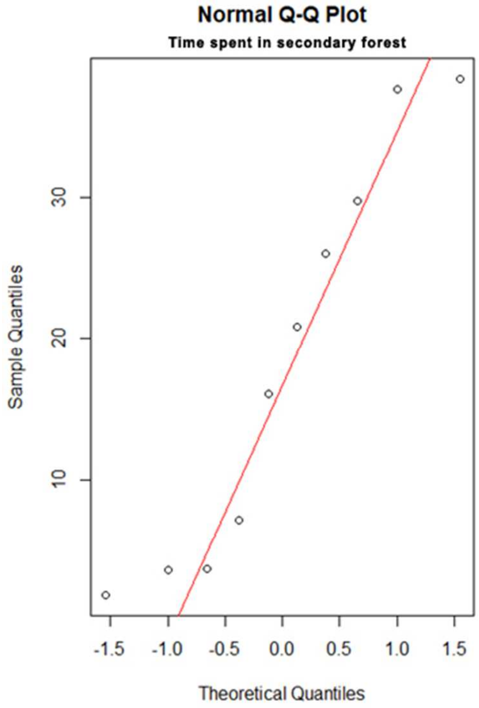


FIGURE S6A. Quantile-quantile plot for percentage values of time spent in secondary forest. Shapiro-Wilk normality test: `W = 0.89811, p-value = 0.2089`

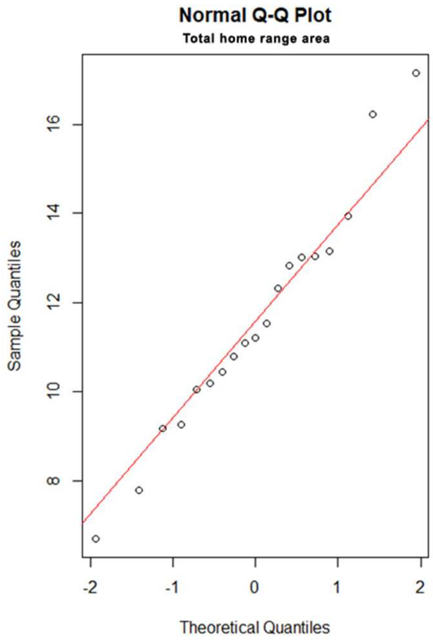


FIGURE S6B. Quantile-quantile plot for percentage values of home range area. Shapiro-Wilk normality test: W = 0.97656, p-value = 0.8954

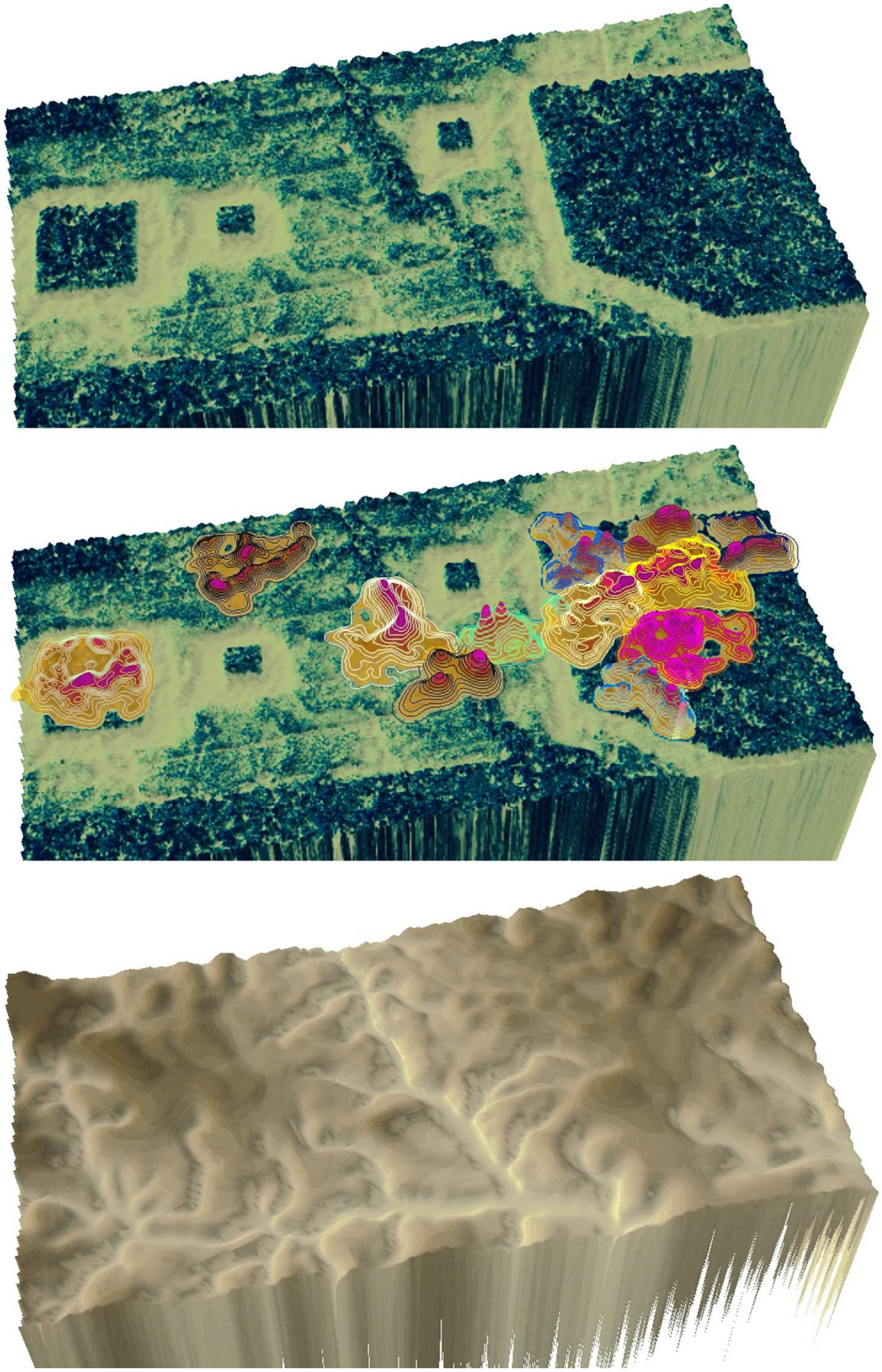


FIGURE S7. Flock territorial configuration. **A.** vegetation height map. **B.** flock kernels overlaid on vegetation map. Each color represents a different territory. Areas of higher proportion of use are represented as peaks and in red. **C.** Topographic map for the same area. Lighter colors represent lower elevation. Empty areas were not visited, but are assumed to hold territories, given the previous evidence that the landscape is saturated with flocks where vegetation conditions are appropriate.

TABLE S7. Sampling effort for each flock ordinated by date.

Site	Flock	Date	start	end	locations (30s)	hours
Porto Alegre	**PA3**	9-jun-09	7:35	12:36	604	5,03
Porto Alegre	**PA4**	9-jun-09	14:40	15:25	91	0,76
Porto Alegre	**PA_Cap**	10-jun-09	11:46	12:09	47	0,39
Porto Alegre	**PA2**	10-jun-09	13:44	14:25	82	0,68
Porto Alegre	**PA4**	10-jun-09	6:01	8:48	335	2,79
Porto Alegre	**PA4**	10-jun-09	9:34	10:55	163	1,36
Porto Alegre	**PA_10ha**	11-jun-09	6:09	11:22	627	5,23
Porto Alegre	**PA_10ha**	11-jun-09	11:30	12:17	95	0,79
Porto Alegre	**PA_10ha**	11-jun-09	12:55	13:40	90	0,75
Porto Alegre	**PA_10ha**	11-jun-09	14:50	15:22	65	0,54
Porto Alegre	**PA1**	12-jun-09	13:54	16:11	274	2,28
Porto Alegre	**PA1**	13-jun-09	6:02	15:49	1174	9,78
Porto Alegre	**PA2**	14-jun-09	7:20	10:14	350	2,92
Porto Alegre	**PA2**	14-jun-09	10:21	13:14	349	2,91
Porto Alegre	**PA2**	14-jun-09	13:22	13:26	9	0,08
Porto Alegre	**PA3**	15-jun-09	6:17	8:41	288	2,40
Porto Alegre	**PA3**	15-jun-09	8:43	9:43	121	1,01
Porto Alegre	**PA_10ha**	18-jun-09	6:46	14:31	932	7,77
Porto Alegre	**PA_10ha**	18-jun-09	14:40	15:18	77	0,64
Porto Alegre	**PA_10ha**	19-jun-09	12:13	14:09	232	1,93
Porto Alegre	**PA_10ha**	19-jun-09	6:32	12:07	671	5,59
Porto Alegre	**PA3**	21-jun-09	6:26	7:56	180	1,50
Dimona	**Dim_10ha**	24-jun-09	6:10	6:43	67	0,56
Dimona	**Dim_10ha**	24-jun-09	7:57	8:01	11	0,09
Dimona	**Dim_10ha**	24-jun-09	9:46	10:45	120	1,00
Dimona	**Dim_10ha**	25-jun-09	6:00	13:00	819	6,83
Dimona	**South_Central**	26-jun-09	13:57	15:10	147	1,23
Dimona	**E400**	27-jun-09	15:45	16:55	142	1,18
Dimona	**Central**	29-jun-09	9:32	9:41	19	0,16
Dimona	**Southwest**	29-jun-09	6:04	7:26	165	1,38
Dimona	**Dim_10ha**	30-jun-09	8:46	14:14	657	5,48
Dimona	**Dim_10ha**	1-jul-09	8:45	10:32	214	1,78
Dimona	**Dim_10ha**	1-jul-09	10:36	14:29	469	3,91
Dimona	**Dim_10ha**	9-jul-09	6:07	12:02	712	5,93
Dimona	**Central**	10-jul-09	6:17	14:13	846	7,05
Dimona	**Central**	11-jul-09	6:02	11:52	700	5,83
Dimona	**Central**	12-jul-09	6:10	16:34	1251	10,43
Dimona	**Central**	13-jul-09	12:25	16:56	543	4,53
Dimona	**Central**	14-jul-09	6:13	13:01	818	6,82

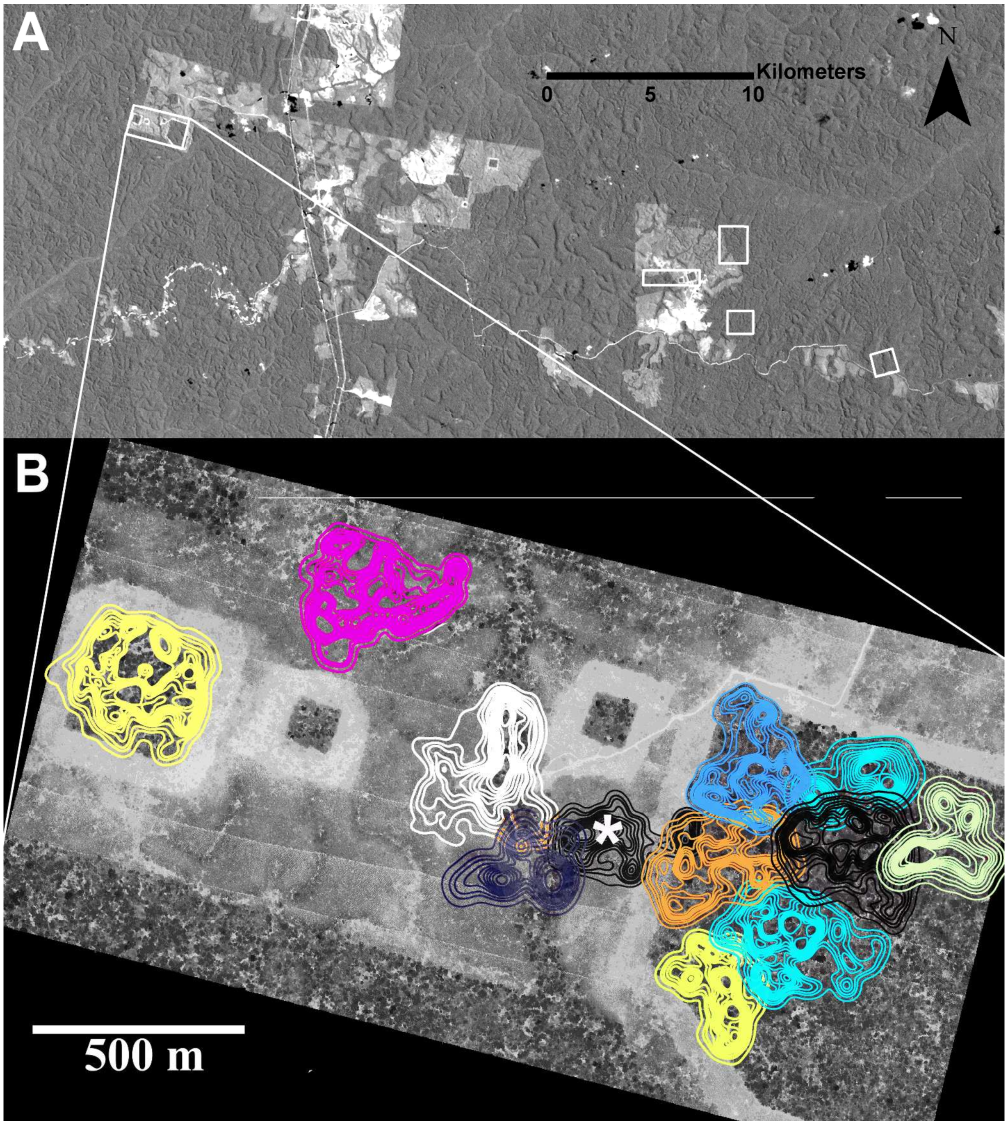
Dimona	**South_Central**	15-jul-09	6:10	11:59	699	5,83
Dimona	**W400**	16-jul-09	13:44	15:05	164	1,37
Dimona	**Central**	17-jul-09	12:43	13:05	44	0,37
Dimona	**Central**	17-jul-09	13:26	15:22	213	1,78
Dimona	**Southwest**	17-jul-09	6:05	8:32	296	2,47
Dimona	**E400**	18-jul-09	8:21	11:44	407	3,39
Dimona	**N**	19-jul-09	11:51	12:02	24	0,20
Dimona	**NE**	19-jul-09	9:08	9:13	13	0,11
Dimona	**W400**	19-jul-09	15:04	15:06	6	0,05
Dimona	**NE**	20-jul-09	7:58	9:00	120	1,00
Dimona	**NE**	20-jul-09	7:58	9:00	125	1,04
Dimona	**N**	1-ago-09	12:20	13:03	89	0,74
Dimona	**W400**	1-ago-09	11:20	11:44	51	0,43
Dimona	**N**	2-ago-09	13:20	14:23	127	1,06
Dimona	**NE**	2-ago-09	6:20	7:14	111	0,93
Dimona	**NE**	2-ago-09	12:09	12:52	89	0,74
Dimona	**NE**	2-ago-09	10:21	12:01	201	1,68
Dimona	**N**	3-ago-09	14:35	15:38	126	1,05
Dimona	**NE**	3-ago-09	6:17	9:21	368	3,07
Dimona	**N**	4-ago-09	9:51	12:00	240	2,00
Dimona	**N**	4-ago-09	14:09	15:14	132	1,10
Dimona	**Lake_flk**	5-ago-09	9:50	11:02	147	1,23
Dimona	**Lake_flk**	5-ago-09	6:19	9:37	397	3,31
Dimona	**w400**	5-ago-09	14:24	15:22	116	0,97
Dimona	**Southwest**	6-ago-09	6:22	11:08	574	4,78
Dimona	**W400**	7-ago-09	8:33	11:27	349	2,91
Dimona	**W400**	7-ago-09	14:34	15:47	148	1,23
Dimona	**Cap_II**	10-jun-10	11:59	12:32	66	0,55
Dimona	**Central**	10-jun-10	6:19	9:24	372	3,10
Dimona	**Central**	10-jun-10	10:49	11:27	99	0,83
Dimona	**lg_cmp_flk**	10-jun-10	14:31	15:12	85	0,71
Dimona	**lg_cmp_flk**	12-jun-10	5:42	14:50	59	0,49
Dimona	**lg_cmp_flk**	12-jun-10	16:10	16:25	339	2,83
Dimona	**lg_cmp_flk**	13-jun-10	6:03	11:45	54	0,45
Dimona	**W400**	14-jun-10	5:47	14:21	1028	8,57
Dimona	**Lake_flk**	15-jun-10	6:05	11:58	708	5,90
Dimona	**lg_cmp_flk**	16-jun-10	14:49	16:03	150	1,25
Dimona	**W400**	16-jun-10	6:01	12:53	826	6,88
Dimona	**W400**	17-jun-10	5:53	15:05	1106	9,22
Dimona	**W400**	19-jun-10	6:34	12:47	748	6,23
Dimona	**Cap_S**	20-jun-10	6:42	8:34	227	1,89
Dimona	**Cap_S**	21-jun-10	15:35	16:06	87	0,73
Dimona	**Central**	21-jun-10	6:00	12:56	833	6,94

Dimona	**Central**	22-jun-10	5:58	12:25	775	6,46
Dimona	**Central**	10-jul-10	5:56	11:10	629	5,24
Dimona	**Ig_cmp_flk**	11-jul-10	6:01	13:58	870	7,25
Dimona	**Ig_cmp_flk**	11-jul-10	15:56	16:41	92	0,77
Dimona	**Cap_S**	12-jul-10	14:54	16:19	170	1,42
Dimona	**Dim_10ha**	12-jul-10	6:11	10:37	533	4,44
Dimona	**Ig_cmp_flk**	13-jul-10	5:59	12:13	749	6,24
Dimona	**Ig_cmp_flk**	13-jul-10	14:24	15:26	127	1,06
Dimona	**Ig_cmp_flk**	14-jul-10	6:48	11:04	514	4,28
Dimona	**Cap_II**	15-jul-10	6:00	11:35	425	3,54
Dimona	**Cap_S**	17-jul-10	9:10	10:40	69	0,58
Dimona	**Cap_S**	17-jul-10	11:08	15:01	466	3,88
Dimona	**Dim_10ha**	18-jul-10	6:16	8:41	291	2,43
Dimona	**Dim_10ha**	18-jul-10	10:33	14:01	418	3,48
Dimona	**Cap_II**	19-jul-10	6:22	11:58	673	5,61
Dimona	**Cap_S**	19-jul-10	13:54	15:03	139	1,16
Dimona	**Dim_10ha**	20-jul-10	6:14	14:24	960	8,00
Dimona	**Cap_S**	21-jul-10	15:23	16:06	88	0,73
Dimona	**Ig_cmp_flk**	21-jul-10	6:05	12:28	723	6,03
Dimona	**Cap_II**	22-jul-10	6:05	15:01	1073	8,94
Dimona	**Ig_cmp_flk**	23-jul-10	5:56	14:02	972	8,10
Dimona	**Ig_cmp_flk**	24-jul-10	5:55	12:00	714	5,95
Dimona	**Ig_cmp_flk**	24-jul-10	15:48	16:15	54	0,45
Dimona	**Dim_10ha**	25-jul-10	6:12	13:01	819	6,83
Colosso	**Cap_1ha**	4-ago-10	6:13	10:41	537	4,48
Colosso	**Col_10ha**	5-ago-10	11:05	17:00	705	5,88
Florestal	**Fl_II**	7-ago-10	6:08	14:15	894	7,45
Colosso	**Col_10ha**	8-ago-10	6:03	14:30	1015	8,46
Colosso	**Cap_1ha**	9-ago-10	6:08	15:01	1067	8,89
Florestal	**Fl_III**	10-ago-10	7:02	9:57	350	2,92
Colosso	**Col_10ha**	11-ago-10	6:03	10:01	478	3,98
Florestal	**Fl_II**	13-ago-10	6:05	12:30	1010	8,42
Colosso	**Col_10ha**	14-ago-10	8:30	17:10	1041	8,68
Florestal	**FL_IA**	15-ago-10	11:15	15:00	450	3,75
Florestal	**FL_III**	16-ago-10	9:00	13:05	287	2,39
Colosso	**Cap_1ha**	17-ago-10	6:14	12:30	752	6,27
Colosso	**Col_10ha**	19-ago-10	6:06	13:03	805	6,71
Colosso	**Col_10ha**	10-set-10	8:20	14:26	655	5,46
Colosso	**CaboFrio_I**	11-set-10	6:30	9:05	231	1,93
Colosso	**CaboFrio_I**	11-set-10	13:05	15:05	245	2,04
Colosso	**Cap_1ha**	11-set-10	15:30	16:05	65	0,54
Florestal	**Fl_II**	12-set-10	11:55	15:05	383	3,19
Colosso	**Col_10ha**	13-set-10	6:00	12:00	725	6,04

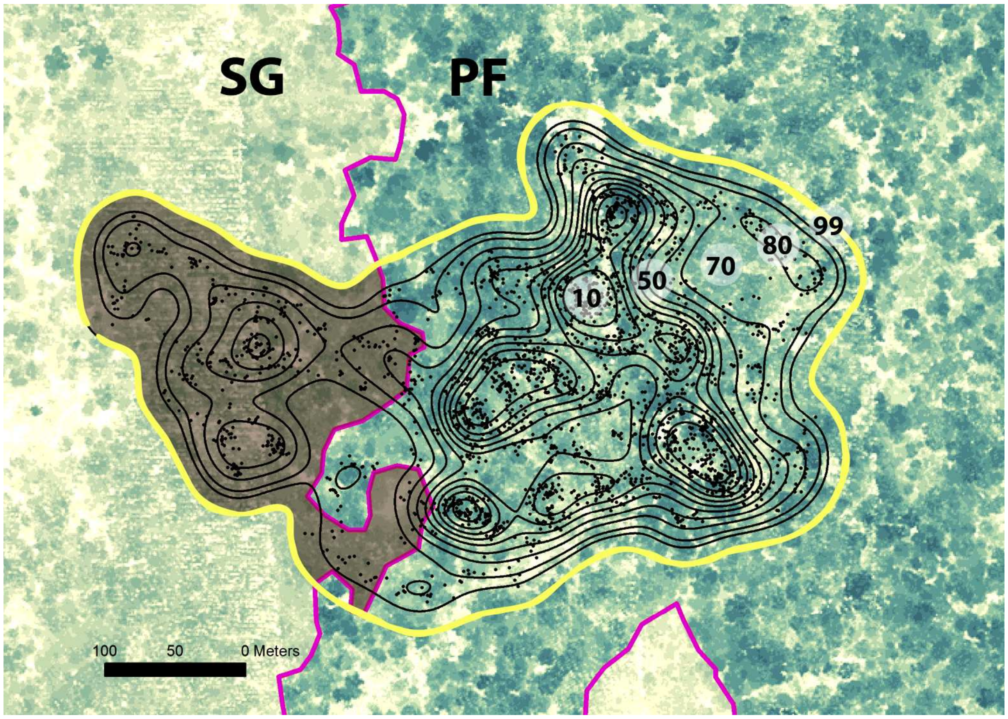
Colosso	**Cap_1ha**	15-set-10	6:00	15:00	1080	9,00
Colosso	**Cap_1ha**	16-set-10	6:00	12:00	740	6,17
Florestal	**Fl_II**	17-set-10	6:00	15:00	1009	8,41
Florestal	**Fl_II**	18-set-10	6:00	14:30	1075	8,96
Colosso	**Cap_1ha**	19-set-10	11:00	16:00	582	4,85
Colosso	**Col_10ha**	20-set-10	6:00	8:00	240	2,00
Gavião	**Gavião_I**	30-set-10	9:25	11:10	230	1,92
Gavião	**Gavião_I**	1-out-10	6:35	13:45	858	7,15
Gavião	**Gavião_I**	2-out-10	14:15	14:55	503	4,19
Gavião	**Gavião_II**	2-out-10	8:15	11:50	427	3,56
Gavião	**Gavião_II**	4-out-10	6:18	13:50	797	6,64
Gavião	**Gavião_II**	5-out-10	6:33	10:00	412	3,43
Dimona	**Ig_cmp_flk**	9-out-10	6:00	12:31	763	6,36
Dimona	**Ig_cmp_flk**	10-out-10	5:53	13:00	852	7,10
Dimona	**Ig_cmp_flk**	11-out-10	5:55	11:11	648	5,40
Dimona	**Ig_cmp_flk**	11-out-10	13:20	16:43	407	3,39
Dimona	**Ig_cmp_flk**	12-out-10	5:50	8:18	296	2,47
Dimona	**Ig_cmp_flk**	12-out-10	11:10	16:40	658	5,48
Dimona	**Ig_cmp_flk**	9-nov-10	6:00	12:00	719	5,99
Dimona	**Central**	10-nov-10	5:55	8:35	579	4,83
Dimona	**Central**	11-nov-10	6:35	10:30	413	3,44
Dimona	**Dim_10ha**	13-nov-10	6:45	15:10	881	7,34
Dimona	**Dim_10ha**	14-nov-10	5:55	15:18	1086	9,05
Dimona	**Ig_cmp_flk**	15-nov-10	16:41	17:50	139	1,16
Dimona	**Central**	16-nov-10	5:50	13:33	878	7,32
Dimona	**Central**	17-nov-10	5:50	10:47	509	4,24
Dimona	**Central**	18-nov-10	5:45	14:34	1000	8,33
Dimona	**Dim_10ha**	19-nov-10	8:35	17:00	690	5,75
Dimona	**Dim_10ha**	20-nov-10	8:45	15:00	775	6,46
Dimona	**Central**	21-nov-10	5:50	11:50	776	6,47
Dimona	**W400**	21-nov-10	15:35	16:40	120	1,00
Dimona	**Central**	22-nov-10	5:50	10:30	550	4,58
Dimona	**Central**	22-nov-10	14:30	16:50	286	2,38
Dimona	**Dim_10ha**	23-nov-10	9:45	17:00	867	7,23
Dimona	**Dim_10ha**	24-nov-10	5:50	9:05	370	3,08
Dimona	**Ig_cmp_flk**	26-nov-10	5:53	8:10	250	2,20
Colosso	**Cap_1ha**	3-fev-11	6:00	12:00	701	5,84
Colosso	**Col_10ha**	4-fev-11	6:00	9:05	189	1,58
Colosso	**Col_10ha**	4-fev-11	14:50	17:12	276	2,30
Colosso	**Cap_1ha**	5-fev-11	6:00	13:20	923	7,69
Colosso	**Col_10ha**	6-fev-11	6:15	11:25	620	5,17
Colosso	**Col_10ha**	8-fev-11	6:15	9:50	513	4,28
Colosso	**Col_10ha**	8-fev-11	11:17	12:10	109	0,91

Colosso	**Col_10ha**	9-fev-11	6:08	8:34	292	2,43
Colosso	**Cap_1ha**	10-fev-11	11:25	15:00	419	3,49
Colosso	**Col_10ha**	11-fev-11	6:10	11:00	505	4,21
Colosso	**Col_10ha**	11-fev-11	14:52	17:00	335	2,79
Colosso	**Col_10ha**	12-fev-11	12:15	17:15	585	4,88
Colosso	**Cap_1ha**	13-fev-11	12:55	15:00	240	2,00
Colosso	**Col_10ha**	14-fev-11	7:00	11:08	427	3,56
Colosso	**Cap_1ha**	15-fev-11	6:00	12:00	715	5,96
Colosso	**Col_10ha**	24-fev-11	6:53	10:42	459	3,83
Colosso	**Col_10ha**	24-fev-11	14:00	16:00	239	1,99
Colosso	**Col_10ha**	26-fev-11	6:35	10:00	413	3,44
Colosso	**Col_10ha**	27-fev-11	6:00	11:52	701	5,84
Colosso	**Cap_1ha**	28-fev-11	6:50	12:50	721	6,01
Colosso	**CaboFrio_I**	1-mar-11	10:00	13:10	360	3,00
Colosso	**Cap_1ha**	1-mar-11	6:00	9:30	370	3,08
Colosso	**Col_10ha**	18-mar-11	15:30	16:00	60	0,50
Florestal	**Fl_II**	19-mar-11	6:00	8:10	272	2,27
Florestal	**Fl_II**	20-mar-11	12:00	16:00	384	3,2
Florestal	**Fl_II**	21-mar-11	6:00	13:15	905	7,54
Florestal	**Fl_II**	22-mar-11	6:00	7:10	120	1,00
Colosso	**Cap_1ha**	23-mar-11	6:00	14:00	931	7,76
Florestal	**Fl_II**	24-mar-11	6:00	14:30	1036	8,63
Florestal	**Fl_II**	31-mar-11	7:30	14:10	801	6,68
Florestal	**Fl_II**	3-abr-11	11:33	17:10	662	5,52
Florestal	**Fl_II**	4-abr-11	13:20	16:55	240	2,00
Florestal	**FL_II**	5-abr-11	14:25	15:38	120	1,00
Florestal	**FL_II**	6-abr-11	6:00	8:05	240	2,00
Dimona	**dim_10ha**	4-mai-11	5:50	14:00	965	8,04
Dimona	**Cap_North_I**	5-mai-11	6:40	14:00	871	7,26
Dimona	**South_Central**	7-mai-11	6:00	9:22	451	3,76
Dimona	**Southwest**	7-mai-11	9:22	13:05	402	3,35
Dimona	**Dim_10ha**	8-mai-11	12:38	16:49	500	4,17
Dimona	**Cap_North_I**	9-mai-11	9:40	11:25	210	1,75
Dimona	**Cap_North_I**	10-mai-11	6:00	11:10	585	4,88
Dimona	**Lake_flk**	11-mai-11	5:40	12:45	770	6,42
Dimona	**Dim_10ha**	13-mai-11	6:00	13:50	918	7,65
Dimona	**N**	18-mai-11	14:25	14:55	62	0,52
Dimona	**South_Central**	19-mai-11	6:00	11:00	602	5,02
Dimona	**Dim_10ha**	20-mai-11	6:00	13:00	840	7,00
Dimona	**Lake_flk**	21-mai-11	11:37	14:04	294	2,45
Dimona	**W400**	21-mai-11	10:31	11:31	120	1,00
Dimona	**Dim_10ha**	22-mai-11	6:00	12:00	732	6,10
Dimona	**Cap_North_I**	23-mai-11	6:00	11:50	740	6,17

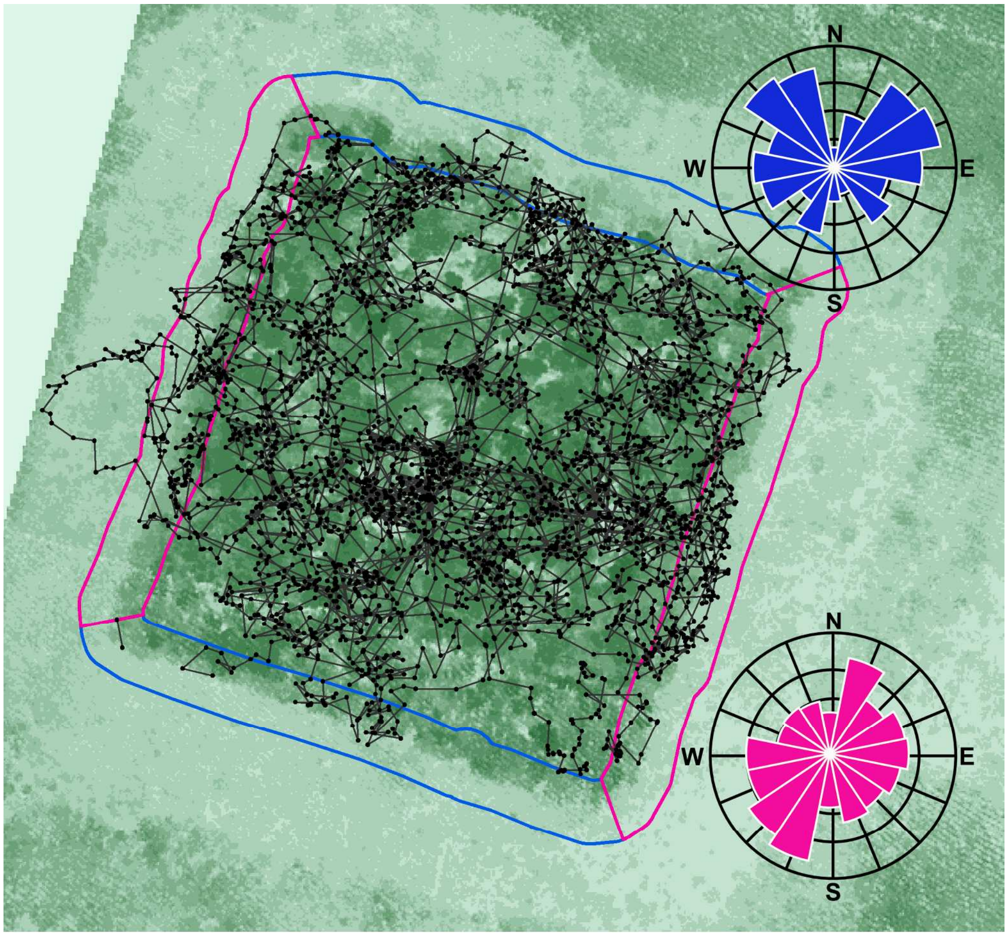
Dimona	**Lake_flk**	23-mai-11	14:32	15:30	116	0,97
Dimona	**Dim_10ha**	24-mai-11	9:28	16:30	819	6,83
Dimona	**Southwest**	7-jun-11	6:00	14:00	965	8,04
Dimona	**South_Central**	8-jun-11	8:55	12:37	505	4,21
Dimona	**Cap_II**	9-jun-11	12:25	15:45	405	3,38
Dimona	**N**	9-jun-11	9:12	10:30	160	1,33
Florestal	**Fl_III**	28-jun-11	7:40	12:15	548	4,57
Florestal	**FL_IB**	29-jun-11	6:15	13:00	721	6,01
Florestal	**Fl_IA**	30-jun-11	7:25	13:20	717	5,98
Florestal	**FL_IB**	2-jul-11	6:10	11:00	566	4,72
Florestal	**Fl_IA**	3-jul-11	6:15	12:00	727	6,06
Florestal	**FL_IB**	4-jul-11	6:10	14:00	992	8,27
Florestal	**Fl_IA**	6-jul-11	11:55	14:30	317	2,64
Florestal	**Fl_III**	6-jul-11	6:00	9:50	452	3,77
Colosso	**CaboFrio_I**	7-jul-11	11:30	14:30	258	2,15
Colosso	**CaboFrio_I**	8-jul-11	11:00	15:00	480	4,00
Florestal	**Fl_IA**	9-jul-11	9:39	12:30	336	2,80
Florestal	**FL_IB**	9-jul-11	12:40	13:40	123	1,03
Florestal	**Fl_III**	21-jul-11	6:00	12:00	728	6,07
Colosso	**CaboFrio_I**	22-jul-11	7:40	13:00	644	5,37
Colosso	**CaboFrio_I**	23-jul-11	6:00	11:00	480	4,00
Gavião	**Gavião_I**	26-jul-11	6:15	11:30	662	5,52
Gavião	**Gavião_I**	27-jul-11	6:00	11:30	700	5,83
Gavião	**Gavião_I**	28-jul-11	12:35	14:00	178	1,48
Gavião	**Gav_10_ha**	29-jul-11	7:00	13:50	799	6,66
Gavião	**Gavião_II**	30-jul-11	6:15	11:35	630	5,25
Gavião	**Gav_10_ha**	31-jul-11	6:00	14:30	1020	8,50
Gavião	**Gav_10_ha**	1-ago-11	6:00	10:30	550	4,58
Km37	**Km37_III**	2-ago-11	9:45	14:30	550	5,80
Km37	**Km37_III**	3-ago-11	9:00	12:15	405	3,38
Km37	**Km37_IV**	3-ago-11	8:20	9:00	80	0,70
Km37	**Km37_III**	4-ago-11	6:10	13:00	840	7,00
Km37	**Km37_III**	5-ago-11	7:00	11:00	489	4,08
Km37	**Km37_V**	6-ago-11	8:15	15:10	845	7,04
Km37	**Km37_V**	7-ago-11	6:40	14:30	940	7,83
Km37	**Km37_V**	8-ago-11	8:00	10:00	268	2,23



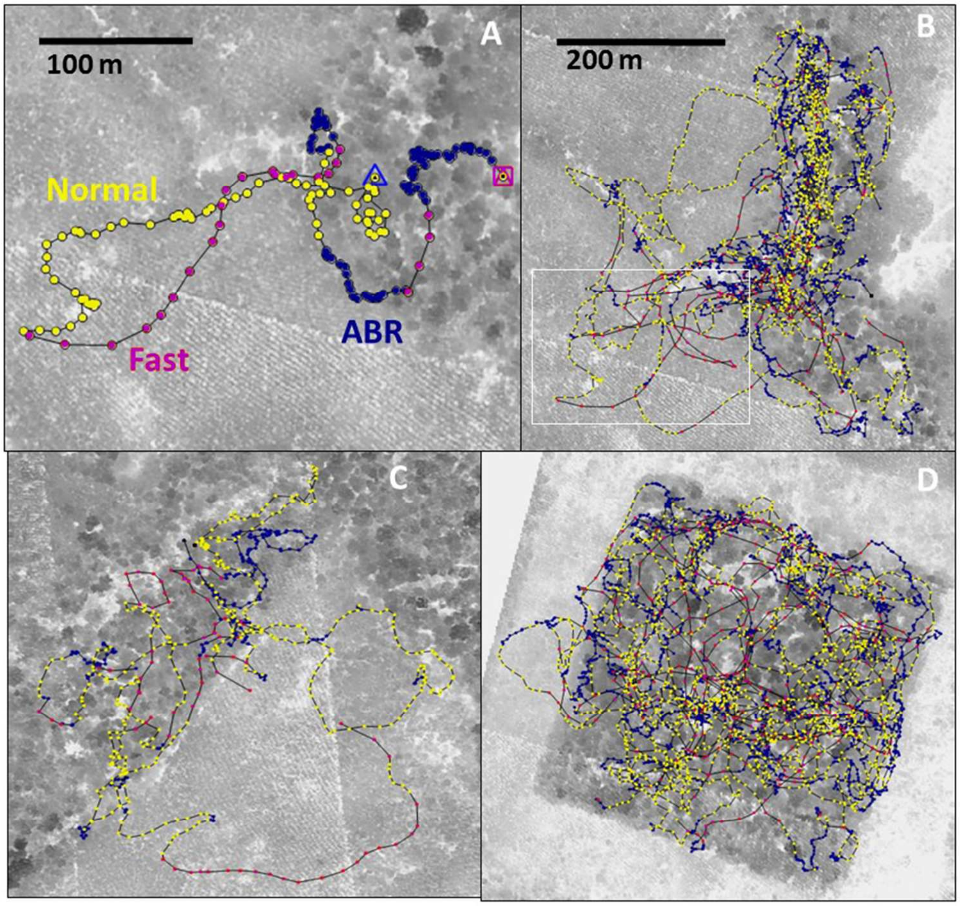
263x294mm (300 x 300 DPI)



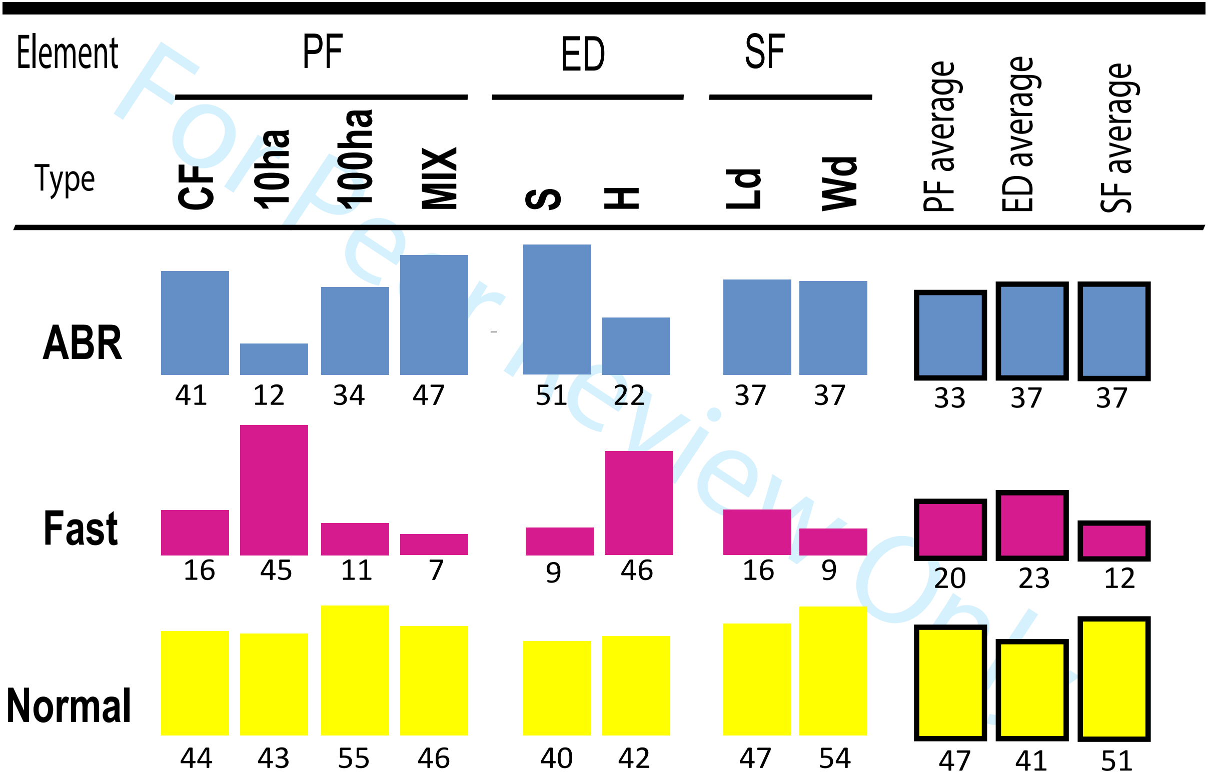
230x163mm (300 x 300 DPI)



203x188mm (300 x 300 DPI)



232x220mm (96 x 96 DPI)


Element
PF
ED
SF
Type
CF
10ha
100ha
MIX
S
H
Ld
Wd
PF average
ED average
SF average
ABR
41
12
34
47
51
22
37
37
33
37
37
Fast
16
45
11
7
9
46
16
9
20
23
12
Normal
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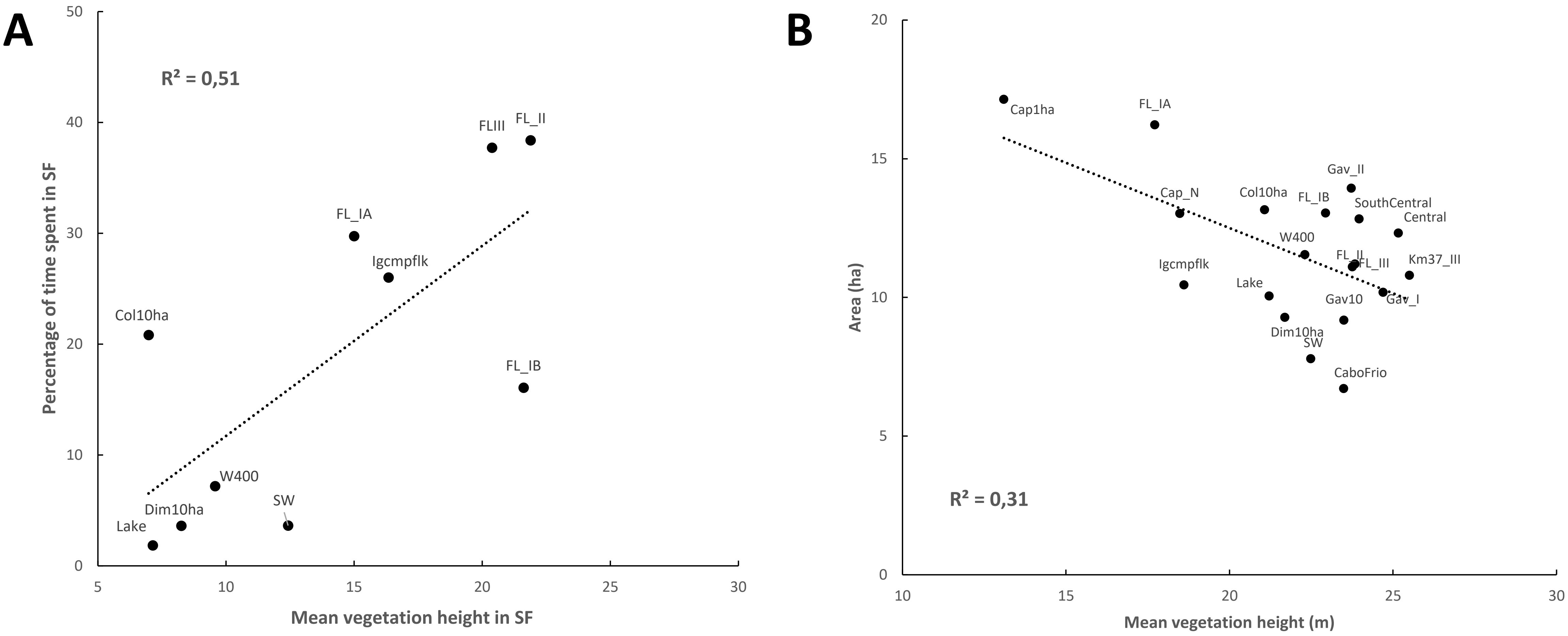
42
47
54
47
41
51


A
R² = 0,51
Percentage of time spent in SF
Mean vegetation height in SF
50
40
30
20
10
0
5
10
15
20
25
30
FLIII
FL_II
FL_IA
Igcmpflk
Col10ha
FL_IB
W400
SW
Dim10ha
Lake
B
R² = 0,31
Area (ha)
Mean vegetation height (m)
20
15
10
5
0
10
15
20
25
30
Cap1ha
FL_IA
Gav_II
Cap_N
Col10ha
FL_IB
SouthCentral
Central
W400
FL_II
FL_III
Km37_III
Igcmpflk
Lake
Gav_I
Gav10
Dim10ha
SW
CaboFrio