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INFLUENCE OF ENVIRONMENTAL FACTORS ON THE MOVEMENT PATTERNS OF AFRICAN ELEPHANTS IN THE SELATI GAME RESERVE, SOUTH AFRICA.

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ABSTRACT

Animal movement patterns are influenced by a combination of internal and external drivers that interact synergistically and ultimately drive animals' behaviour. Examining the factors behind these influences and their role in guiding animals' choices is crucial for comprehending movement patterns. Exploring the spatial ecology of African savanna elephants (*Loxodonta africana*) provides vital information, particularly within the context of a fenced reserve in South Africa, that is important for the effective and efficient management and conservation of both the species and its habitat. In pursuit of this objective, Hidden Markov Models (HMMs) and hourly Global Positioning System fixes were used to distinguish movements of two matriarchs within the Selati Game Reserve (SGR) into three distinct states. Subsequently, the analysis of the influence of four environmental variables (terrain roughness, distance to nearest road/path, distance to nearest water source, and NDVI) on the probability of persistence in, and transition to, a particular state between June 2022 and December 2022 was conducted. The results showed that all the different covariates consistently influenced elephant movements. Particularly, when the terrain was rougher, matriarchs tended to switch to state 1. Moreover, they showed to use the road network to navigate the landscape faster during the dry season, and to exploit roadside vegetation during the wet season. Additionally, persistence in state 3, the farthest from water sources, was found with direct and accurate movement patterns. Finally, matriarchs consistently occurred in state 1, when NDVI values were highest, and in state 3, when NDVI values were lowest. More in-depth analyses can be carried out to assess whether these results are confirmed on a larger scale, for example over subsequent years. Thus, this study has provided vital information for improving conservation management of elephant within fenced reserves, where their proper management is crucial for the well-being of the entire ecosystem.

Keywords: movement ecology; African elephant; fenced reserve; external drivers; HMMs; South Africa.

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1 INTRODUCTION

1.1 Animal movements

The field of movement ecology aims to understand why organisms move through space following certain patterns and the possible constraints that condition them (Patterson *et al.*, 2017). Animal movement patterns inherently involve internal and external drivers, which interact synergistically, thus impacting animal choices (Mckellar *et al.*, 2015). Therefore, the study of these movement patterns allows ecologists to identify the spatio-temporal distribution of the species analysed, as well as the influencing factors of their movement patterns between different environments (Birkett *et al.*, 2012). Despite the growing importance of animal movement studies in ecology and conservation biology, due to considerable interest in this topic over the past decades, research has commenced to emphasise animal movements in a quantitative manner only in the last decade (Mckellar *et al.*, 2015).

Both marine and terrestrial animals move to optimize their chances of survival and reproductive success, ultimately leading to their physical growth and overall fitness (Whoriskey *et al.*, 2017). Furthermore, animal movements offer advantages by potentially reducing competition within a species and facilitating the discovery of new or improved resources (Bowler *et al.*, 2005). Consequently, risk scenarios might thus be avoided and the probability of finding new mates enhanced (Vogel *et al.*, 2020). Additionally, understanding movement patterns concerning different habitats can aid in discovering the motivations behind the choice of a specific habitat (Nathan *et al.*, 2008). For instance, several papers have found that in richer and more varied landscapes, large herbivores show slower movements and more frequent turning behaviour, whereas, in areas with less forage value, they turn less and show faster pacing patterns (Venter *et al.*, 2015; Fryxell *et al.*, 2008; Senft *et al.*, 1987). This change in movement pattern may indicate that forage availability influences the spatial behaviour of the animals (Vogel *et al.*, 2020). In this regard, it has been demonstrated that spatial variations in animal movement patterns are the result of the non-homogeneous distribution of vital resources, including habitat type, water resources and high-value foraging areas (De Knegt *et al.*, 2007; Apps *et al.*, 2001). Furthermore, movements are also influenced by variations in time, i.e., the seasonal or annual periods when essential resources are accessible to the animals themselves. In turn, abiotic factors, such as rainfall and temperature, influence the seasonal availability of the resources (Birkett *et al.*, 2012). As evidence, the latter has been widely ascertained for mountain caribou (Apps *et al.*, 2001), as well as for large African herbivores (de Knegt *et al.*, 2007).

Animal movements play a crucial role in maintaining key ecosystem processes, including also seed and natural fertiliser dispersal (Doughty *et al.*, 2013; Guimaraes *et al.*, 2008). In turn, such ecosystem processes contribute to ecosystem health and steadiness (Gravel *et al.*, 2016), as well as enhancing biodiversity (Berti *et al.*, 2023). Despite this, movements also carry a significant energy expenditure and an increased risk of mortality. Fahrig (2007) found a certain association between fast, linear movements and the crossing of risky habitats. This has been to some extent confirmed by several authors who have found an increase in stepping speeds in landscapes with high anthropogenic presence (Karelus *et al.*, 2017; Stillfried *et al.*, 2017; Wang *et al.*, 2017). Human-occupied landscapes influence animal movements, as although they occasionally have high foraging areas, they are still avoided by wildlife given the increased risk of mortality or conflict (Vogel *et al.*, 2020).

Movement is at the core of individual biology and the decisions made are reflected in the movements that are performed, with both direct and indirect repercussions on various levels (Beirne *et al.*, 2021). At the individual level, the movement patterns exhibited by individuals directly determine their fitness, as their capacity for self-sufficiency, survival, and mating depend on them (Kays *et al.*, 2015; Owen-Smith *et al.*, 2010). At the population level, the movement trends of one population can affect those of other populations, modifying possible future interactions (Spiegel *et al.*, 2017; Morales *et al.*, 2010). At the ecosystem level, the movement choices of animals play an important role in the mobilisation of dispersed nutrients in the ecosystem, as well as regulating the degree of impact of the individual within the ecosystem it inhabits (Earl and Zollner, 2017). In light of the above, the conservation not only of a focal species but also of the entire ecosystem, of which it is a part, is highly dependent on understanding and learning about how animals move, the motivations behind the choices that govern these movements, and the consequences of such choices (Beirne *et al.*, 2021). The pervasive recognition of the vital role of the identification of such patterns and the variation they entail is increasingly supported by high-performance tracking technologies (Beirne *et al.*, 2021; Birkett *et al.*, 2012). Such GPS devices have allowed a quantitative collection of fine-scale animal movements data (Kays *et al.*, 2015; Cagnacci *et al.*, 2010;), fostering the emergence of increasingly up-to-date, accurate and precise statistical models capable of correctly analysing this type of data (Hooten et al., 2017).

1.2 Statistical modelling on movement data

A significant number of papers on statistical modelling of animal movement have been concerned with the insight-based attempt to distinguish between time series of movement in different behavioural states through the application of state-switching modelling (Michelot *et al.*, 2023). The main explanation for this common choice is that displacement patterns are a reflection of animal behaviour, which in turn is a product of the individual's reaction to physiological impulses and the ecosystem (Whoriskey *et al.*, 2017). Therefore, the identification of these hidden drivers of animal movement (a.k.a. behavioural states) is necessary to further the knowledge of how and why animals decide to exploit available areas (Whoriskey *et al.*, 2017). As evidence, in the last 20 years, different research has classified displacement routes into distinct states, on the basis of individual motivations; among these papers, the following is the most exhaustive: Morales *et al.* (2004) distinguished encamped and exploratory states of elk individuals (*Cervus elaphus*); Pomerleau *et al.* (2011) classified bowhead whales (*Balaena mysticetus*) movement patterns as transient and resident; Franke *et al.* (2004) described three different states, namely bedding, feeding and relocating, in woodland caribou (*Rangifer tarandus*); and Bagniewska *et al.* (2013) determined three distinct dive states in the semi-aquatic American mink (*Neovison vison*). Through the analysis of such behavioural states, it is possible to comprehend how animals utilise resources within the ecosystem (Fryxell *et al.*, 2008; Forester *et al.*, 2007) and, to a greater extent, to investigate population dynamics (Morales *et al.*, 2010). The identification of these characteristics, especially in endangered species, can be a crucial tool in the service of conservation decision-makers (Anadón *et al.*, 2012; Pomerleau *et al.*, 2011; Lusseau, 2003). Moreover, with regard to migrating animal populations, it is critical to determine their movement patterns in space and time and the factors that drive them, when the objective is their conservation and management (Schick *et al.*, 2008; Berger, 2004; Thirgood *et al.*, 2004). A lack of knowledge of these dynamics can pose a risk to animal safety and, indirectly, can lead to an intensification of human-wildlife conflicts (Harris *et al.*, 2009; Bolger *et al.*, 2008).

Refinements in location devices have enabled data to be recorded on fine spatial and temporal scales. Thus, such high-precision data can be combined with external variables, for instance, environmental and topographical covariates, providing meaningful information on how extrinsic factors affect movement behaviour (see Langrock *et al.*, 2014; Patterson *et al.*, 2009; Morales *et al.*, 2004). As a result, numerous works have determined the fine-scale movement behaviour of large mammalian species, including elk (Fryxell *et al.*, 2008), moose (*Alces alces*) (Demarchi, 2003), caribou (Apps *et al.*, 2001) and African elephant (*Loxodonta africana*) (Wittemyer *et al.*, 2008; Cushman *et al.*, 2005). Many of these fine-scale movement studies define different behavioural states between seasons and consider multiple time scales (e.g., days, weeks, months). The authors often analyse seasonal patterns using meteorological proxies, which generally include temperature and precipitation.

Statistical modelling for partitioning movement patterns into distinct unobserved states has generally been developed and adapted using more generalist State-Space Models (SSMs) (Jonsen *et al.*, 2013; Patterson *et al.*, 2008; Schick *et al.*, 2008; Jonsen *et al.*, 2005) or Hidden Markov Models (HMMs) (Langrock *et al.*, 2012; Patterson *et al.*, 2009; Holzmann *et al.*, 2006; Morales *et al.*, 2004), usually assuming a discrete or continuous time structure (Blackwell, 2003). HMMs have been applied for studying movement patterns of a variety of animals, including marine animals, such as tunas (Patterson *et al.*, 2009) and white sharks (Towner *et al.*, 2016), birds, in particular, woodpeckers (Mckellar *et al.*, 2015), insects, with a study on fruit flies (Holzmann *et al.*, 2006), and mammals, including caribous (Franke *et al.*, 2004), and panthers (van de Kerk *et al.*, 2015).

1.3 *African Elephant (Loxodonta africana)*

1.3.1 Taxonomy, distribution, and biology

Belonging to the class *Mammalia* and order *Proboscidea*, the elephant is classified within the family *Elephantidea*, of which only two genus have extant species: the genera *Loxodonta* and *Elephas* (Shoshani and Tassy, 2004). The latter is represented only by the species of the Asian elephant (*Elephas maximum*), which in turn comprises three subspecies (Soshani *et al.*, 2001). Two species belongs to the genus *Loxodonta*, the African savanna elephant (*Loxodonta africana*, Blumenbach, 1797) and the African forest elephant (*Loxodonta cyclotis*, Matschie, 1900) (Grubb *et al.*, 2000). From this point forward, this study exclusively pertains to the African savanna elephant, which will be referred to as the African elephant or simply as ‘elephant’.

Once characterised by a large-scale homogeneous presence across the African continent, the African elephant is currently distributed across a highly fragmented and discontinuous landscape (Shaffer *et al.*, 2019). Despite this, it is still present in 37 countries in sub-Saharan Africa, with a total population estimated at between 550,000 and 700,000 individuals (Shaffer *et al.*, 2019). According to the latest IUCN report, of all 37 countries, southern Africa has the largest number of elephants of all four regions. East Africa is in second place, followed by Central Africa and West Africa, with the lowest number of individuals per region (Thouless *et al.*, 2016). Due to high habitat loss and fragmentation, elephant’s current range is 3.3 million km², which is only 22% of the African continent (Campos-Arceiz and Blake, 2011; Blanc *et al.*, 2007).

The African elephant is one of the most dominant animals across the Sub-Saharan African countries. It is the largest extant terrestrial species, where adult males reach a body weight of about six tonnes and adult females between two and three tonnes (Laursen and Bekoff, 1978). African elephants are long-lived animals, which can attain the age of 65. However, the average longevity in their natural environment is estimated at 24 and 41 years for males and females, respectively (Moss, 2001). Elephants exhibit allometric growth between the sexes: females grow until the age of 30, after which they show an abrupt slowdown in growth rate (Hanks, 1972), while males continue to grow beyond the age of 45 (Poole *et al.*, 2011). Furthermore, females are already sexually mature at around nine years old, recording an average age of successful procreation in nature of around 14 years

(Moss, 2001). In contrast, although males reach sexual maturity at 11 years old, they do not manage to compete with more mature males in their natural environment until their 20s, thus becoming truly reproductive no earlier than that age (Poole *et al.*, 2011; Slotow *et al.*, 2000).

1.3.2 Ecological role and impact on the ecosystem

African elephants are keystone species and ecological engineers of African savanna ecosystems (Haynes, 2012; Western, 1989) given their disproportionate effect on ecosystem structure and functionalities (Chibeya *et al.*, 2021; Ripple *et al.,* 2015; Kohi *et al.*, 2011; Estes *et al.*, 2011). Additionally, elephants play a crucial role in the dispersal of seeds across the different habitats within their range (Campos-Arceiz and Blake, 2011). Dudley (2000) estimated a dispersal rate of 2054 seeds per square kilometres per day, and Campos-Arceiz and Blake (2011) reported an improvement in the germination stage in seeds dispersed by elephants. They are also recognised as an umbrella species, which means they have a significant impact on other species in the same ecosystem (Gross and Heinsohn, 2023). Their movement and foraging activities foster biodiversity at the environmental and faunal levels (Thompson *et al.*, 2022; Shaffer *et al.*, 2019). As evidence, long-term studies in savanna ecosystems have demonstrated the key role of elephants in reshaping landscapes through damage to canopies, saplings, and shrubs (Fritz, 2017; Coverdale *et al.*, 2016; Kohi *et al.*, 2011).

As one of the most influential species in African landscapes (de Beer *et al.*, 2006), its impact on vegetation radically alters the plant composition (Guldemond *et al.*, 2017; Baxter and Getz, 2008; Baxter and Getz, 2005; Augustine and McNaughton, 2004; Eckhardt *et al.*, 2001), however, if not properly balanced in space and time, it can be detrimental to the recovery and survival of plant species (Chui, 2021; Jacobs and Biggs, 2002; Lombard *et al.*, 2001). Notwithstanding, the impact of this alteration on the savanna habitat is a debated topic, as the literature reports contrasting outcomes (Howes *et al.*, 2020). Several studies have highlighted how elephants can effectively induce irreversible damage to trees and riparian habitats, where they repeatedly impact over time, thus impeding natural regeneration (Cook and Henley, 2019; Teren *et al.*, 2018; Guldemond and Van Aarde, 2007; Dublin, 2003; Owen-Smith, 1988; Mwalyosi, 1987). Furthermore, this phenomenon is exacerbated when the number of elephants exceeds the maximum carrying capacity of the ecosystem (Thouless *et al.*, 2016; Coverdale *et al.*, 2016; Landman and Kerley, 2014; Wittemyer *et al.*, 2013). However, Stevens *et al.* (2016) suggested that the heterogeneousness of savanna ecosystems can counteract the possible negative elephants' impact, which thus becomes a contributor to the preservation of the optimal state of the savanna. Similarly, the effect on species richness is still not entirely clear. Guldemond *et al.* (2017) stated that the disturbance of elephants on the landscape can generate new niches that can be populated by other species, which in turn leads to an increase in biodiversity. Conversely, in Amboseli National Park, two antelope species (bushbuck *Tragelaphus scriptus* and lesser kudu *Tragelaphus imberbis*) have disappeared precisely because of the damage caused by elephants to the ecosystem (Howes *et al.*, 2020; Cummings *et al.*, 1997). Likewise, within the same park, other mammal species (giraffe *Giraffa camelopardalis*, gerenuk *Litocranius walleri*, and baboon *Papio ursinus*) have diminished in total abundance due to elephant-induced habitat changes (Whyte, 2001). Nevertheless, a study conducted in 2011 revealed that meso-browser, including impalas, showed a preference to feed in areas highly impacted by elephants (Valeix *et al.*, 2011), whilst Nasseri *et al.* (2011) determined an increase in diversity and abundance of herpetofauna in habitats with a high degree of elephant disturbance. A systematic review of studies on elephant impact concluded that elephants certainly have a significant effect on vegetation, but with no evident knock-on effect on the other species with which they coexist (Guldemond *et al.*, 2017).

1.3.3 Habitat selection, home range, and diet

Elephants are capable of living in a wide variety of environments, given their adaptability to large differences in altitude, which allows them to occupy areas from sea level to mountain altitudes (c.a. 1200 metres above sea level), as well as their ability to persist in multiple habitat types, from desert to tropical forest (Jiang *et al.*, 2020; Laws, 1970). It is widely documented that elephant herds expand their range during the wet period of summer compared to the winter season, during which they confine themselves to areas with high proximity to water sources (Lindeque and Lindeque 1991; Ottichilo 1986;

Norton-Griffiths 1975; Jarman 1972; but see also Shannon *et al.*, 2006). However, Shannon *et al.* (2006) pointed out that in an environment of food scarcity during the dry season, the elephant herd's habitat selection may increase in size compared to the wet season, thus widening their home range to increase the likelihood of food availability. When food resources are in abundance, elephants exhibit less accuracy in habitat selection (William *et al.*, 2018; Mabille *et al.*, 2012). Given the high availability and variety of food, they mix multiple food types to obtain a wide nutritional spectrum rather than mere energy intake (Codron *et al.*, 2012). In the opposite scenario - during a period of food scarcity - they specifically select a habitat with a secure food provision, preferring quantity over quality (Tsalyuk *et al.*, 2019; Young *et al.*, 2009a). Chui (2021) showed that elephants select habitats according to seasonal ecological changes and plant production regimes. However, habitat selection also depends on the choices of the individual, where personal traits such as memory, personality and social behaviour are the main driving factors (Hertel *et al.*, 2020; Webber and Vander Wal, 2018; Polansky *et al.*, 2015; Dingemanse *et al.*, 2010; Wittemyer *et al.*, 2007). Therefore, individual heterogeneity plays an equally important role in habitat selection and use (Chui, 2021).

Due to their elevated alimentary tolerance (Chui, 2021), elephants are classified as mixed feeders, which means they can alternate feeding behaviour between seasons depending on which type of food is most abundant (Chibeya *et al.*, 2021). According to recent studies, they seem to mainly browse during the dry season and graze during the wet season (Kos *et al.*, 2012). Consequently, depending on the season, between 60% and 95% of their diet consists of grasses (Archie *et al.*, 2006a). When feeding on trees or shrubs, they generally choose species with high nutrient levels (Holdo, 2003), avoiding plants with defence strategies such as high presence of tannin polyphenols (Sheil and Salim, 2006). Likewise, they tend to choose trees with large canopies in order to maximise the energy gain per plant (Howes *et al.*, 2020), debarking the larger branches and toppling the smaller ones (Thompson *et al.*, 2022; Ssali *et al.*, 2013; Ihwagi *et al.*, 2012; Boundja and Midgley, 2010).

1.3.4 Social hierarchy and reproductive behaviour

The social hierarchy of African elephants is one of the most complex among mammal species. Genetic studies have shown that groups of elephants are matrilineally related, which means that their social organisation is driven by kinship bonds between female elephants (Archie *et al.*, 2006b). Indeed, females represent the core of elephant society, maintaining ties with other female individuals throughout their lives (Schulte and LaDue, 2021; Schuttler *et al.*, 2014; Fishlock and Lee, 2013; Wittemyer and Getz, 2007; Moss and Poole, 1983). In the organisation within these groups of females, the older ones play the dominant role over the younger ones, establishing a clear hierarchy in the group, creating fission-fusion types of society (de Silva and Wittemyer, 2012; Wittemyer and Getz, 2007; Archie *et al.*, 2006b; Wittemyer *et al.*, 2005). Each herd has its matriarch, who will fulfil her role until her death. However, when competition between adult females occurs, it leads to the separation of one of them from the original herd, together with other herd members, who will assume the role of matriarch for the new group (Chui, 2021; Wittemyer *et al.*, 2005). Despite this, the matriarchs still have kinship ties, so they will likely fuse again, forming a two-herd bond group (Archie *et al.*, 2006b; Wittemyer *et al.*, 2005).

Contrastingly, males move away from their native herds around the age of 14 (Lee *et al.*, 2011), commencing to migrate between solitary groups of young males only, or with non-natal herds of females, alternately (Chui, 2021; Chiyo *et al.*, 2014; Lee *et al.*, 2011). Male and female individuals are normally spatially segregated, except for the breeding season, when females are in oestrus and males are in 'musth', i.e., a highly reproductive period when the aggressiveness level increases considerably (Schulte and LaDue, 2021; Rasmussen *et al.*, 1996; Poole, 1987; Poole *et al.*, 1984).

However, while musth happens on a regular basis, albeit temporally staggered among males, females are only in oestrus for a couple of weeks with a gap of 4-5 years (Brown, 2014; Moss and Lee, 2011; Freeman *et al.*, 2009). Furthermore, the gestation period is approximately 22 months (Chui, 2021). Therefore, the latter, combined with the physiological interval between two fertile periods, results in a low reproductive rate (Chui, 2021). Adult males in musth could represent a social advantage for young males. They move, in fact, between different female herds, representing an opportunity for young males to separate from their parental groups. The possibility of learning ecological and social skills from males in musth (Chiyo *et al.*, 2012; Slotow *et al.*, 2000) may represent one of the main factors in the dispersal of young males from their natal herds (Chui, 2021). Once displaced, the young males' associations with adult elephants modify their socio-behavioural knowledge, a crucial step in the transition to adulthood (Murphy *et al.*, 2020; Lee *et al.*, 2011; Evans and Harris, 2008). Despite these interactions, young males are likely to bond with other elephants of the same age to engage in activities, such as sparring, in order to assess their strength to be ready to establish dominance in their future adulthood (Chiyo *et al.*, 2011; Evans and Harris, 2008).

Therefore, although the social structure of females is stronger, as their hierarchical organisation is crucial for their fitness and survival and for the transfer of eco-social knowledge across generations, the social organisation of males is also influenced by several factors, such as age, kinship, reproductive status and dominant behaviour, which are the main drivers of their social bonds (Goldenberg *et al.*, 2014; Chiyo *et al.*, 2011; O'Connell-Rodwell *et al.*, 2011).

1.3.5 Movement patterns and environmental drivers

African elephants are physiologically predisposed to travel long distances (Birkett *et al.*, 2012). Their movement patterns are extremely complex in time and space, as well as highly influenced by seasons (Young *et al.*, 2009a; Young *et al.*, 2009b; de Beer and van Aarde, 2008; Leggett, 2006; Cushman *et al.*, 2005; Douglas-Hamilton *et al.*, 2005); therefore, they are highly variable depending on the scale applied (Birkett *et al.*, 2012; Owen-Smith, 2002; Senft *et al.*, 1987): fine-scale movement patterns may involve periods of one hour, while prolonged periods on larger scales may include weekly, monthly, seasonal, annual and interannual movement patterns (Fryxell *et al.*, 2008; Senft *et al.*, 1987). When elephant populations flourish, it is essential to know their movement behaviour and how they use the habitat in the long term in order to pursue appropriate management (Loarie *et al.*, 2009). External factors, such as the presence of artificial water sources and fences, can have an impact on elephant populations' growth rate and movement behaviour (Loarie *et al.*, 2009). Additionally, a diversified environment results in a non-homogeneous allocation of resources, including habitats, foraging areas, and water (de Knegt *et al.*, 2007; Apps *et al.*, 2001). However, each resource is available to the individual according to its own timeframe, which may depend on the seasons, abiotic factors, or the presence/absence of other environmental resources (Birkett *et al.*, 2012). In African savanna ecosystems, food availability is linked to seasonal variations, therefore elephants adapt to these changes by modifying their displacement patterns throughout the seasons (Birkett *et al.*, 2012; Fryxell *et al.*, 2008). Hence, the presence and distribution of environmental resources influence the seasonal ranges of elephants. In turn, these highlight which factors are limiting and how demographic variables are affected. Therefore, these dynamics and their drivers are crucial to answering the question of how elephant herds can be limited (Shannon *et al.*, 2006).

It has been pointed out that the movement patterns of elephants are influenced by the type of vegetation, as high-density areas, e.g., clusters of trees, are favoured by these pachyderms because of the higher levels of fibre and nutrients they can gain compared to savanna grasses (Vogel *et al.*, 2020; Ludwig *et al.*, 2008). However, despite the high dietary value of some areas, the energetic costs of travelling, in terms of duration and danger, to reach the habitat may reduce its desirability (Vogel *et al.*, 2020). Local ecology and risk components may in fact represent additional environmental factors influencing the spatial behaviour of elephants (Mramba *et al.*, 2019; Goldenberg *et al.*, 2018; Wittemyer *et al.*, 2017; Shannon *et al.*, 2010; Shannon *et al.*, 2008). Furthermore, when elephants have to choose their route, they are notorious for preferring well-known and well-trodden paths or corridors (Songhurst *et al.*, 2016; Von Gerhardt *et al.*, 2014; Jachowski *et al.*, 2013; Guerbois *et al.*, 2012; Gerhardt-Weber, 2011). Lastly, water is one of the main environmental drivers influencing the movement patterns of elephants, also affecting their use of space (de Beer and van Aarde, 2008; Leggett, 2006; Stokke and du Toit, 2002). Elephants are reliant on water as they have a great turnover, due to water loss through dermal and respiratory evaporation when environmental temperatures are elevated (Purdon and Van Aarde, 2017). Moreover, elephants heavily depend on practices associated with water use, such as mud bathing, swimming, and splashing to thermoregulate themselves (Mole et al., 2016; Dunkin *et al.*, 2013). Thus, it is becoming evident that the combined availability of food and water, are key driving factors in elephant movement patterns and habitat use; therefore, knowledge of how these factors influence elephant ecology and behaviour is critical for conservation (Bohrer *et al.*, 2014).

1.3.6 Changes in spatial behaviour within fenced reserves

At the present time, 84% of African elephants are found within Protected Areas (PAs) (Gross and Heinsohn, 2023). Particularly, South Africa has been a pioneer in the development of fenced reserves aimed at protecting wildlife (e.g., Slotow, 2012; Gusset *et al.*, 2008; Grant *et al.*, 2008; Hayward *et al.*, 2007). Elephants were removed from most of the South African lands by 1900 (Whyte *et al.*, 1999). When reintroduction programs commenced to become successful, large numbers of elephants were relocated within private reserves, i.e., closed systems where the presence of fences restricted any kind of migration (Slotow *et al.*, 2005). One of the main reasons for creating a fenced reserve is the conservation of the species, ensuring an environment protected from external dangers (Slotow, 2012). Despite this, PAs have often recorded elevated elephant mortality, due to illegal killing within the reserve, such as poaching or subsistence hunting (Chase *et al.*, 2016; Woodroffe *et al.*, 2014). Nevertheless, an increasing number of fenced reserves are experiencing an overpopulation of elephants (Gross and Heinsohn, 2023; Selier *et al.*, 2018), which greatly affects the maintenance of balanced ecosystems (Gross and Heinsohn, 2023). PAs often host other threatened species, therefore the ecosystem imbalance created by elephant surplus may have an indirect impact on the survival of these species (Wall *et al.*, 2013). However, in unfenced areas, the steady decline of elephants is similarly leading to ecological dysfunction of the ecosystem, compromising inter-species and environmental dynamics (Gross and Heinsohn, 2023).

Spatial confinement of elephants within fenced reserves may exaggerate their impact on habitat (Thompson *et al.*, 2022; Baxter and Getz, 2005; Hoare, 1999; Laws, 1970). The presence of fences can lead to a decrease in seasonal movements and, therefore, a concentration of foraging impacts in selected areas (Guldemond and Van Aarde, 2008; Lombard *et al.*, 2001; Cummings *et al.*, 1997). Therefore, in fenced reserves the likelihood for elephants to repeatedly use the same patches of vegetation increases, due to limited dispersal possibilities across the landscape in relation to food supply (Thompson *et al.*, 2022; Howes *et al.*, 2020; de Boer *et al.*, 2015; Mackey *et al.*, 2006; Slotow *et al.*, 2005). Furthermore, the fence line may itself pose a problem, as Loarie *et al.* (2009) showed how it sometimes induced elephants to group against it. Additionally, movement patterns are also affected by proximity to fences, with articles showing an increase in habitat use as distance from the fences increases (see e.g., Thompson *et al.*, 2022; Vanak *et al.*, 2010).

1.4 Hypotheses, Aims and Objectives

Through the use of hourly GPS fixes, this research aimed to explore the movement patterns of two matriarchs within a fenced reserve in South Africa over a 7-month period. Utilising Hidden Markov Models (HMMs), the study's objective was to determine the most suitable multi-state model for the two matriarchs. This aimed to evaluate their baseline movement patterns and variations in behavioural states, both on a monthly scale and over a combined period of seven months. Afterward, the study proceeded to assess the influence of four distinct extrinsic factors: terrain roughness, distance to the nearest road/path, distance to the nearest water source, and NDVI. This evaluation aimed to determine whether these factors played a pivotal role in shaping the movement patterns of the two matriarchs and to what degree. All four predictor variables were examined independently to assess their direct influence on elephant movements. By explicitly testing their influence on a monthly and collective scale, the aim of the study was to clarify the extent to which movement patterns depend on such covariates, providing a better understanding of the elephants' choices and preferences that drove their movement within the reserve. Thus, in turn, this research aimed to provide information of critical importance for the successful and effective management of the species and, consequently, the entire ecosystem.

2 METHOD

2.1 Study location

Selati Game Reserve (SGR) is located in South Africa, specifically in Limpopo Province, north of the Olifants River (23º54'S - 24º06'S, and 30º36'E - 30º55'E) (Fig.1). The SGR was founded in 1993 when several private landowners joined together 16 properties, with the aim of safeguarding and supporting wildlife and plants richness of the site (Siegel, 2023; Peel and Martindale, 2020). Being surrounded by electrified fences, the SGR is an enclosed reserve, covering a total area of 258 km² (Selati Game Reserve, 2017). To the northwest of the reserve lies the Gravelotte Emerald Mine. Along the western border is the town of Gravelotte, while near the eastern border, the community managed Marakapula Reserve is based. This latter reserve serves as a barrier between the SGR and the Namakgale rural area, as well as between Abelana and Balule Private Nature Reserve (Comley, 2019; Peel and Martindale, 2020). The SGR is bordered by other protected lands to the south, specifically Makalali-Pidwa and Karongwe Reserves, while to the north by community livestock farms. The entire reserve is located within the Ba-Phalaborwa Local Municipality, which is part of Mopani District Municipality of Limpopo Province (Peel and Martindale, 2020). At the present time, the reserve is based on low-impact ecotourism (Siegel, 2023) and authorised low-impact hunting, which partially supports the reserve at the economic level (Peel and Martindale, 2020).

The SGR is characterised by hot summers and warm-to-cold winters. The reserve experiences about 500 mm of precipitation per year (Kottek et al., 2006; Peel and Martindale, 2020). Evapotranspiration rates have occasionally exceeded rainfall, causing a strong impact on plants (Peel and Martindale, 2020). Precipitation is mainly concentrated between October and March, reaching the maximum amount of mm per month between December and January (Fig.) (Comley, 2019).

The scarcity and inconsistency of rainfall are characteristic features of semi-arid savanna ecosystems. In this context, only two seasons characterise the area over the course of the year: a five-month hot and wet season (November-March) and a cold and dry season between May and September, with April and October as transition periods between the two seasons (Peel and Martindale, 2020). During the summer, temperatures vary between 18°C and 45°C, whereas in the winter, they range from 8°C to 23°C. The average highest monthly temperature typically reaches around 40°C, while the lowest mean minimum temperature hovers around 0°C (Peel and Martindale, 2020).

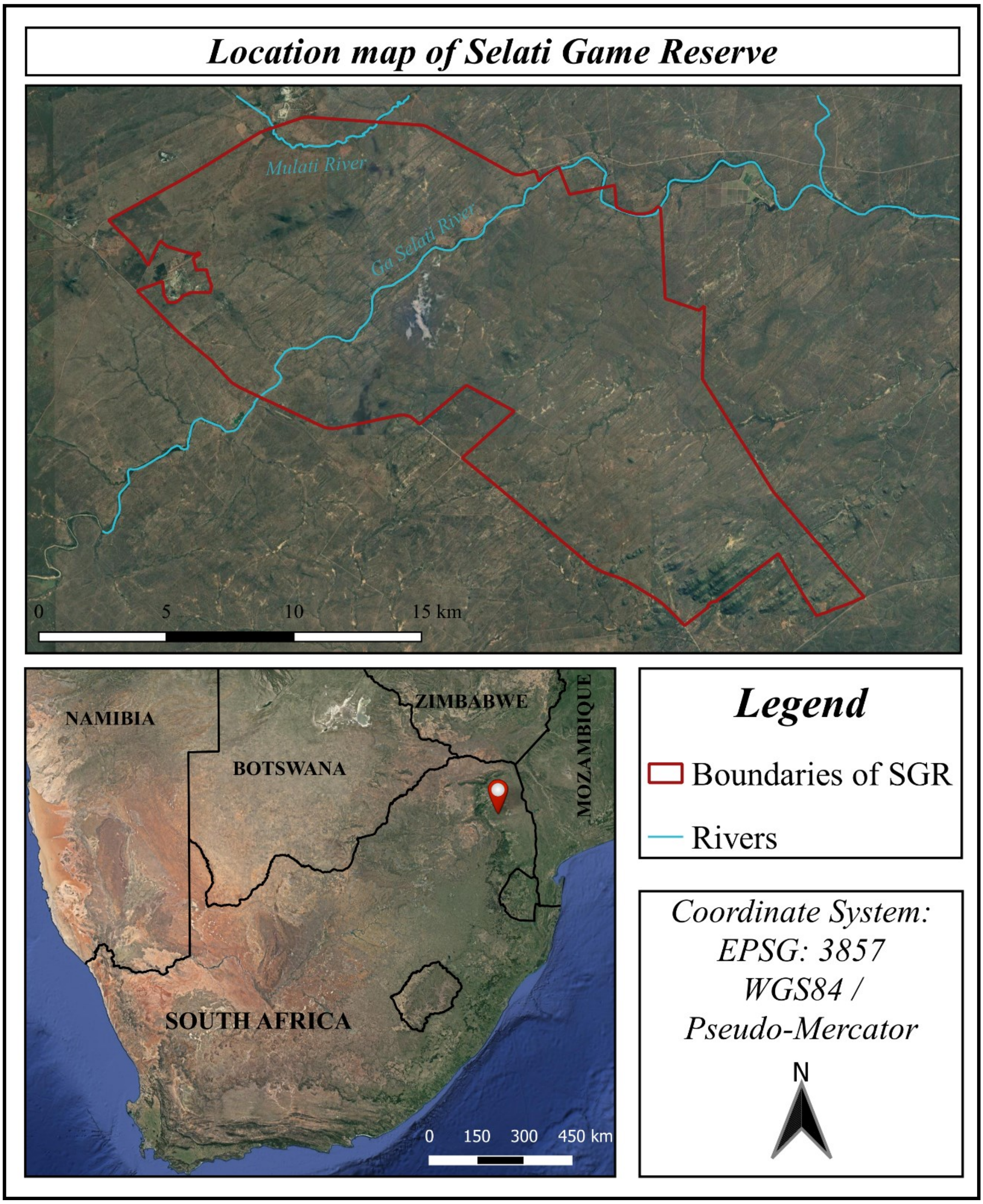

Figure 1. Location map of Selati Game Reserve. Created with QGIS Desktop by Zelia Romano.

The SGR is at an elevation averaging 530 m above sea level (a.s.l.), reaching 778 m a.s.l in the southernmost part of the reserve, with the Ga-Mashishimale Hills. The Selati River flows through the reserve from west to northeast, and along with other drainage streams, flows as a tributary into the Olifants River, partly creating the Greater Olifants River Basin (Peel and Martindale, 2020).

Within the SGR boundaries, multiple water points are present for wildlife, scattered throughout the reserve (Fig.). These include 38 seasonal pans, 22 artificial water sources, 7 reservoirs and at least 10 boreholes, of which only about half are active. The seasonal pans are designed so that rainwater runoff flows into them, however supplementary water can come from surrounding boreholes as well. In the section of the Selati River that lies within the reserve, six dams were built in the past: currently only three are still intact (Comley, 2019; Siegel, 2023).

The SGR is entirely within the South African Savanna Biome, including three different bioregions within its boundaries (Rutherford *et al.*, 2006) (Fig.2):

i) The Phalaborwa-Timbavati Mopaneveld bioregion, which covers 61% of the reserve, fully dominate the central areas of the reserve. It covers an area with a wide variation in elevation, ranging from 300 m to 600 a.s.l. It is dominated by red bushwillow (*Combretum apiculatum*), silver cluster-leaf (*Terminalia sericea*) and mopane (*Colophospermum mopane*) (Rutherford *et al.*, 2006), across mopane forests, mixed mopane-bushwillow forests and mixed mopane-bushwillow-*Acacia spp.* forests (Peel and Martindale, 2020). The abundance of termite mounds scattered throughout the bioregion is another distinctive feature of the area (Mucina and Rutherford, 2006).

ii) The Granite Lowveld bioregion represents only the 33% of the SGR, and it is mainly distributed in the northern and southern areas. It extends over a wide range of elevations, particularly between 250 and 700 m a.s.l., resulting in major changes in soil composition throughout this elevation range. Ancient granites and Makhutswi gneiss, which represent the bedrock geology, form sandy soils at higher elevations and clay soils in lower areas (Rutherford *et al.*, 2006). The bioregion is represented by scattered shrubland and low, fairly dense forests in the sandy areas, where three main species dominated, namely silver cluster-leaf, large-fruited bushwillow (*Combretum zeyheri*) and red bushwillow (Mucina and Rutherford, 2006). In contrast, in dense and open savanna areas, knob thorn (*Senegalia nigrescens*), sicklebush (*Dichrostachys cinerea*) and brandy bush (*Grewia bicolor*) dominate (Mucina and Rutherford, 2006). Red bushwillow veld, mixed red bushwillow-marula (*Sclerocarya birrea*) veld, and silver cluster-leaf veld are found within this bioregion (Mucina and Rutherford, 2006).

iii) The Gravelotte Rocky Bushveld bioregion constitutes only the mountainous zones, scattered at west and east of the reserve, with a total cover of about 6%. It lies between 450 and 950 m a.sl. and is characterised by open deciduous and semi-deciduous woodlands on rocky areas and isolated hill that stands above well-developed plains (Mucina and Rutherford, 2006). Indeed, rocky soils differentiate this bioregion from the others, generally shallow with rocky outcrops and slopes all around the woodlands. The main tree species typical of this bioregion are African teak (*Pterocarpus angolensis*), hook-thorn (*Senegalia caffra*), bushveld candelabra (*Euphorbia cooperi*) and red bushwillow (Comley, 2019).

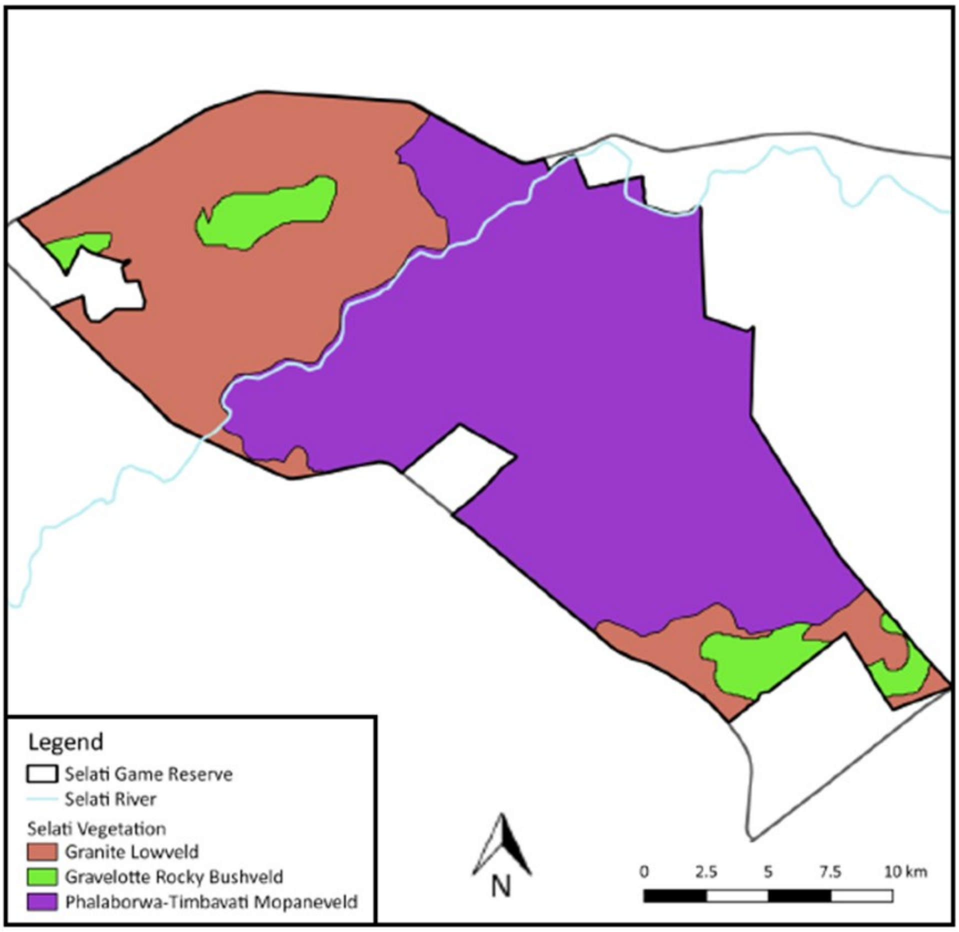

Figure 2. Distribution of the three different bioregions inside SGR (Mucina and Rutherford, 2006).

2.2 GPS Collar Data collection

In 2022, two matriarchs, Elza and Jean (Appendix I), were collared with the Long Range (LoRa) collar devices in the Selati Game Reserve in June. These types of collars enabled GPS positions to be acquired on an hourly basis. Therefore, to study the movements of each matriarch, and thus also those of their herds, GPS-fixes were used from the day the collar was fitted - which is the 1st of June for Elza, and the 8th of June for Jean - until 31st December 2022, the end date for both the matriarchs studied. Throughout the reserve, three gateways were installed in order to have total signal reception coverage of the collars (Seager, 2023). The LoRa collars are a type of tracking device that use LoRaWAN (Long Range Wide Area Network) technology to monitor and collect data about elephant movements (Meenakshi *et al.*, 2022). The collar collects data from the GPS receiver and sensors installed inside it. This data includes the elephant's coordinates, movement patterns, speed, and environmental conditions. The LoRa technology allows the collar to transmit the collected data over long distances using low-power, wide-area networks (Meenakshi *et al.*, 2022). Subsequently, gateways located within the reserve pick up the transmitted data from the collar. Finally, the received data is sent to an Amazon Web Service Stack (AWS Stack) and then to ArcGis Online, where it is stored (Seager, 2023).

The LoRa collars involved in this study have a spatial accuracy of 5 metres and a temporal error between 0 and 2 minutes every hour, i.e., a GPS fix is recorded every 60-62 minutes (Seager, 2023). GPS reception problems resulted in missing position data. These were imputed using a customised R function that interpolated values for intervals greater than 65 minutes. In the 7-month period analysed in this study, LoRa collars recorded 2.18% and 1.67% missing data from Elza and Jean respectively, ensuring reasonable completeness (Table 1).

Table 1. Missing detections of GPS fixes for each analysed month per matriarch. Additionally, the total number of GPS points divided per month and matriarch.

GPS fixes				
	Elza		***Jean***	
	Missing detections	*Total records*	*Missing detections*	*Total records*
June	6	711	6	542
July	5	742	2	743
August	71	742	63	740
September	14	720	4	719
October	7	743	5	743
November	4	718	3	719
December	5	742	3	742

2.3 Data preparation for covariates and Remote Sensing Data

The model built to analyse each matriarch movement pattern included four covariates: terrain roughness, distance to nearest road/path, distance to nearest water source, and NDVI.

Selati Game Reserve shared essential shapefiles to carry out this project, particularly concerning the distribution of all the main and secondary gravel roads (see Appendix II), and the location of all water sources within the reserve, both natural and artificial (see Appendix II). The water points were then divided into seasonal and perennial, so that during the dry season only the active ones were applied. The distance from each GPS fix to the nearest water source and road was calculated in R for both matriarchs. Terrain roughness and elevation of the entire reserve were calculated using ‘terra’ and ‘elevatr’ packages, respectively (Hijmans *et al.*, 2023; Hollister *et al.*, 2023). Even though previous research pointed out that elevation could indirectly influence preferences by having an effect on the other covariates (Asner *et al.*, 2016; Berti *et al.*, 2022; Chibeya *et al.*, 2021; Ngene *et al.*, 2009; Taher *et al.*, 2021; Talukdar *et al.*, 2020), the elevation variable was excluded because the best performing model did not include elevation. Instead, terrain roughness was included as a covariate since it was in the best approximating model.

The Normalized Difference Vegetation Index (NDVI) was calculated to be added as another covariate in order to assess habitat preferences. The satellite images used to calculate the NDVI value were downloaded from Planet (https://www.planet.com/). Their spatial resolution is 3 metres per pixel. One image per month was downloaded, choosing a date close to the middle of that month and having a cloud cover below 5%. The chosen image was used as representative of the entire month to which it referred (details of all satellite tiles use are given in Appendix III). The NDVI calculation was performed separately for each month on QGIS Desktop (version 3.30.1 “s-Hertogenbosch”), using the raster calculator tool. Only the near-infrared (NIR) and red (RED) bands were utilized as input for the calculation, following the formula NDVI= NIR−RED/NIR+RED. The NDVI value obtained from the satellite image for a particular month was consistently applied to every day within that same month (see Appendix II).

2.4 Hidden Markov Model (HMM)

Elephant movement patterns were statistically analysed through a Hidden Markov Model (HMM). HMM is a state-space models that outline animal behaviours as a series of states delineated by both movement parameters and transition probabilities between states (Jonsen *et al.*, 2005; McClintock *et al.*, 2020). In detail, it consists of two dependent parts: a set of observations Z1; . . .; ZT and a sequence of unobservable states S1; . . .; ST (Fig.3). The latter take on values between {1,. . .,N}, respecting the Markov first-order finite-state Markov chain (Langrock *et al.*, 2012). Therefore, at any time t, the execution of Z_t is assumed to have been extracted from one of N constituent distributions, determined in turn by the value of the state at time t. In this study, the unobservable states are represented by the different behavioural states (Michelot *et al.*, 2016).

The HMM was adapted to this study using the R package moveHMM, which applies HMMs and associated tools for modelling animal movement (see Michelot *et al.*, 2023). The package was employed to pre-process the data for analysis, to fit HMM to the data and to diagnose fitted models (Michelot *et al.*, 2023).

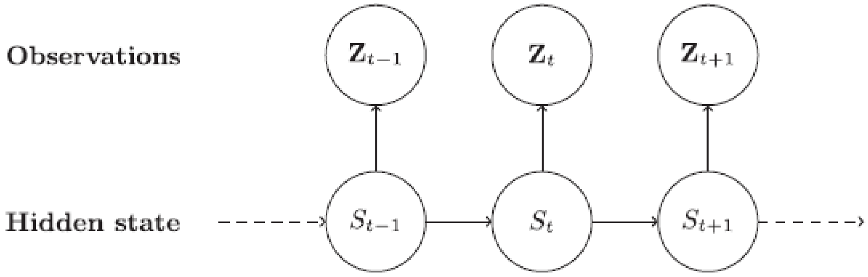

Figure 3. Structure of dependency in Hidden Markov Model (Michelot *et al*., 2016).

2.5 Data processing and fitting HMM

The HMM procedure for modelling animal movements concerns a bivariate time series with $z_t = (l_t, \phi_t)$, where l_t is the step length, i.e., the Euclidean distance between two subsequent GPS fixes (x_t, y_t) and (x_{t+1}, y_{t+1}), and , ϕ_t is the turning angle, i.e. the change in direction in the intervals [t −1,t] and [t, t + 1] of the analysed animal (Fig.4) (Patterson *et al.*, 2017). Therefore, for being able to fit an HMM using moveHMM, the series of step lengths (meters) and turning angles (radians) were calculated through the prepData function from the GPS fixes.

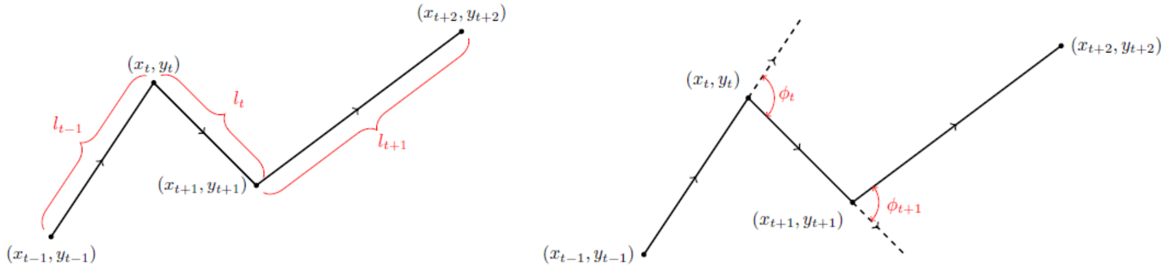

Figure 4. Graphic overview of step lengths and turning angles calculation (Michelot *et al.*, 2023).

Step lengths were modelled with a Gamma (*Γ*) distribution, dependent on two initial parameters: the step mean (mu μ) and the step standard deviation (sigma σ). Turning angles were modelled with a Von Mises (*VM*) distribution, dependent on two initial parameters: the angle-mean and the concentration of the distribution around the mean (kappa k). At a given time, these parameters are governed by the unobserved state corresponding to that fix (Michelot *et al.*, 2023).

The number of states (i.e., behavioural categories) must be entered, along with their state transition probabilities. Likewise, the initial parameters exemplifying the state-dependent distributions, must be stated. As Michelot *et al.* (2016) stressed, these choices are fundamental as the starting values influence the algorithm governing the function for the maximum likelihood estimation (MLE). Furthermore, the choice can influence the outputs of the HMM, since a different estimate of the starting parameters depends on the number of states chosen, thus a change in the parameters can lead to different fitted estimations (Berti *et al.*, 2023). Therefore, if the starting parameters and the number of states are inadequately selected, this affects the fitting of the HMM.

To overcome these possible biases, several trials were conducted in order to find the most suitable number of behavioural states for this study. In particular, a two-state model and a three-state model were adapted as a trial. Both the graphical outputs and the analysis through the Akaike Information Criterion (AIC) confirmed a better fit of the three-state model for the specific case of this research. In addition, this is in line with the findings of Taylor *et al.* (2020), who found that the three-state model was the best fit when analysing elephant movements. Once the number of behavioural states was defined, a function was created to generate random initial parameter values for each state of the HMM's step model (mu and sigma) and angle model (angleMean and kappa). These values were generated within specified ranges, following the methodology explained by Berti *et al.* (2023). Specifically, the initial parameters were ranged between the 10%-90% quantiles of the movement values obtained from the GPS fixes; since the chosen model was three-state, this interval of quantiles' was split into three sub-intervals, one for each state, as follows: U(q10%, q40%), U(q40%, q70%), U(q70%, q90%), respectively (Berti *et al.*, 2023). The function was set on 100 iterations for which the HMM were fitted with different initial parameter values for each state. Subsequently, the model with the lowest negative log-likelihood was chosen as the best-fitted three-state HMM model, thus its parameters were used for all the matriarchs.

Once the starting parameters were set, the model calculated the regression coefficients for the transition probabilities. These coefficients returned an estimate of the probability of transition from one state to the other, based on the values of the predictor variables (Michelot *et al.*, 2023). Additionally, the stationary state probabilities were also performed by the model. They comprised the long-term probabilities of occurring in each state at different values of the covariate (Michelot *et al.*, 2023).

Pseudo-residuals - also called quantile residuals - were applied to assess the correctness and accuracy of the chosen fitted HMM. If the model has analysed the data correctly, the pseudo-residuals must have an approximately normal distribution. Therefore, a deviation from a standard normal distribution suggests a lack of fit of the HMM (Michelot *et al.*, 2023; Michelot *et al.*, 2016). The sequence of behavioural states of the unobserved Markov chain was also decoded to analyse more in deep the state-switching process, using the Viterbi algorithm. The latter provides the most probable succession of states that generated the observation (Michelot *et al.*, 2023; Michelot *et al.*, 2016). Therefore, the Viterbi function was applied to estimate the percentage of time spent in each state. Additionally, the state probabilities, i.e., the probability of occurrence of each state in the model for each GPS time point, given the fitted model, were calculated with a function already present in the moveHMM package. For an HMM with N states and a series of GPS fixes recorded following a succession in time of length T, the function used generates a matrix T x N, where in each row is given the probability that the Markov chain was in each of the N states at the time of row T (Michelot *et al.*, 2023). The state with the greatest likelihood found with the latter function may not correspond with the state in the most likely sequence calculated by the Viterbi algorithm. The reason lies in the different type of execution between the two functions, which can be described as ‘local decoding’ and ‘global decoding’, respectively (Michelot *et al.*, 2023).

The modelling was created to analyse the matriarchs’ movement patterns with the influence of four covariates on a monthly scale. In addition, matriarchs’ movement patterns were also evaluated by combining all months together, in order to gain an overall understanding. The maximum period analysed for a single elephant was seven months (1st of June to 31st of December), of which five months (June to October) were classified as the 'dry season' and the last two (November and December) as the 'wet season', based on the weather conditions of that year, combined with empirical evidence recorded by the reserve managers. Based on the AIC evaluation, the best HMMs model identified three distinct states in all individuals. These states can be classified into broad categories of behaviour: state 1, represented by the short steps, was mainly characterised by slower movements without a specific direction; state 3, represented by the long steps, was the fastest state with a specific direction traced throughout; finally, state 2, represented by the medium steps, had characteristics intermediate between the other two states, i.e., a cadenced speed of movement with both non-directed and directed directions.

During the analysis of Jean's movement patterns, two months, July and November, were notably absent. This absence stemmed from a recurring error in the initial parameters, preventing the extraction of any meaningful results from the GPS data for these particular months. Nevertheless, both July and November were factored into the analysis of all months combined, contributing to the overall assessment.

For maps of monthly movement patterns, see Appendix IV.

3 RESULTS

A total of 10,066 GPS fixes (n) were analysed to study the movement patterns of two matriarchs, Elza (n = 5,118) and Jean (n = 4,948), within the Selati Game Reserve, between June and December 2022.

3.1 Elza

The step length means for each state fluctuated in a month-scale analysis: state 1 had a minimum of 55 metres c.a. (in June) and a maximum of 102 metres c.a. (in October); state 2 ranged from a minimum of 157 metres c.a. (in October) and a maximum of 369 metres c.a. (in December); state 3 exhibited a minimum of 754 metres c.a. (in September) and a maximum of 1129 metres c.a. (in December). Overall, on a 7-month period, the step length means were 61.5, 272, and 994 meters, for states 1,2, and 3 respectively. Fluctuations were also recorded for the standard deviation (SD) of the step length, as well as for the mean and concentration of the turning angle (see Table 2 and 3).

Table 2. Step length parameters showing the mean (expressed in km) and standard deviation (SD) for each month and for all the months combined (last row). The step length mean corresponds to the average distance covered in a single step for each state.

Step length parameters						
	Mean			*SD*		
	State 1	*State 2*	*State 3*	*State 1*	*State 2*	*State 3*
June	0.055	0.310	1.077	0.055	0.221	0.543
July	0.066	0.270	0.953	0.064	0.160	0.533
August	0.074	0.222	0.857	0.071	0.104	0.579
September	0.063	0.182	0.754	0.063	0.127	0.511
October	0.102	0.157	1.001	0.125	0.131	0.710
November	0.066	0.305	0.983	0.061	0.182	0.404
December	0.079	0.369	1.129	0.077	0.201	0.430
June-December	**0.061**	**0.272**	**0.994**	**0.058**	**0.166**	**0.556**

Table 3. The turning angle parameters, showing the mean and the concentration for each month and for all the months combined (last row). The turning angle mean corresponds to the average angle performed in a single step for each state.

Turning angle parameters						
	Mean			*Concentration*		
	State 1	*State 2*	*State 3*	*State 1*	*State 2*	*State 3*
June	0.300	0.012	-0.147	0.541	1.165	2.279
July	-0.029	0.070	-0.030	0.627	1.619	1.551
August	0.205	0.027	0.052	0.721	1.872	1.737
September	0.501	-0.028	0.044	0.267	2.212	1.867
October	-2.692	0.095	0.054	0.889	1.416	2.101
November	-0.030	-0.027	0.076	0.239	1.123	2.051
December	0.414	-0.097	-0.024	0.663	1.231	2.157
June-December	**0.178**	**0.021**	**-0.015**	**0.484**	**1.407**	**1.824**

A clear difference was found in the time spent in state 3 (long step) between the dry and wet seasons, with an average for all dry months of around 35% of the total time spent walking long distances, in contrast to only 14.5% during the wet months (Table 4). In particular, in November, the first month after the dry season, there is a peak in the percentage of time spent in state 1 (short step), with a value of 41% (Table 4).

Table 4. Percentage of time spent for each state obtained with the Viterbi algorithm, included in the Viterbi function of the moveHMM package. It provides the most probable sequence of states that generated the observation, based on the fitted model.

	Percentage of time spent on each state		
	State 1	*State 2*	*State 3*
June	0.319	0.462	0.217
July	0.364	0.426	0.215
August	0.318	0.384	0.402
September	0.267	0.361	0.390
October	0.131	0.588	0.289
November	0.413	0.476	0.116
December	0.312	0.508	0.185
June-December	**0.319**	**0.462**	**0.217**

In June (Table 5, Fig. 5-8), when all covariates are set to zero, the baseline probability of transitioning from state 1 to state 2 (*1→2*) was +0.71. Under the influence of the NDVI variable, this probability became -3.09, indicating that an increase in the value of this predictor variable was associated with a decrease in the odds of the event occurring. Conversely, the baseline probability of moving from state 1 to state 3 (*1→3*) and from state 2 to state 1 (*2→1*) exhibited considerable negative values (-15.50 and -5.15, respectively). In contrast, when the influence of distance to the water source was considered, the *1→3* probability suggested a positive relationship between the predictor and the outcome (+1.26). This indicated that as the distance from a water source increased, the *1→3* switching probability increased as well. Similarly, when considering the influence of NDVI, the probability of *2→1* transitioning was positively affected, with a value of +6.49. This implied that in greener areas, there was a greater probability of transitioning to state

1. Fig. 5-8 also showed the probability of persistence in a state due to the influence of each covariate: for example, the rougher the terrain, the more likely Elza was to persist in state 1 (Fig.5); just as the lower the roughness value, the higher the probability of persistence in state 3 (Fig.5); furthermore, the higher the NDVI value, the lower the probability of persistence in states 2 and 3 (Fig.8).

Table 5. Regression coefficients for the transition probabilities referred to the month of June. The table shows the probability of transition between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The first row indicates the baseline probability of transition when all the covariates are set to zero. From the second to the fifth row, 4 different covariates and their influence on the transition probabilities are shown.

	Regression coefficients for the transition probabilities					*June*
	1→2	*1→3*	*2→1*	*2→3*	*3→1*	*3→2*
Intercept	0.711	-15.504	-5.159	-0.706	-12.022	-2.608
Terrain roughness	-0.375	1.1585	0.241	0.371	0.413	0.824
Min. road/path distance	0.072	-1.311	0.162	0.146	0.902	0.554
Min. water source distance	0.188	1.264	0.009	0.212	0.029	-0.116
NDVI	-3.090	-8.245	6.497	-2.212	-5.608	3.705

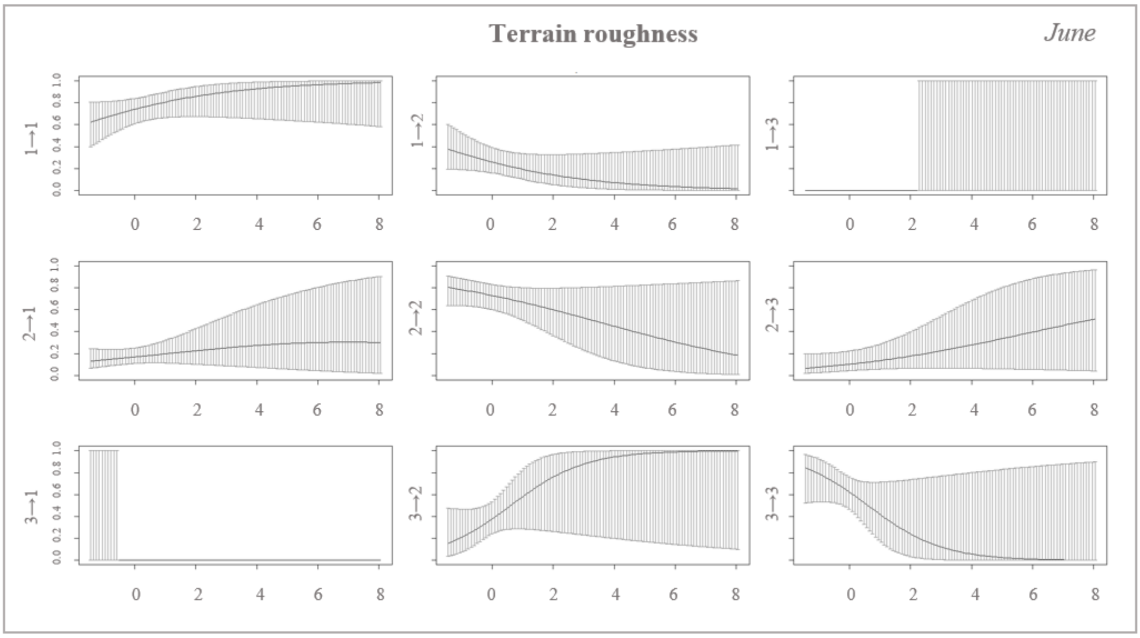

Figure 5. Graph showing transition probabilities under the influence of terrain roughness as a covariate in June, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

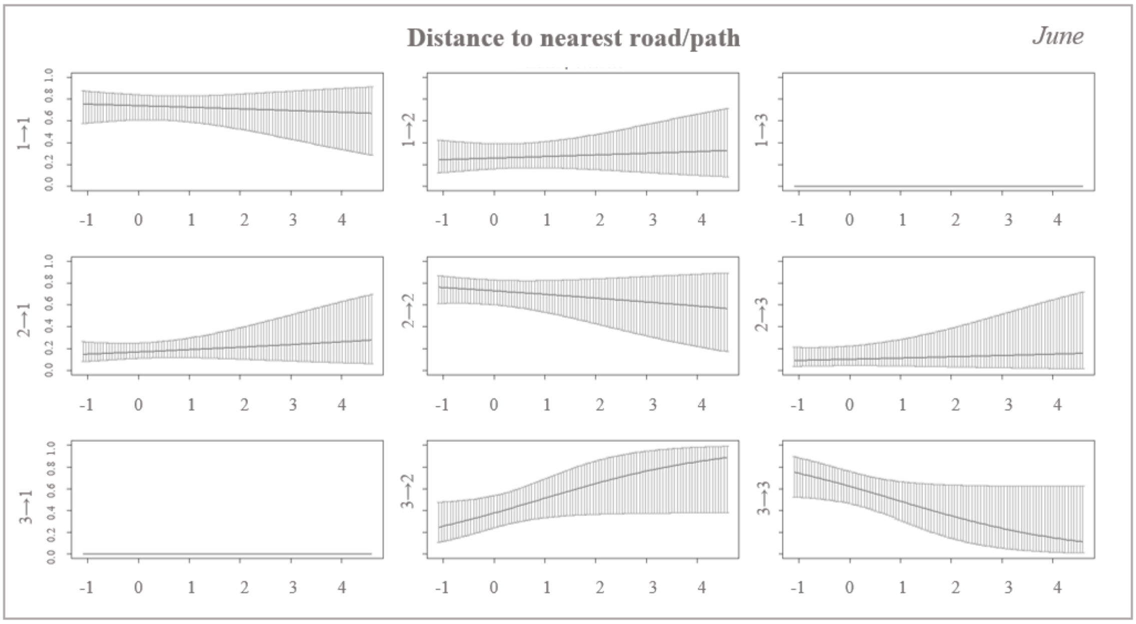

Figure 6. Graph showing transition probabilities under the influence of distance to nearest road/path as a covariate in June, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

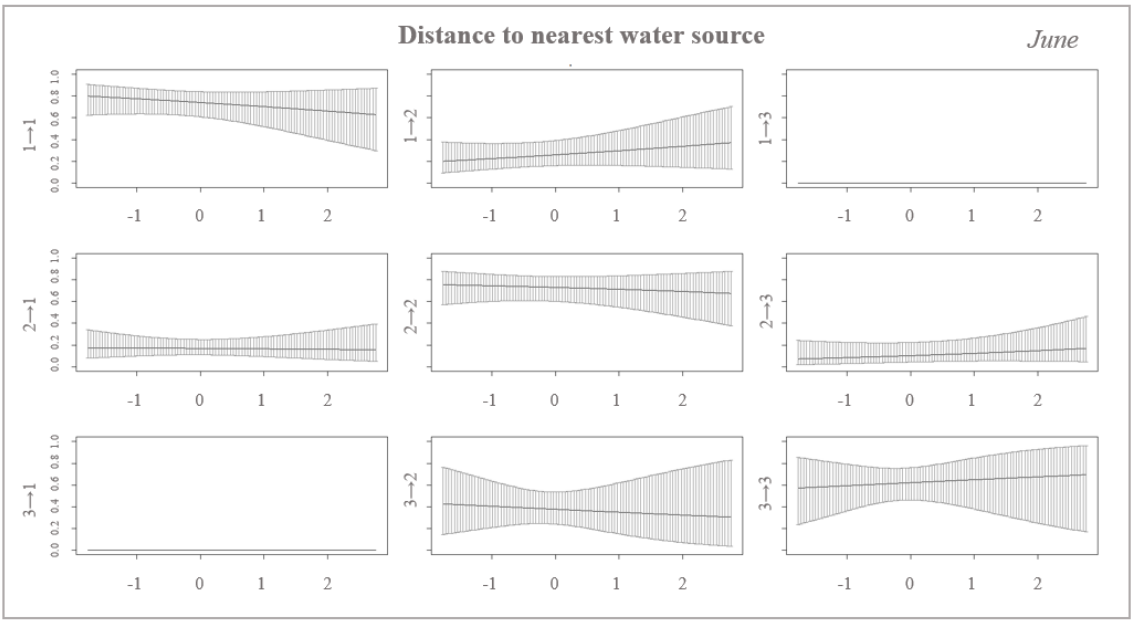

Figure 7. Graph showing transition probabilities under the influence of distance to nearest water source as a covariate in June, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

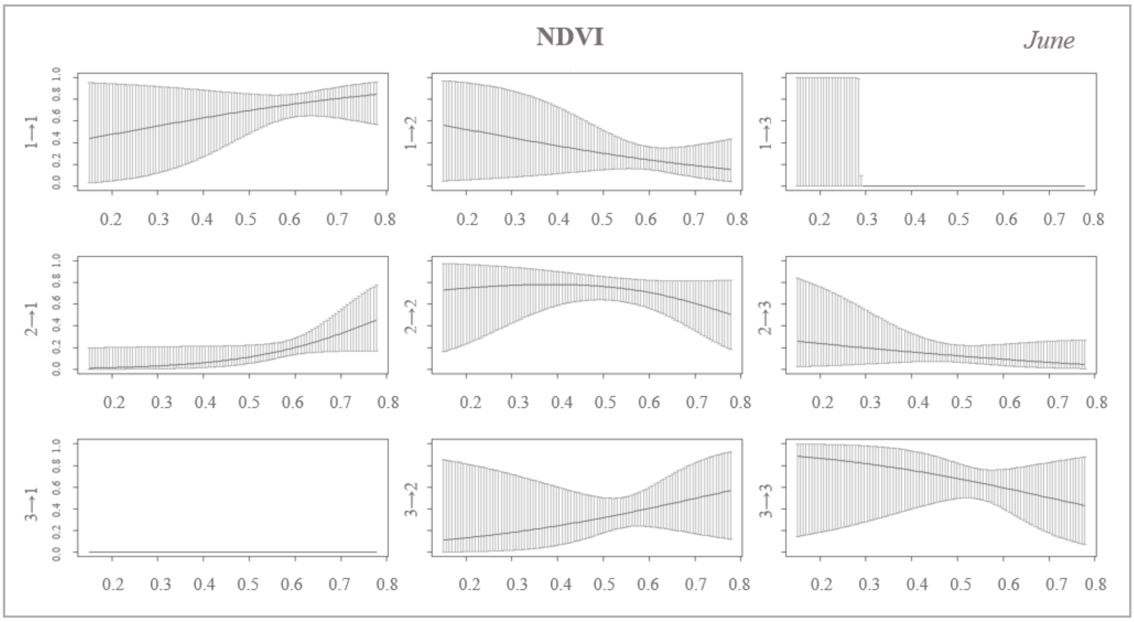

Figure 8. Graph showing transition probabilities under the influence of NDVI as a covariate in June, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

In July (Table 6, Fig. 9-12), Elza presented a tendency to move into state 1 as the terrain was rougher (*3→1* = +0.93), into state 2 as the distance to the nearest road/path increased (*3→2* = +0.80), and into state 3 as the furthest from water sources (*1→3* = +0.21 and *2→3* = +0.29). Under the influence of the NDVI, the *2→1* transition showed a slightly negative value (-0.89); however, a substantially positive value was recorded for the *3→1* switching probability (+9.68), which meant that a large NDVI value promoted the transition. A high probability of persistence in state 3 was indicated at the shortest distance from the road/path (Fig. 10).

Table 6. Regression coefficients for the transition probabilities referred to the month of July. The table shows the probability of transition between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The first row indicates the baseline probability of transition when all the covariates are set to zero. From the second to the fifth row, 4 different covariates and their influence on the transition probabilities are shown.

	Regression coefficients for the transition probabilities					*July*
	1→2	*1→3*	*2→1*	*2→3*	*3→1*	*3→2*
Intercept	0.193	-12.159	-0.920	-0.548	-13.793	-0.570
Terrain roughness	-0.416	-1.215	-0.038	-0.064	0.931	0.999
Min. road/path distance	-0.135	-0.577	-0.048	-0.517	-1.975	0.805
Min. water source distance	-0.077	0.213	-0.160	0.298	-3.568	0.083
NDVI	-2.946	-5.539	-0.893	-1.904	9.684	-0.258

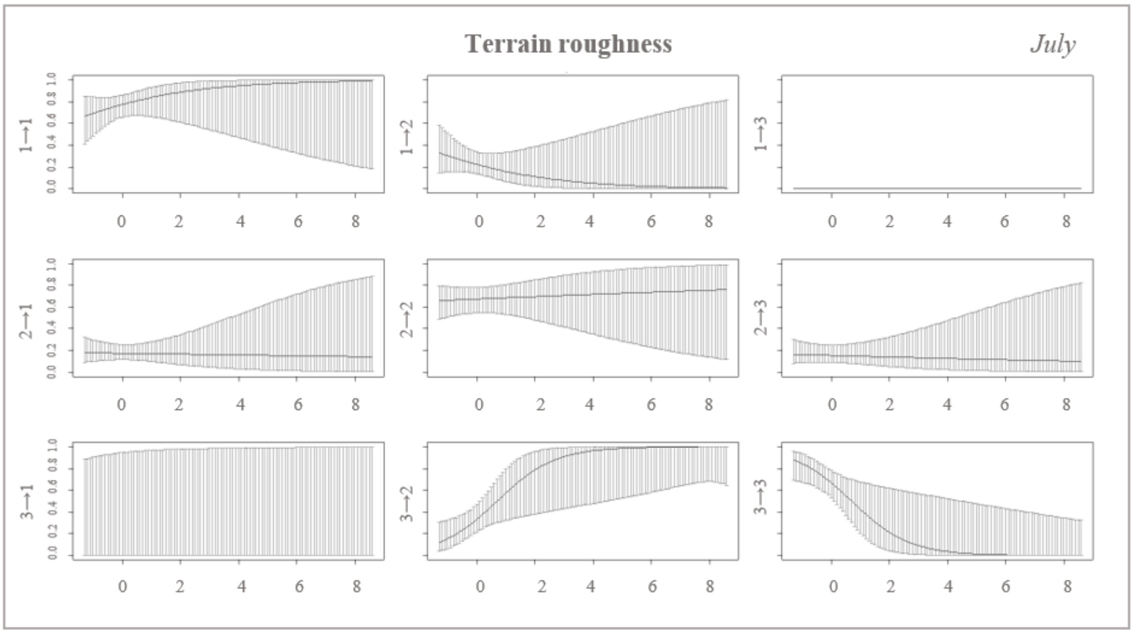

Figure 9. Graph showing transition probabilities under the influence of terrain roughness as a covariate in July, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

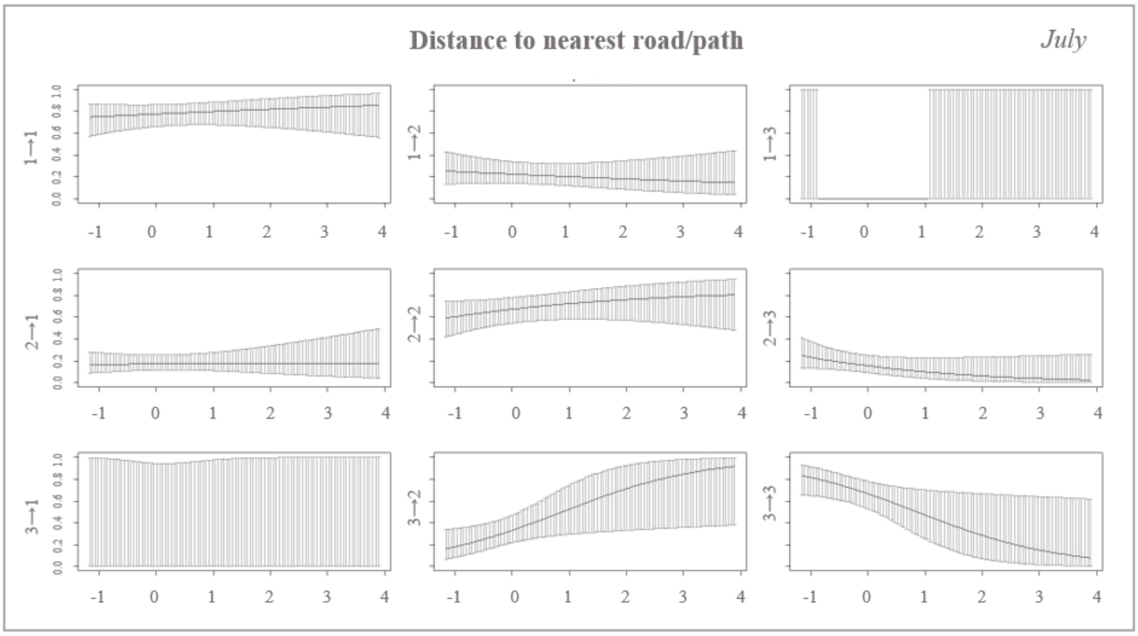

Figure 10. Graph showing transition probabilities under the influence of distance to nearest road/path as a covariate in July, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

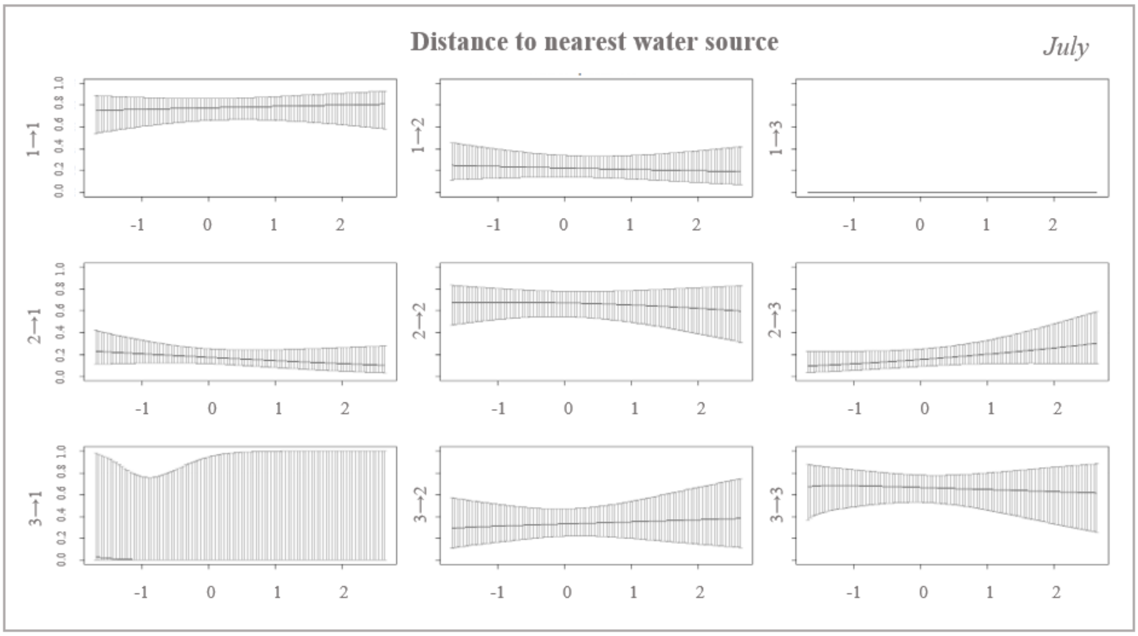

Figure 11. Graph showing transition probabilities under the influence of distance to nearest water source as a covariate in July, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

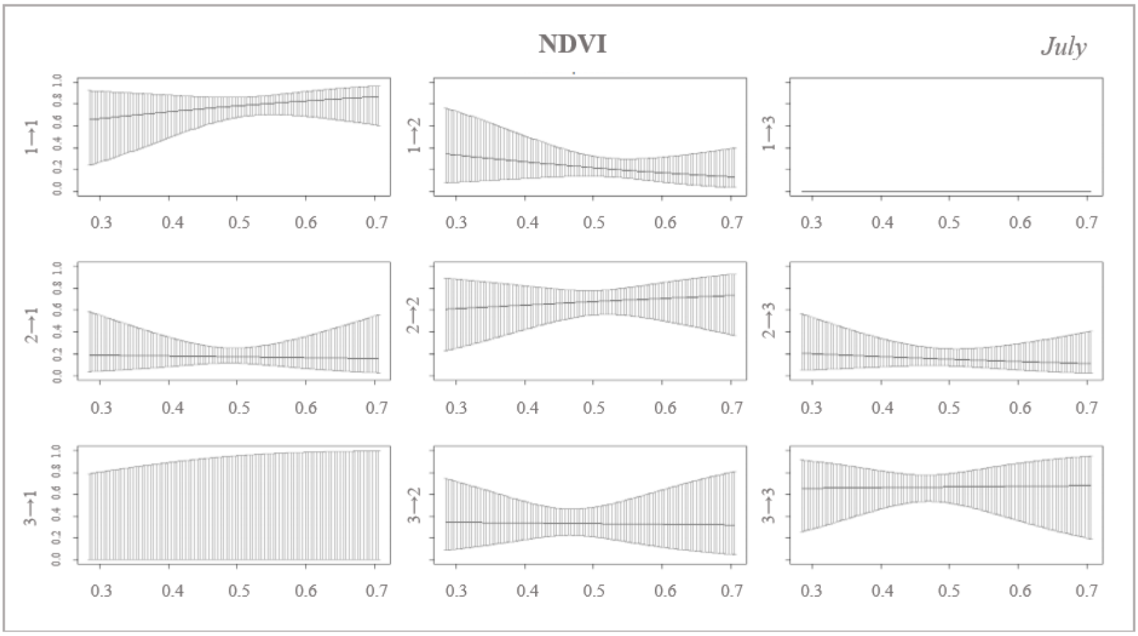

Figure 12. Graph showing transition probabilities under the influence of NDVI as a covariate in July, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

In August (Table 7, Fig. 13-16), when the road predictive variable was set, Elza recorded both positive and negative values, although all very close to zero. In contrast, during the same month, strongly positive values were observed for *2→1* and *3→2* transition probabilities (+11.94 and +20.03, respectively) as the NDVI value increased (Table 7). Additionally, when it was far from the road, Elza was less likely to persist in state 2 (Fig.14); furthermore, it stayed in state 1 when it was closer to the water (Fig.15). Under the influence of the NDVI variable, Elza was likely to be found in state 3 at a low NDVI value (Fig.16).

Table 7. Regression coefficients for the transition probabilities referred to the month of August. The table shows the probability of transition between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The first row indicates the baseline probability of transition when all the covariates are set to zero. From the second to the fifth row, 4 different covariates and their influence on the transition probabilities are shown.

	Regression coefficients for the transition probabilities					*August*
	1→2	*1→3*	*2→1*	*2→3*	*3→1*	*3→2*
Intercept	-0.638	-3.041	-5.672	-0.306	-5.344	-9.230
Terrain roughness	-0.284	-0.203	-0.254	0.347	0.271	-0.045
Min. road/path distance	-0.198	-0.189	-0.141	0.366	0.106	0.160
Min. water source distance	0.114	0.404	-0.206	0.015	0.613	-1.868
NDVI	-2.904	3.072	11.948	-4.643	8.069	20.032

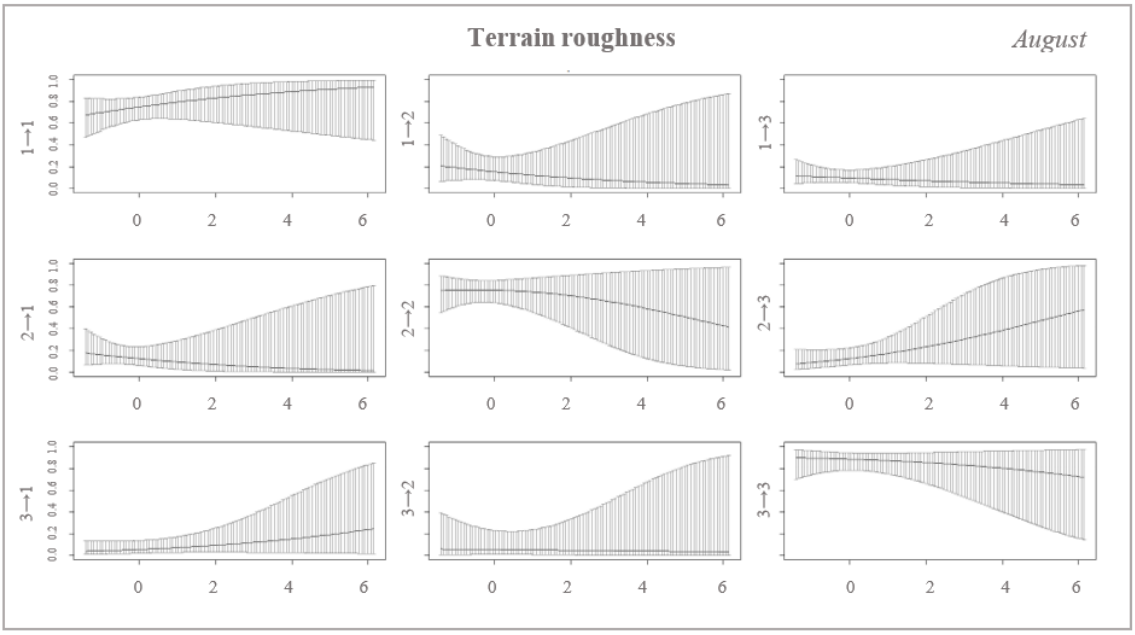

Figure 13. Graph showing transition probabilities under the influence of terrain roughness as a covariate in August, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

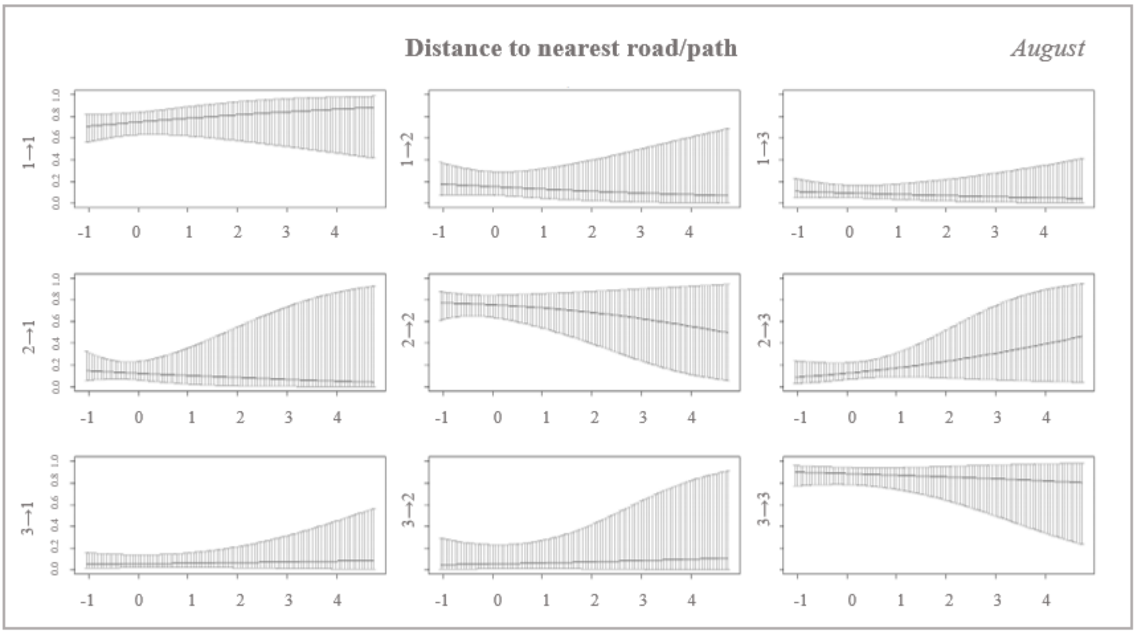

Figure 14. Graph showing transition probabilities under the influence of distance to nearest road/path as a covariate in August, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

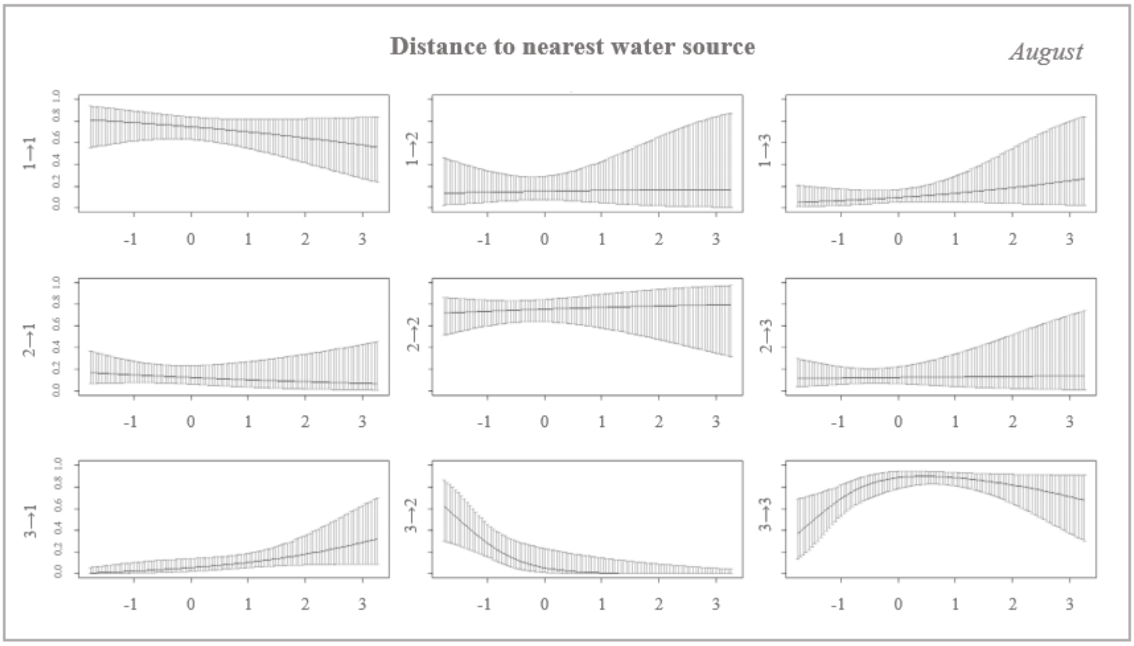

Figure 15. Graph showing transition probabilities under the influence of distance to nearest water source as a covariate in August, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

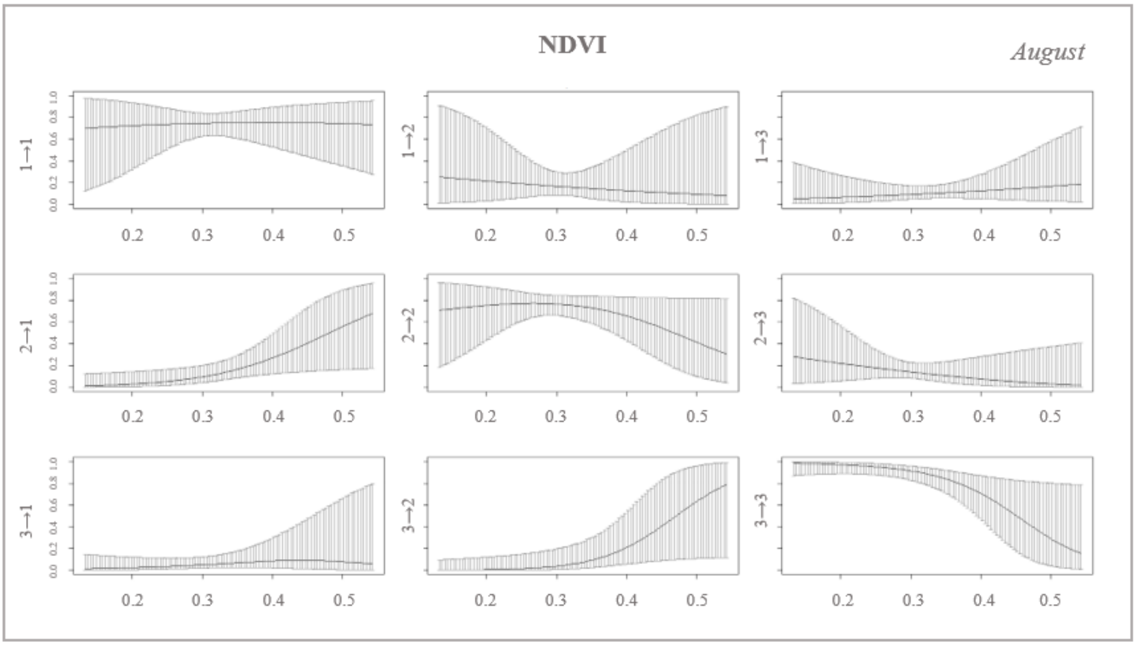

Figure 16. Graph showing transition probabilities under the influence of NDVI as a covariate in August, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

September (Table 8, Fig.13-16) showed extremely high values of *2→1* (+31.50) under the influence of the NDVI (Fig.16). In support of the latter result, Elza persisted in state 2 when at the lowest NDVI values (Fig.16). Regarding the distance from the road, the *3→1* transition was significantly inhibited (-6.00) as the distance from the nearest road increased (Table 8). As evidence, persistence in state 1 was more likely to occur as close to the road as possible (Fig.14). When setting the terrain roughness as a covariate, the *3→1* transition was promoted as the roughness increased (+1.73). Persistence in state 2 was more likely to occur near water sources.

Table 8. Regression coefficients for the transition probabilities referred to the month of September. The table shows the probability of transition between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The first row indicates the baseline probability of transition when all the covariates are set to zero. From the second to the fifth row, 4 different covariates and their influence on the transition probabilities are shown.

	Regression coefficients for the transition probabilities					*September*
	1→2	*1→3*	*2→1*	*2→3*	*3→1*	*3→2*
Intercept	17.761	2.451	-11.419	-2.966	-24.425	-4.667
Terrain roughness	-0.250	0.053	0.076	0.133	1.736	-0.272
Min. road/path distance	-2.294	0.129	-0.486	0.052	-6.008	-0.117
Min. water source distance	0.196	0.125	0.535	0.635	0.318	-0.158
NDVI	-63.557	-9.996	31.507	2.559	-6.257	10.131

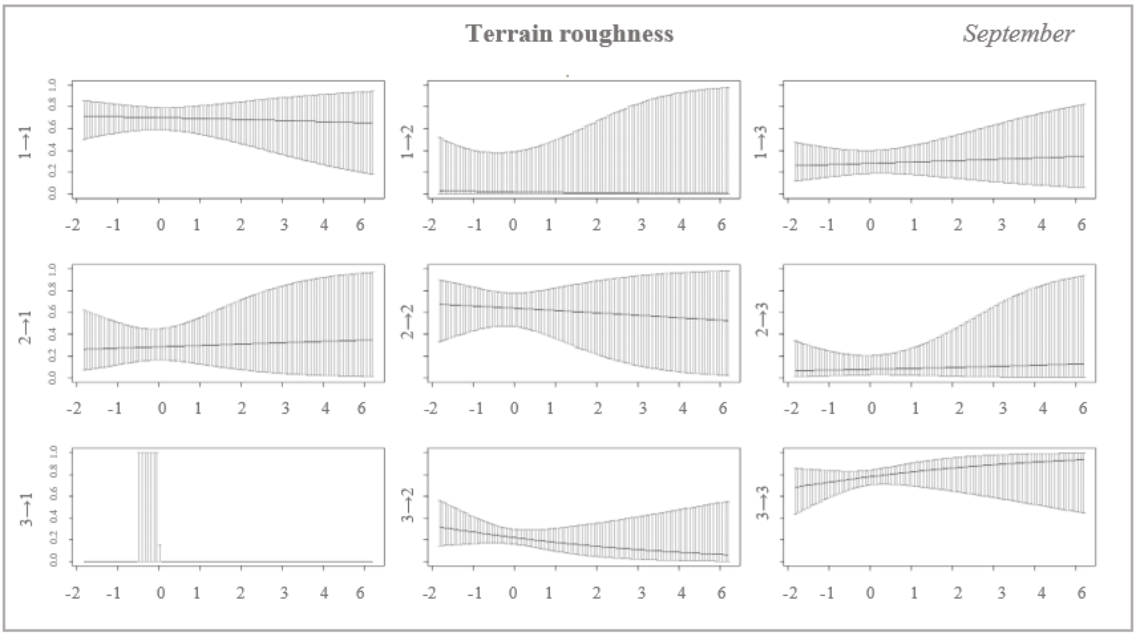

Figure 17. Graph showing transition probabilities under the influence of terrain roughness as a covariate in September, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

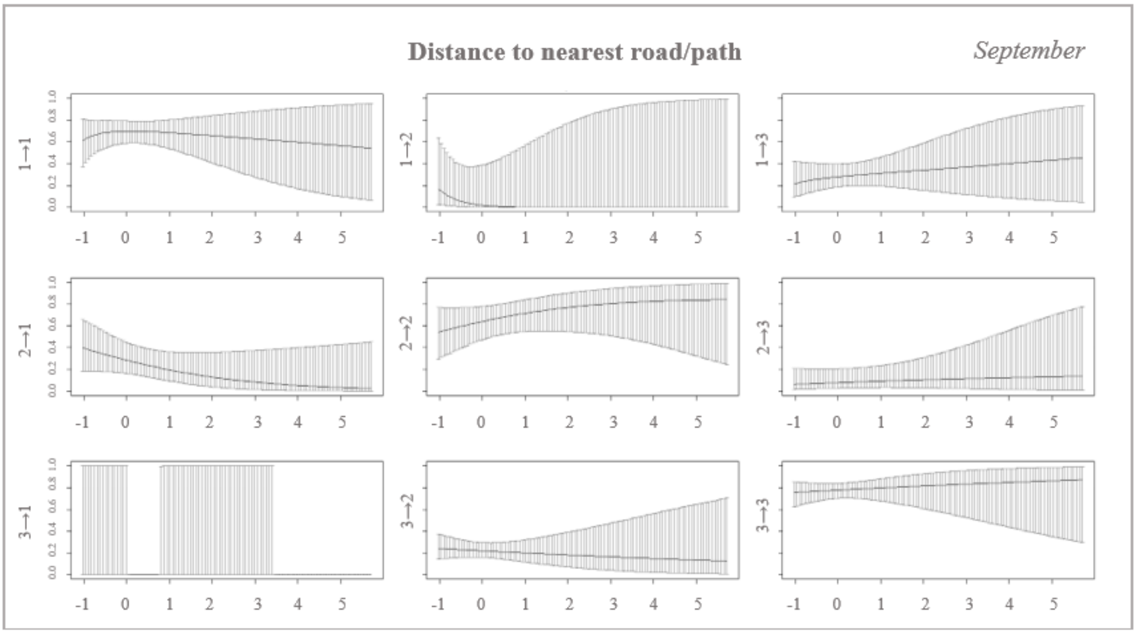

Figure 18. Graph showing transition probabilities under the influence of distance to nearest road/path as a covariate in September, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

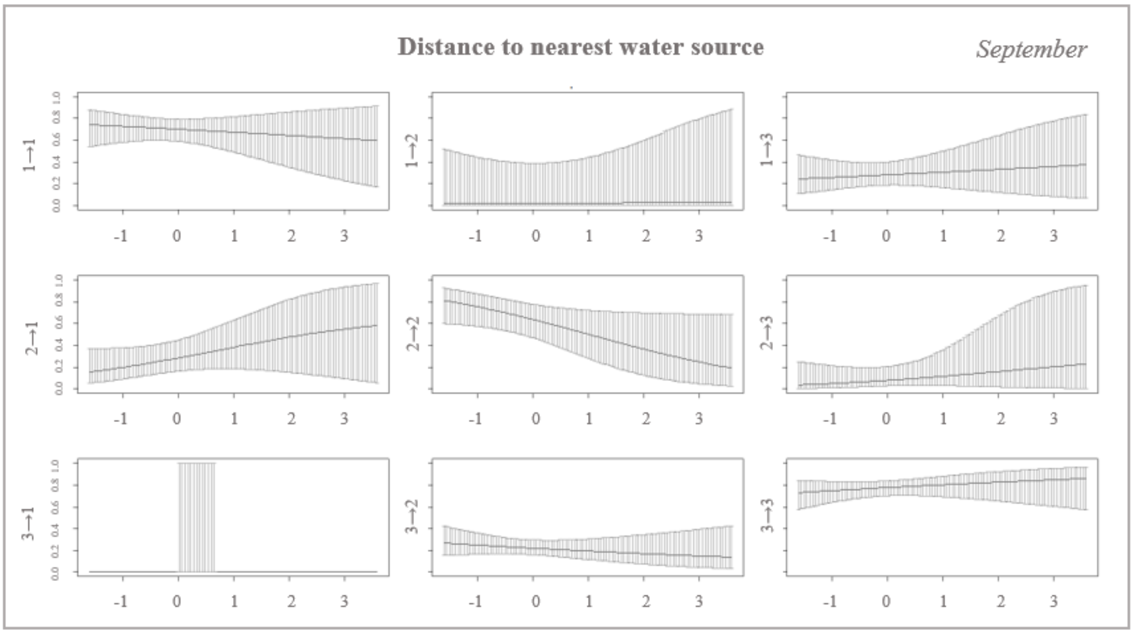

Figure 19. Graph showing transition probabilities under the influence of distance to nearest water source as a covariate in September, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

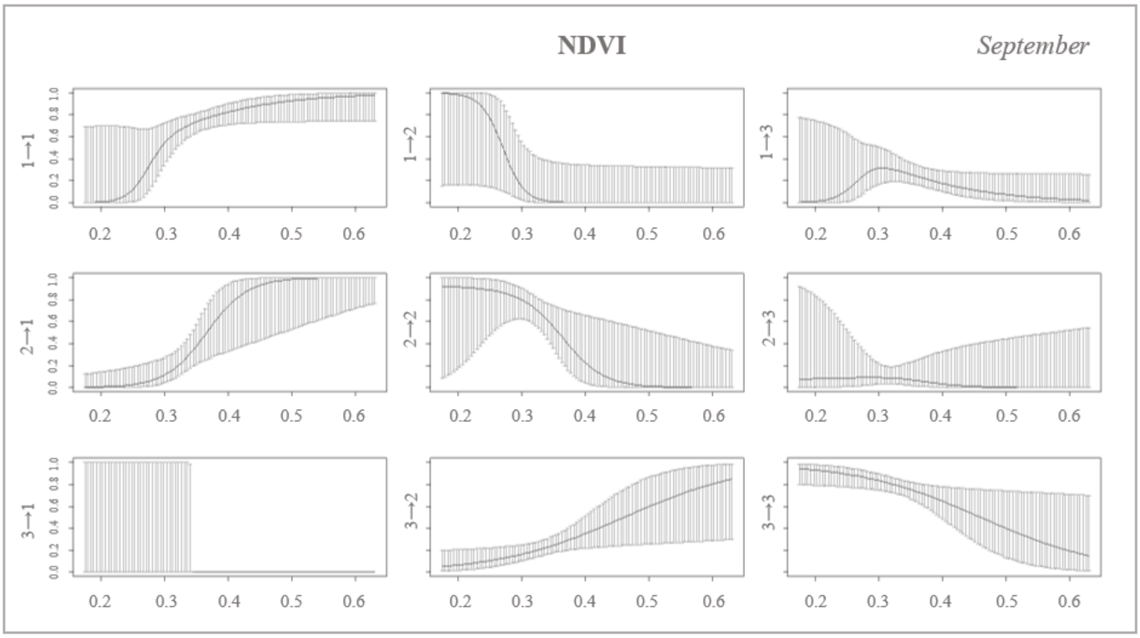

Figure 20. Graph showing transition probabilities under the influence of NDVI as a covariate in September, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

In October (Table 9, Fig.21-24), when NDVI or distance from the road were set as covariates (Fig.22,24), Elza was more likely to be in state 1 (+33.56) as the former increased and the latter at a minimum value. Contrastingly, this month recorded an opposite trend in transition probabilities when terrain roughness was set as a covariate, showing a high probability of persisting in state 1 at the lowest value of roughness (Table 9, Fig.21). Regarding the predictor variable of distance to the nearest water source, the *1→2* switching probability was more probable to occur near the water (Fig.23).

Table 9. Regression coefficients for the transition probabilities referred to the month of October. The table shows the probability of transition between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The first row indicates the baseline probability of transition when all the covariates are set to zero. From the second to the fifth row, 4 different covariates and their influence on the transition probabilities are shown.

	Regression coefficients for the transition probabilities					*October*
	1→2	*1→3*	*2→1*	*2→3*	*3→1*	*3→2*
Intercept	0.195	12.604	-3.924	-3.712	-12.971	-9.022
Terrain roughness	3.458	-1.751	0.359	-0.350	0.286	-0.159
Min. road/path distance	-0.636	2.494	-1.537	-0.363	-0.051	-0.313
Min. water source distance	-4.016	-0.166	-0.962	0.127	-0.330	-0.239
NDVI	-13.550	-45.985	0.534	4.238	33.561	23.391

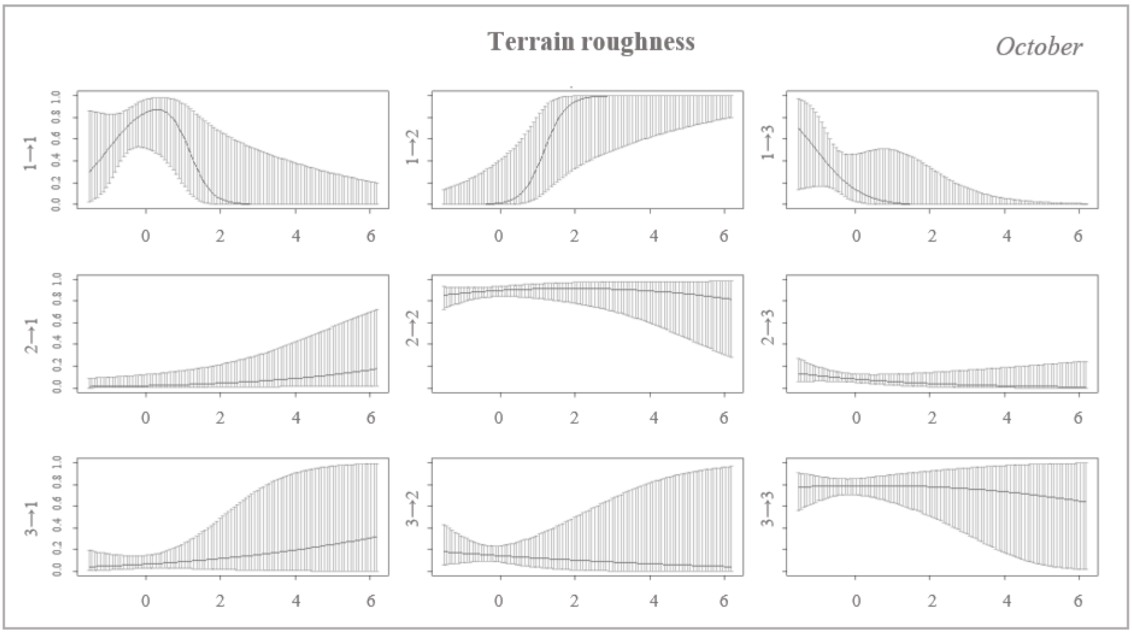

Figure 21. Graph showing transition probabilities under the influence of terrain roughness as a covariate in October, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

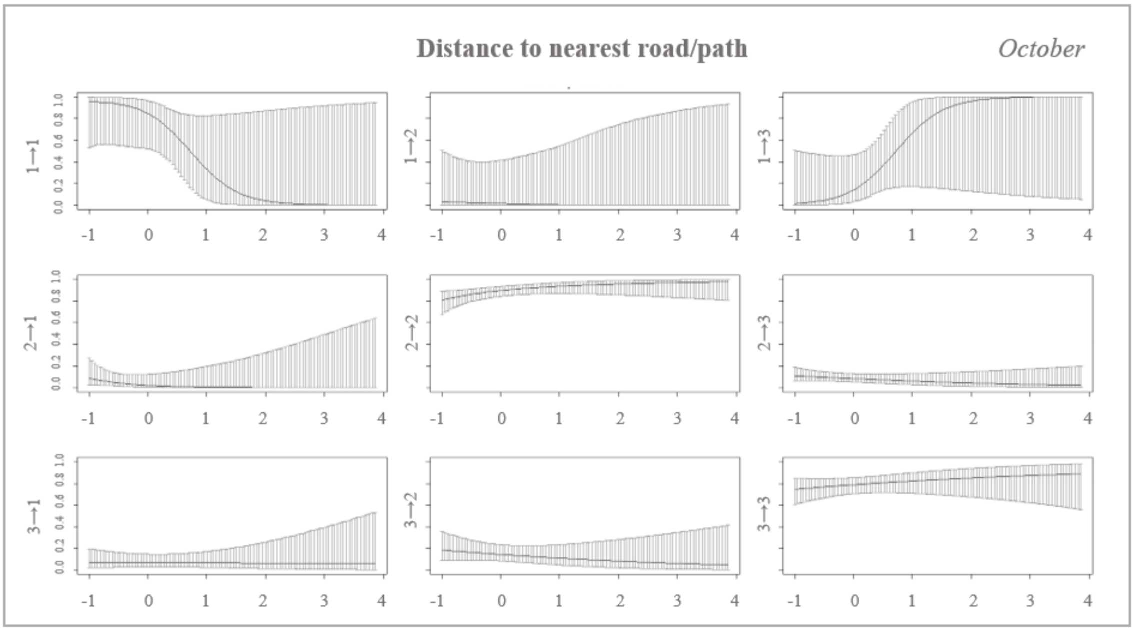

Figure 22. Graph showing transition probabilities under the influence of distance to nearest road/path as a covariate in October, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

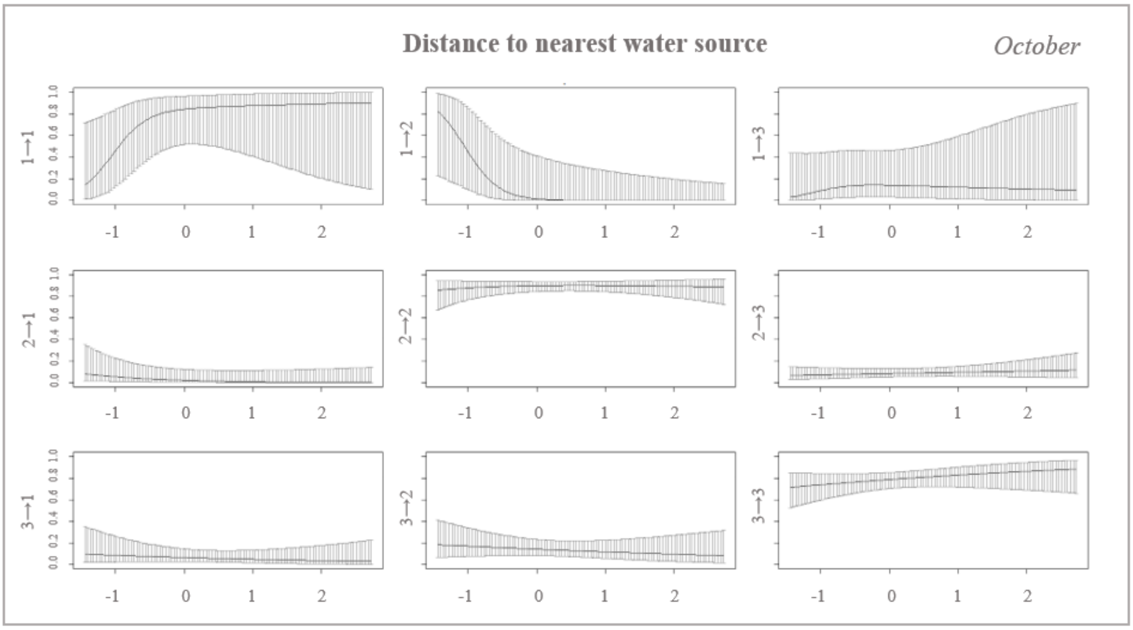

Figure 23. Graph showing transition probabilities under the influence of distance to nearest water source as a covariate in October, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

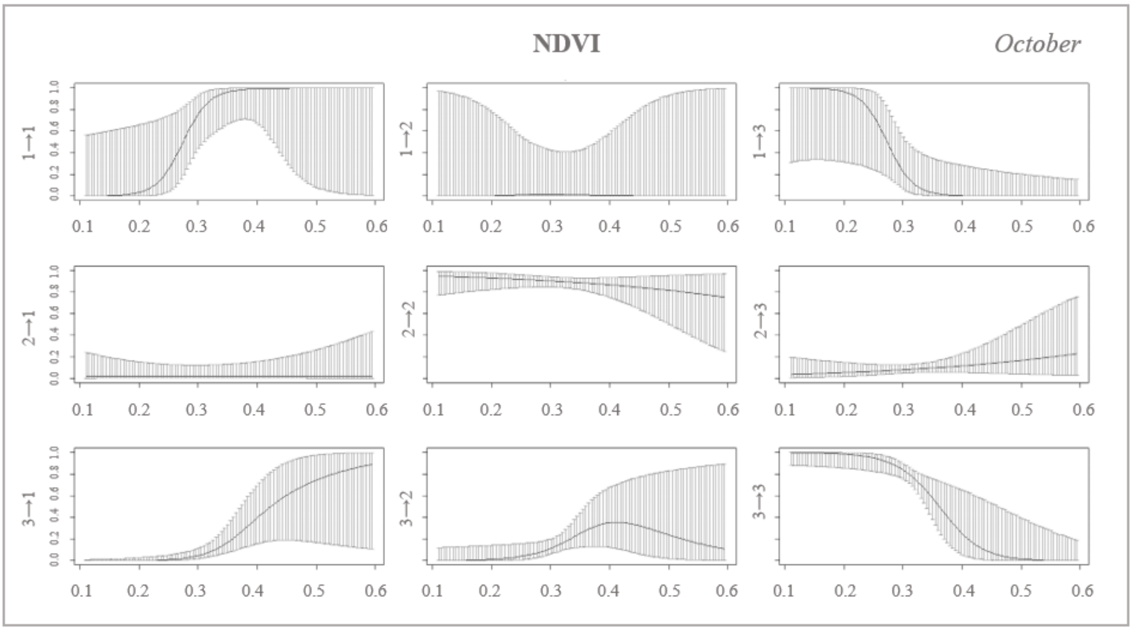

Figure 24. Graph showing transition probabilities under the influence of NDVI as a covariate in October, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

Between November and December, the only two months belonging to the wet season, the results of the transition probabilities followed almost the same patterns for both (Table 10-11, Fig.25-32): a high probability of remaining in state 2 as the terrain was rougher (Fig.25-26); an elevated likelihood of persisting in states 1 and 2 near water and switch into state 3 when the distance from it increased (Fig.29-30); a higher probability of staying in state 3 at a lower NDVI value, moving to state 2, and then to state 1, as the greenness increased (Fig.31-32); and a discrete likelihood of remaining in state 2 when distant from road (Fig.27-28).

Table 10. Regression coefficients for the transition probabilities referred to the month of November. The table shows the probability of transition between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The first row indicates the baseline probability of transition when all the covariates are set to zero. From the second to the fifth row, 4 different covariates and their influence on the transition probabilities are shown.

	Regression coefficients for the transition probabilities					*November*
	1→2	*1→3*	*2→1*	*2→3*	*3→1*	*3→2*
Intercept	-1.722	-37.559	-8.057	-2.799	-27.154	-4.848
Terrain roughness	-0.172	-1.745	-0.118	-1.512	-10.641	-0.110
Min. road/path distance	0.125	3.618	-0.125	0.202	0.625	0.339
Min. water source distance	-0.082	-0.650	-0.090	0.399	-7.341	-0.694
NDVI	0.562	-20.944	11.299	0.904	-9.960	8.594

Table 11. Regression coefficients for the transition probabilities referred to the month of December. The table shows the probability of transition between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The first row indicates the baseline probability of transition when all the covariates are set to zero. From the second to the fifth row, 4 different covariates and their influence on the transition probabilities are shown.

	Regression coefficients for the transition probabilities					*December*
	1→2	*1→3*	*2→1*	*2→3*	*3→1*	*3→2*
Intercept	2.388	14.848	-1.833	-2.405	-481.931	-2.087
Terrain roughness	0.375	-797.052	0.071	-0.317	-40.518	0.301
Min. road/path distance	-0.165	-122.262	-0.082	0.039	10.639	0.009
Min. water source distance	0.011	-241.173	0.142	0.753	-40.660	-0.117
NDVI	-5.153	-2211.85	0.859	0.572	-291.208	2.015

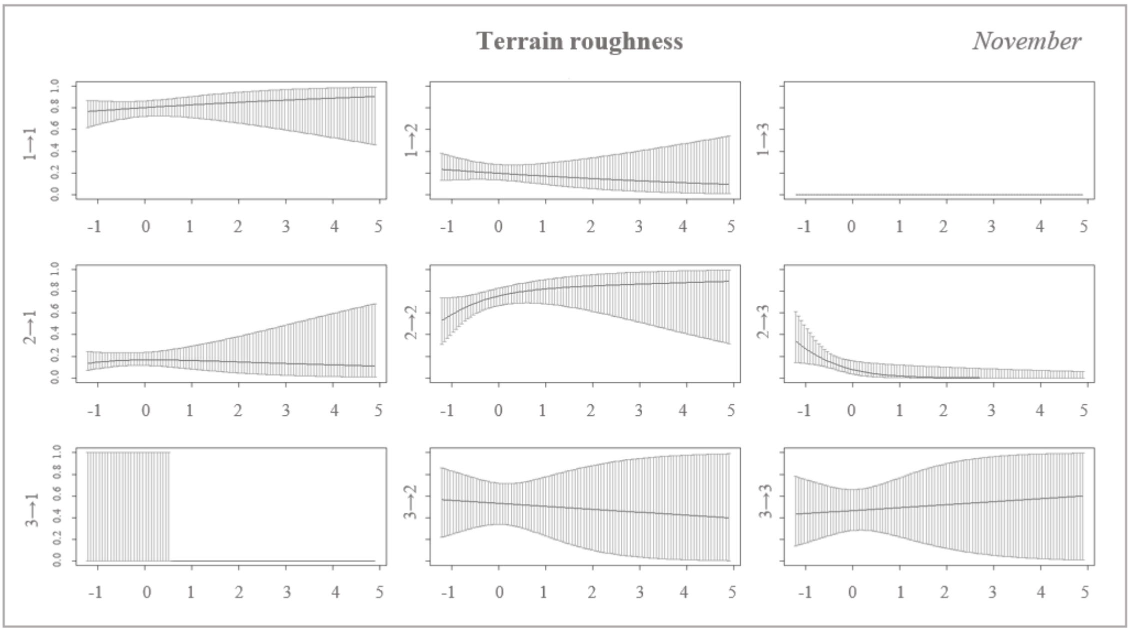

Figure 25. Graph showing transition probabilities under the influence of terrain roughness as a covariate in November, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

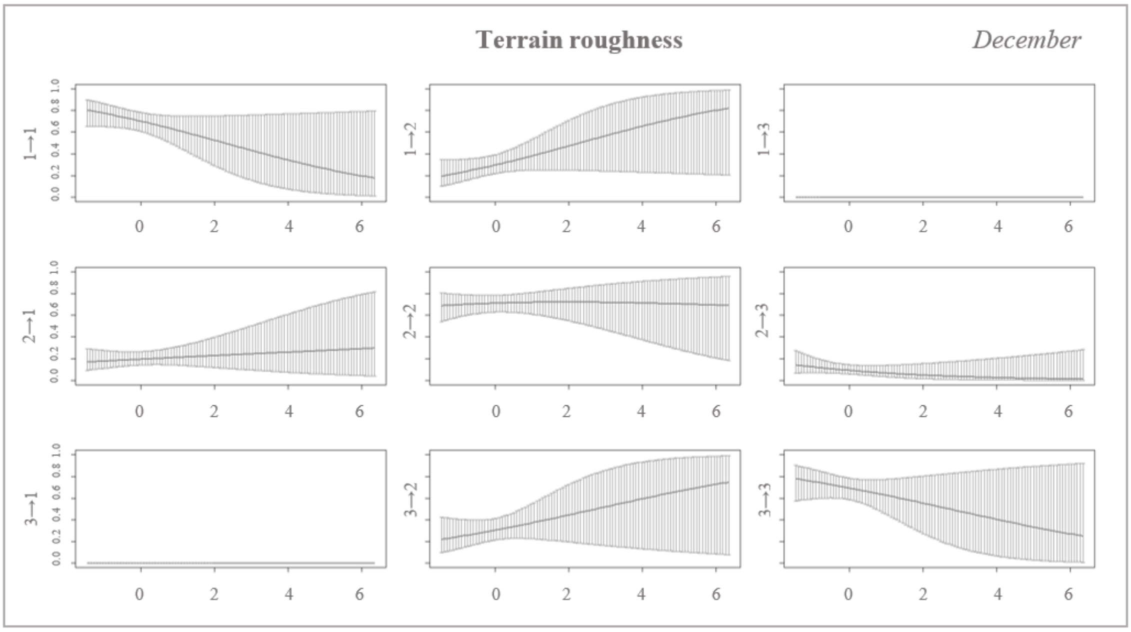

Figure 26. Graph showing transition probabilities under the influence of terrain roughness as a covariate in December, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

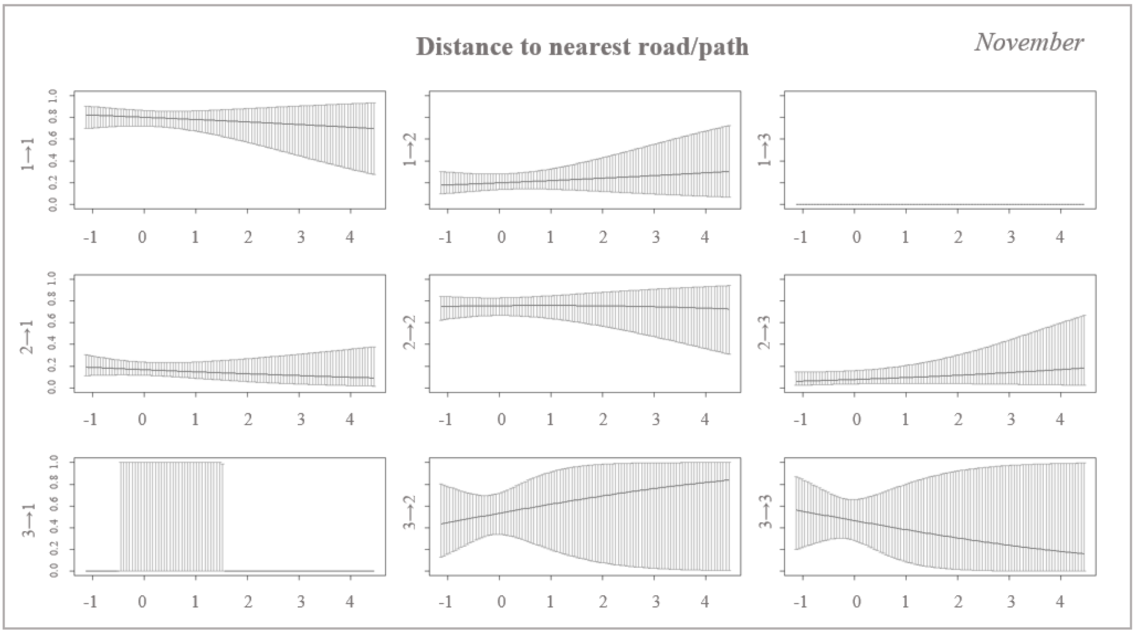

Figure 27. Graph showing transition probabilities under the influence of distance to nearest road/path as a covariate in November, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

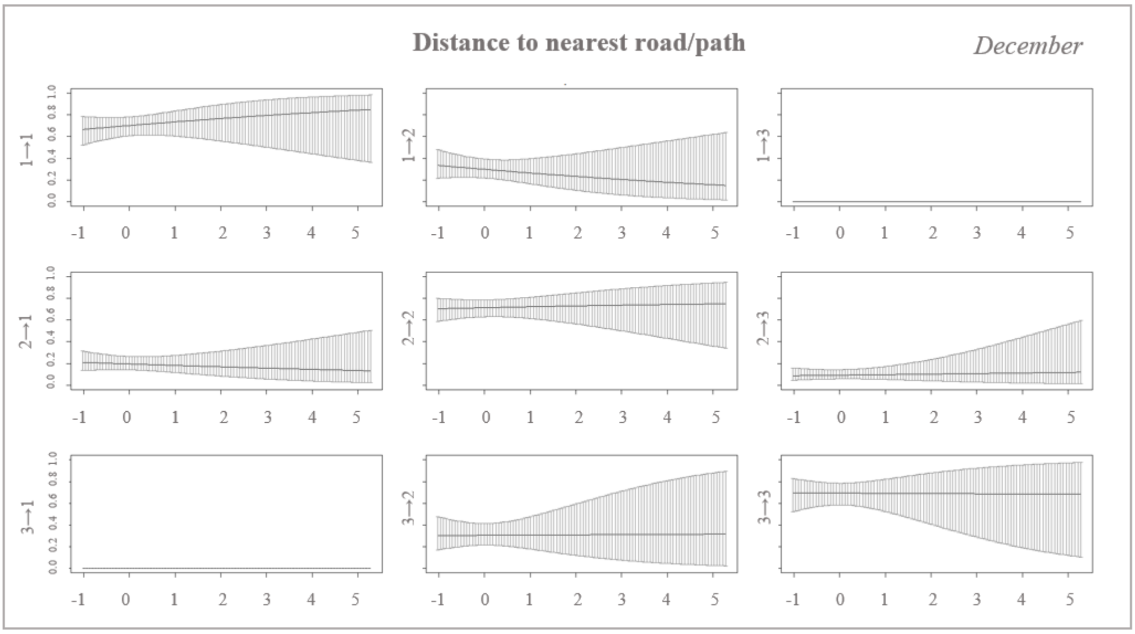

Figure 28. Graph showing transition probabilities under the influence of distance to nearest road/path as a covariate in December, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

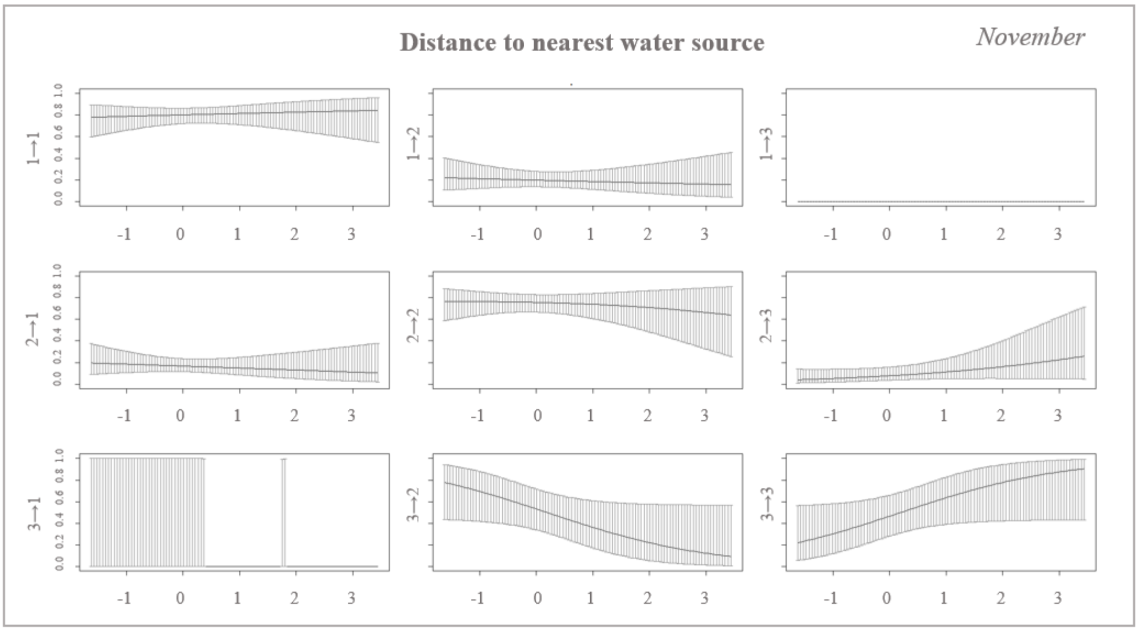

Figure 29. Graph showing transition probabilities under the influence of distance to nearest water source as a covariate in November, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

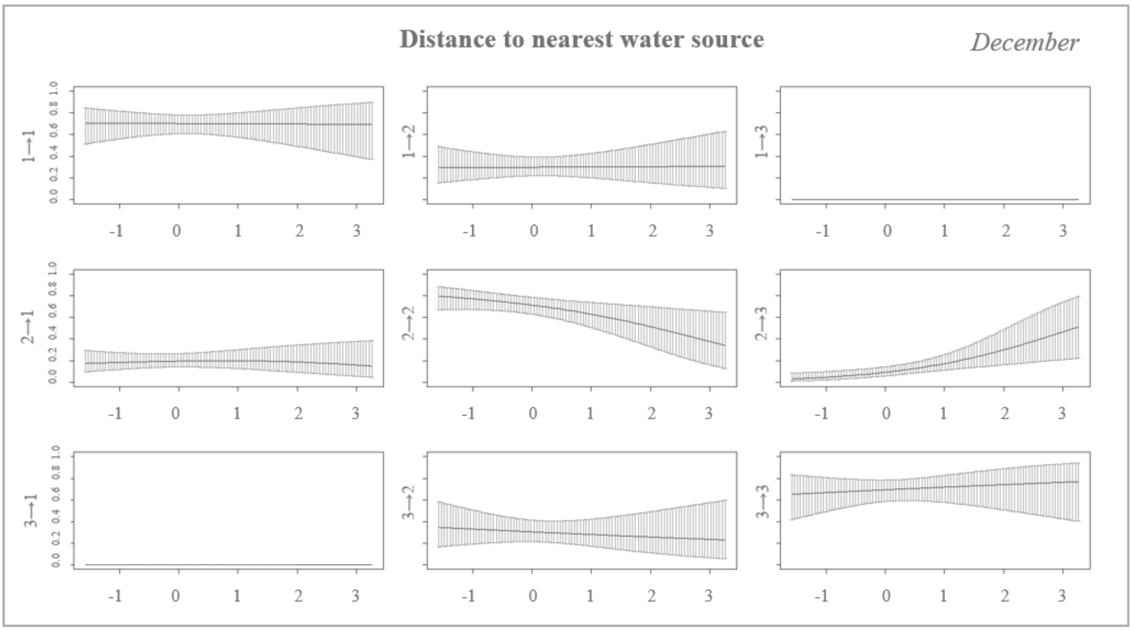

Figure 30. Graph showing transition probabilities under the influence of distance to nearest water source as a covariate in December, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

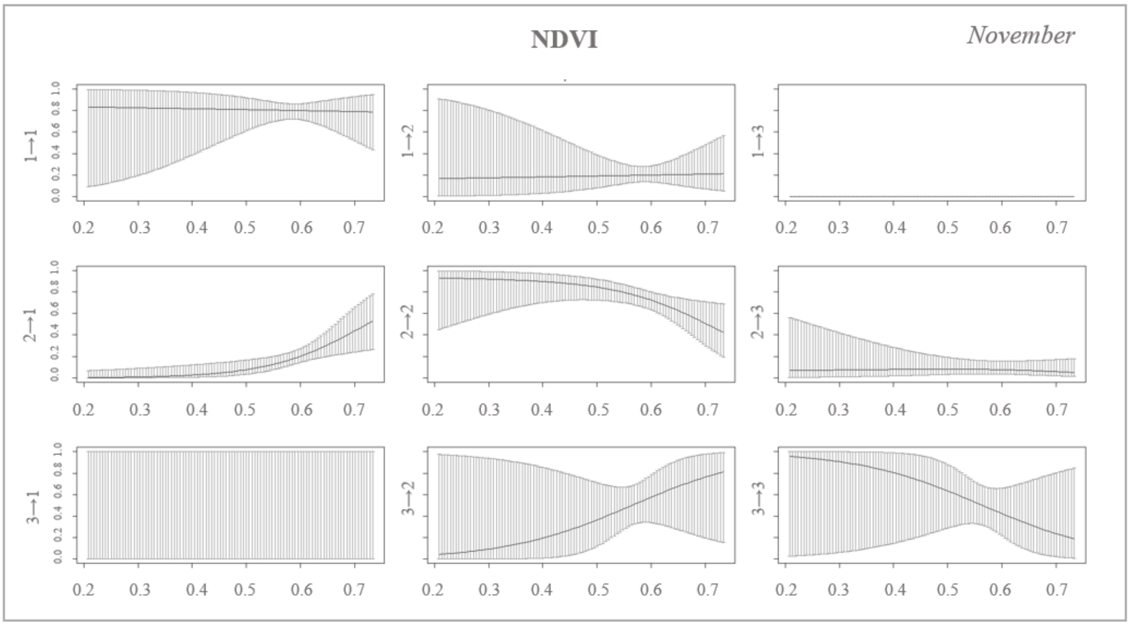

Figure 31. Graph showing transition probabilities under the influence of NDVI as a covariate in November, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

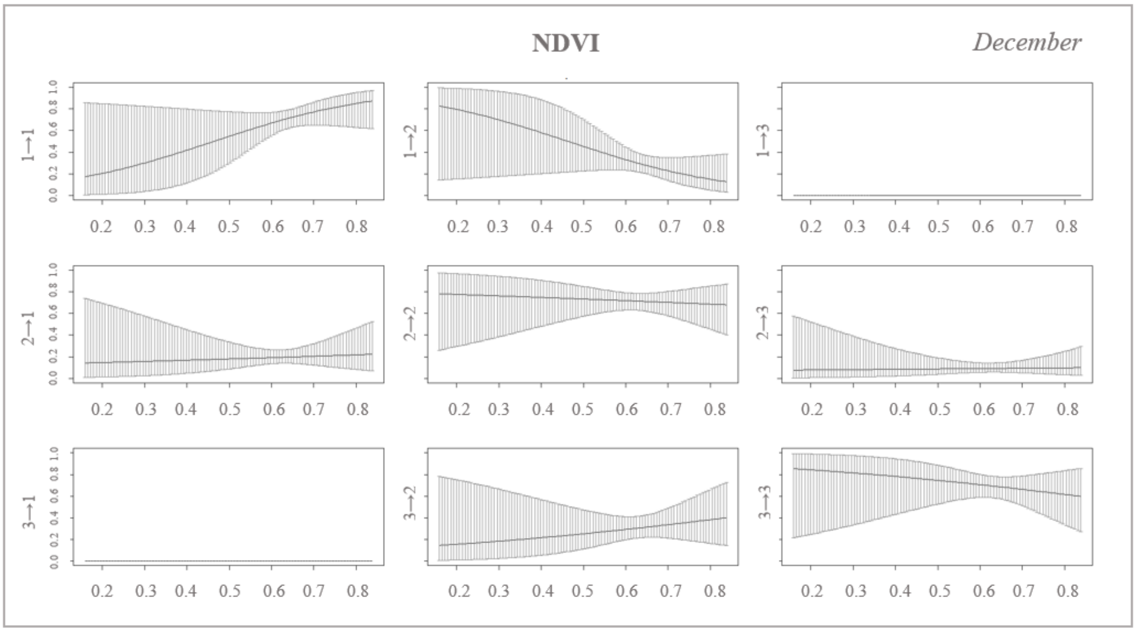

Figure 32. Graph showing transition probabilities under the influence of NDVI as a covariate in December, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

The transition probabilities of all 7 months combined followed the general trends shown month by month (Table 12, Fig.33-36): for example, the terrain roughness influenced the switching probabilities by promoting a transition to state 1 (*2→1*= +0.12) and a persistence in that state as the roughness increased (Fig.33); or considering distance to the nearest water source, as the distance increased, the probability of persistence in state 2 diminished and the probability of *2→3* transition increased (+0.40) (Fig.35).

Table 12. Regression coefficients for the transition probabilities referred to the month from June to December combined as a whole. The table shows the probability of transition between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The first row indicates the baseline probability of transition when all the covariates are set to zero. From the second to the fifth row, 4 different covariates and their influence on the transition probabilities are shown.

Regression coefficients for the transition probabilities						*June-to-December*
	1→2	*1→3*	*2→1*	*2→3*	*3→1*	*3→2*
Intercept	-1.334	-0.382	-1.612	-2.453	-5.588	-1.324
Terrain roughness	-0.150	-0.184	0.128	-0.080	-2.649	0.159
Min. road/path distance	0.028	0.132	-0.147	-0.093	0.494	-0.152
Min. water source distance	0.090	-0.320	0.098	0.404	0.486	-0.139
NDVI	0.243	-5.746	0.475	1.335	0.455	0.814

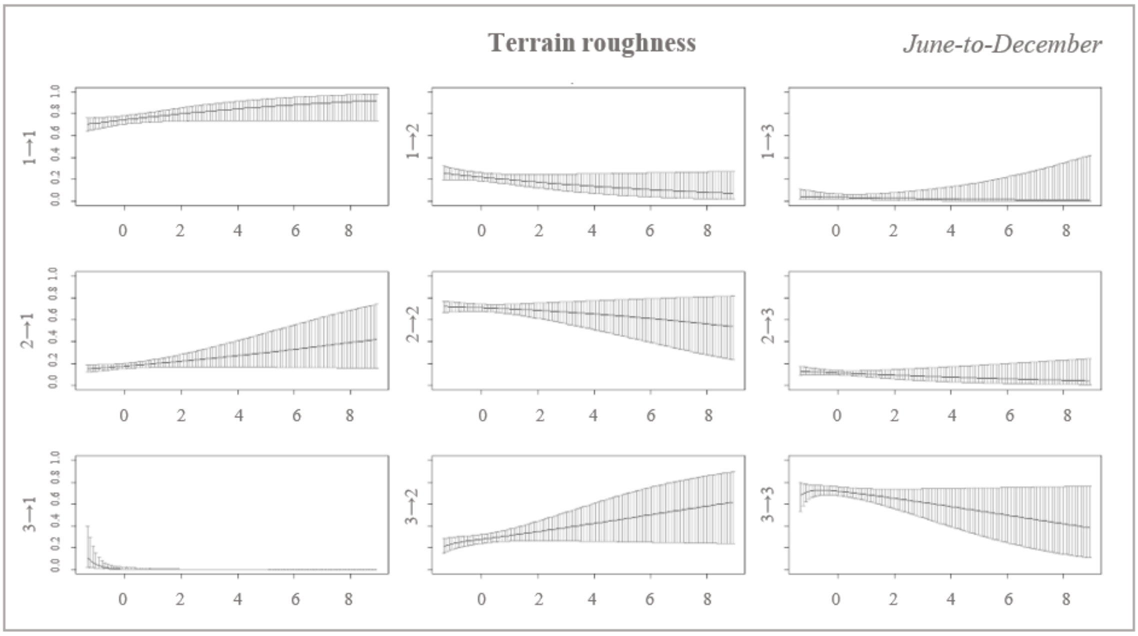

Figure 33. Graph showing transition probabilities under the influence of terrain roughness as a covariate for the 7-month period (June to December), between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

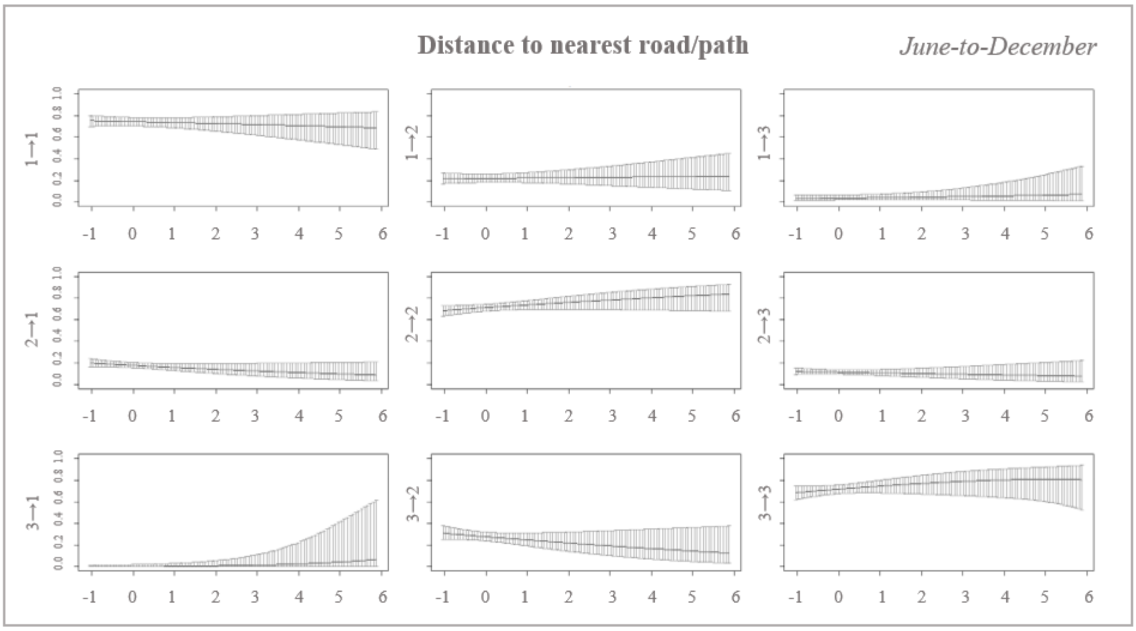

Figure 34. Graph showing transition probabilities under the influence of distance to nearest road/path as a covariate for the 7-month period (June to December), between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

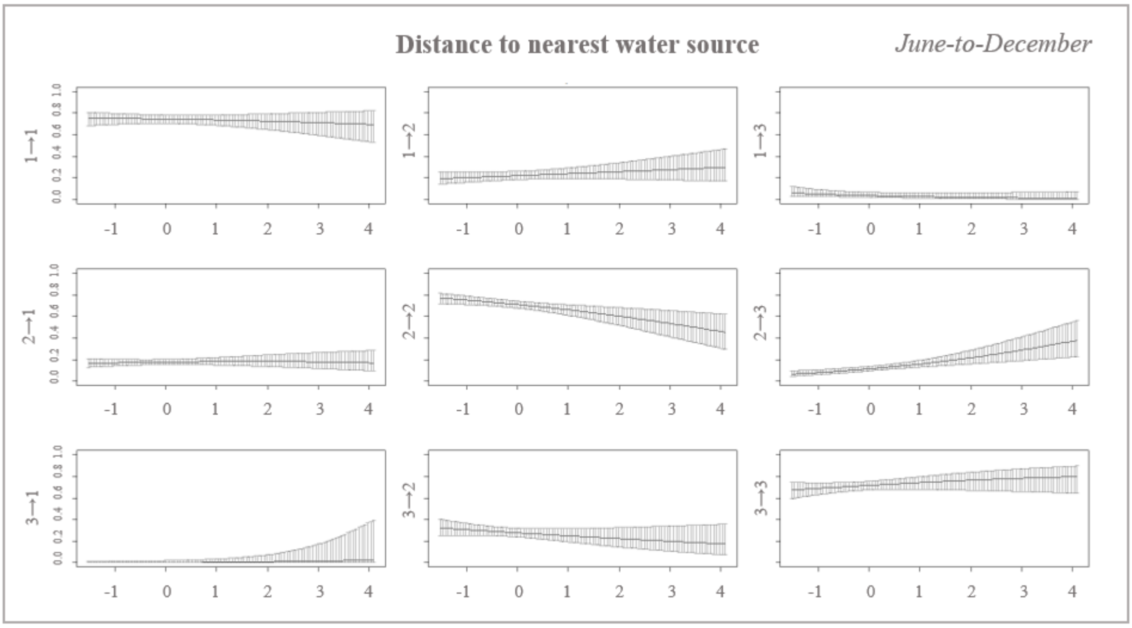

Figure 35. Graph showing transition probabilities under the influence of distance to nearest water source as a covariate for the 7-month period (June to December), between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

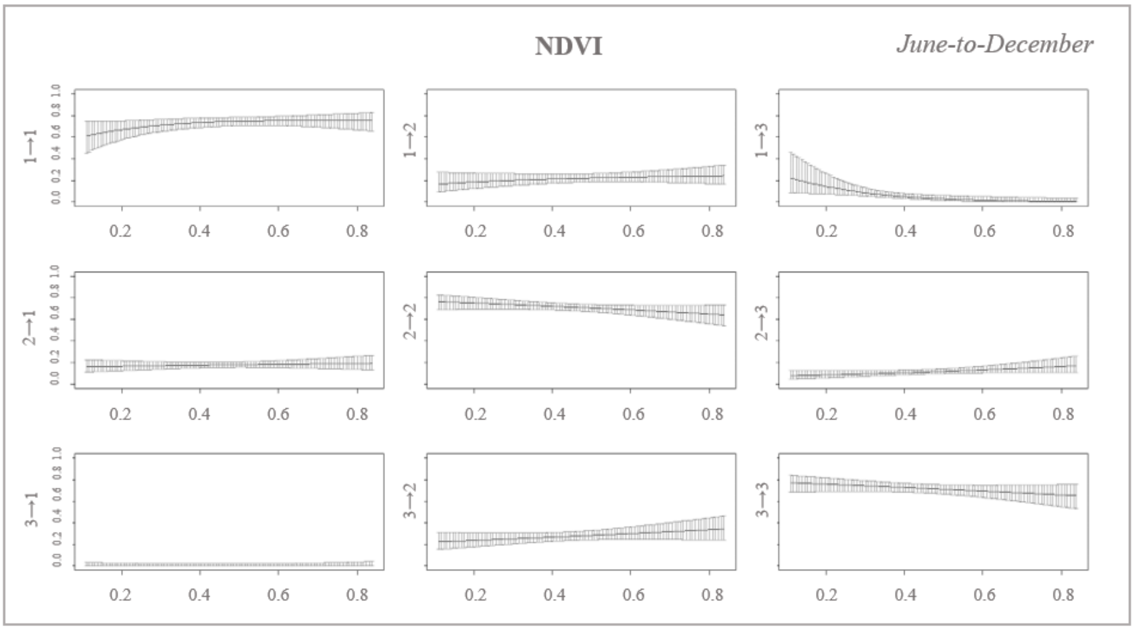

Figure 36. Graph showing transition probabilities under the influence of NDVI as a covariate for the 7-month period (June to December), between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

The results regarding the stationary state probabilities were analysed covariate by covariate (Fig.37-44).

Considering the terrain roughness as covariate, across June, July, and August there was a clear prevalence of occurrence in state 1 at high roughness values (Fig.37-39). In September, the probability of being in state 3 increased with increasing the covariate value, while both state 1 and 2 had a low probability of occurrence at high roughness levels (Fig.40). In October, there was a marked predominance of state 2 at each value of terrain roughness (Fig.41). November and December, instead, registered the same probability of occurrence for the former, and higher odds of being in state 2 for the latter (Fig.42-43). Analysing the 7-month period as a whole, however, showed a strong prevalence of state 1 when the terrain was rougher (Fig.44).

When the distance to the nearest road/path was applied as a variable, in June there was a tendency to remain in state 2 regardless of the distance to the road, while there was a greater likelihood of persisting in state 3 when on the road (Fig.37). In July, a higher probability of being in states 2 and 1 was observed as distance increased, whereas state 3 was more likely at the shortest distance (Fig.38). In August and September, there was a net prevalence of state 3 among the different values of the covariate (Fig.39-40), whereas October showed a predominance of state 1 in the extreme proximity of the road, and of state 2 as the value of the covariate augmented (Fig.41). November and December showed similar patterns, with a preponderance of state 2 across the entire spectrum of covariate values (Fig.42-43). Overall, state 2 was the favourite under the influence of this covariate, with state 1 slightly more likely near the road (Fig.44).

Under the influence of distance from the nearest water source as a predictor variable, state 2 prevailed in June and July, regardless of the distance from the water (Fig.37-38). In August, September, and October, instead, state 2 was the most probable near the water source (with a substantial peak in October), while state 3 increased exponentially as distance from the water increased (Fig.39-41). A similar trend emerged between November and December, with state 1 following the same trend as state 2 with higher occurrence near the water point, but also with a greater likelihood of moving to state 3 once away from the water (Fig.42-43). The same trends as the latter were followed in the 7-month analysis (Fig.44).

With slightly different degrees of probability, when setting NDVI as a covariate, each month indicated a high persistence in state 1 at the highest values of the NDVI, and a high probability of remaining in state 3 at the lowest values of the covariate, with the highest probability of being in state 2 at the mean values of NDVI (Fig.37-44).

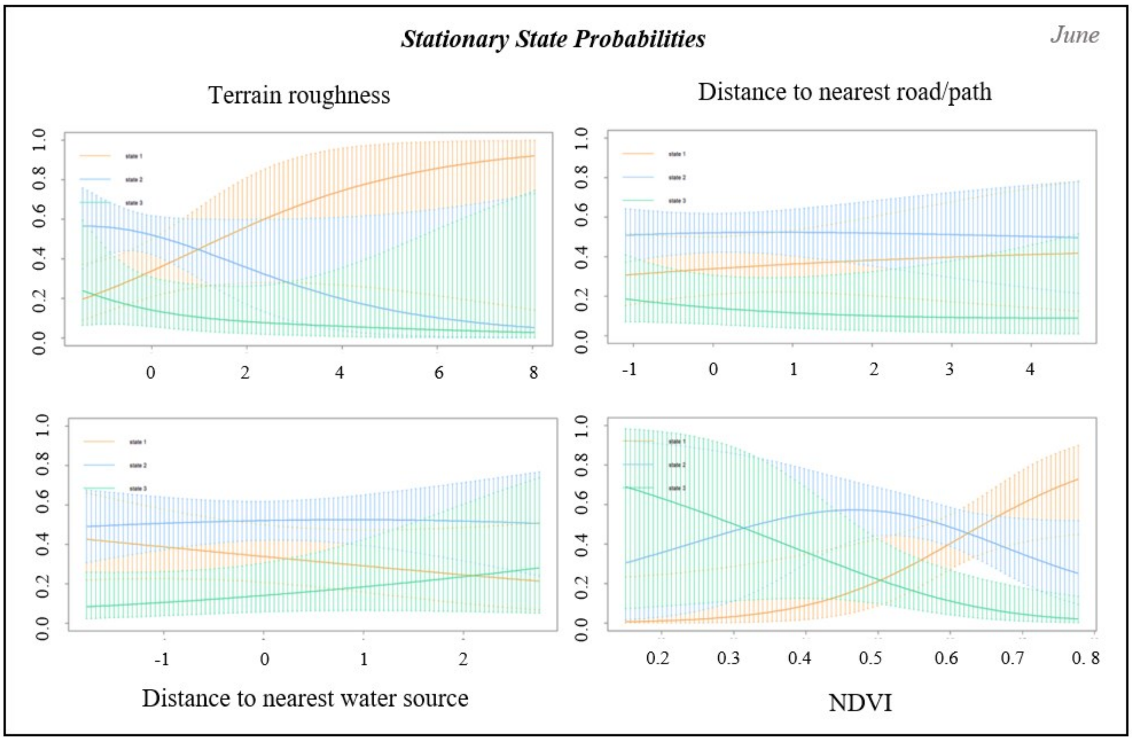

Figure 37. Graph showing stationary state probabilities for each covariate in June.

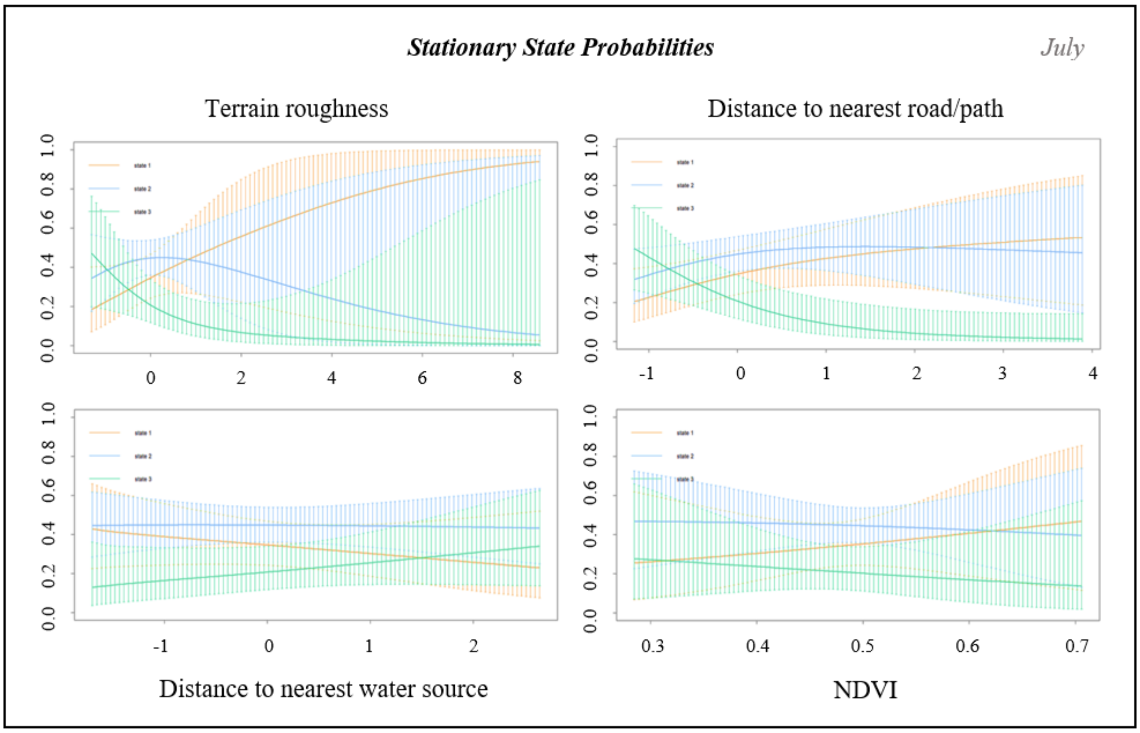

Figure 38. Graph showing stationary state probabilities for each covariate in July.

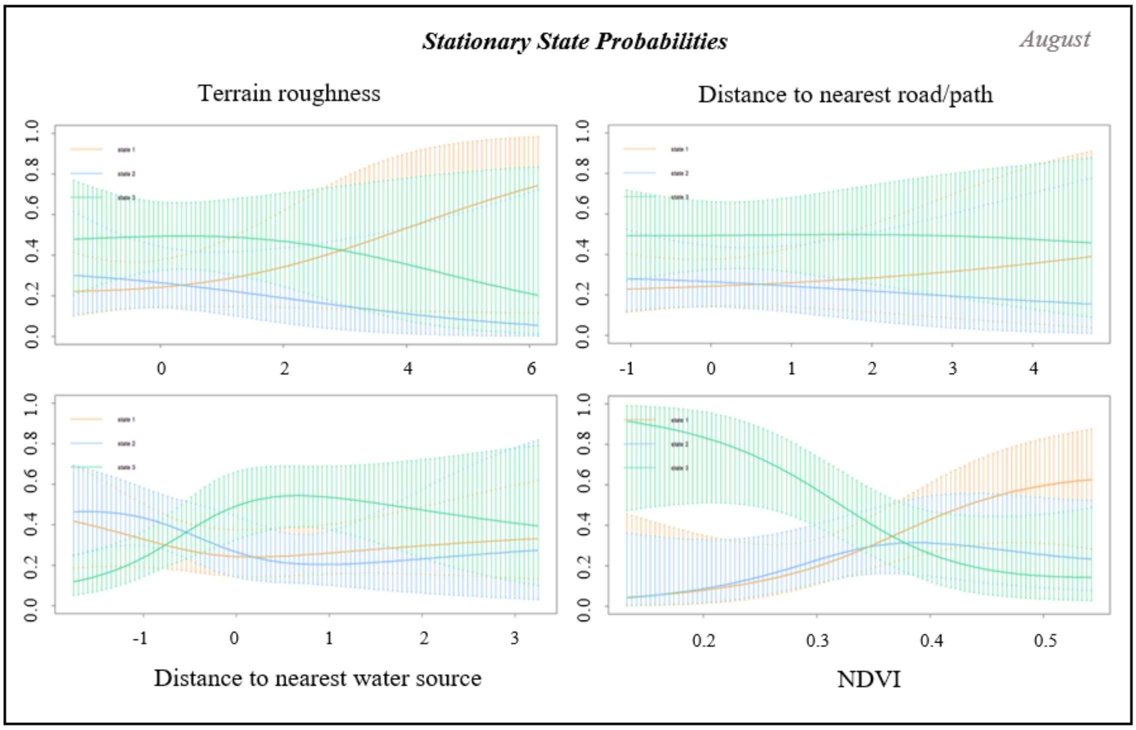

Figure 39. Graph showing stationary state probabilities for each covariate in August.

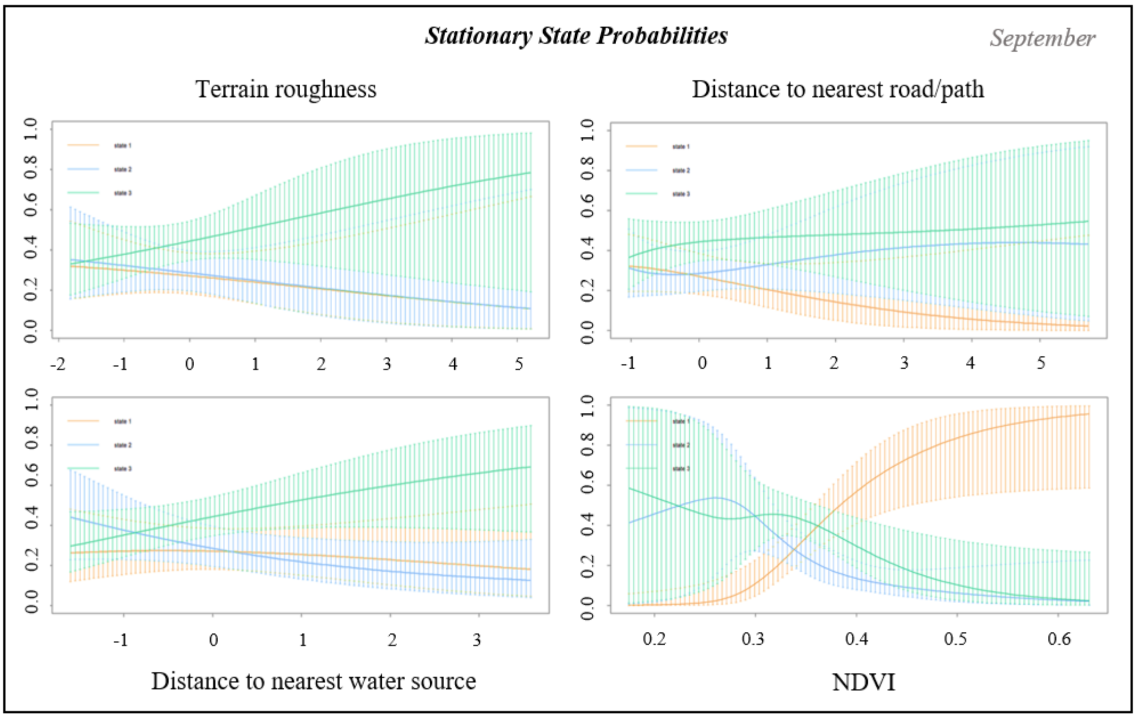

Figure 40. Graph showing stationary state probabilities for each covariate in September.

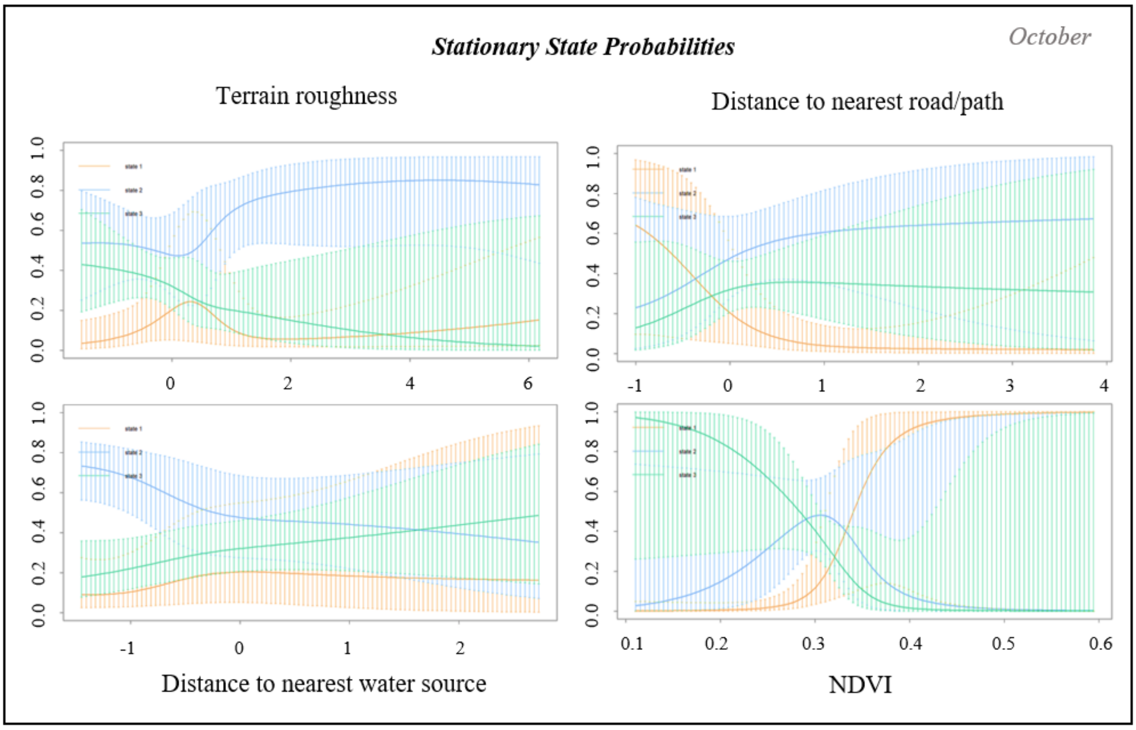

Figure 41. Graph showing stationary state probabilities for each covariate in October.

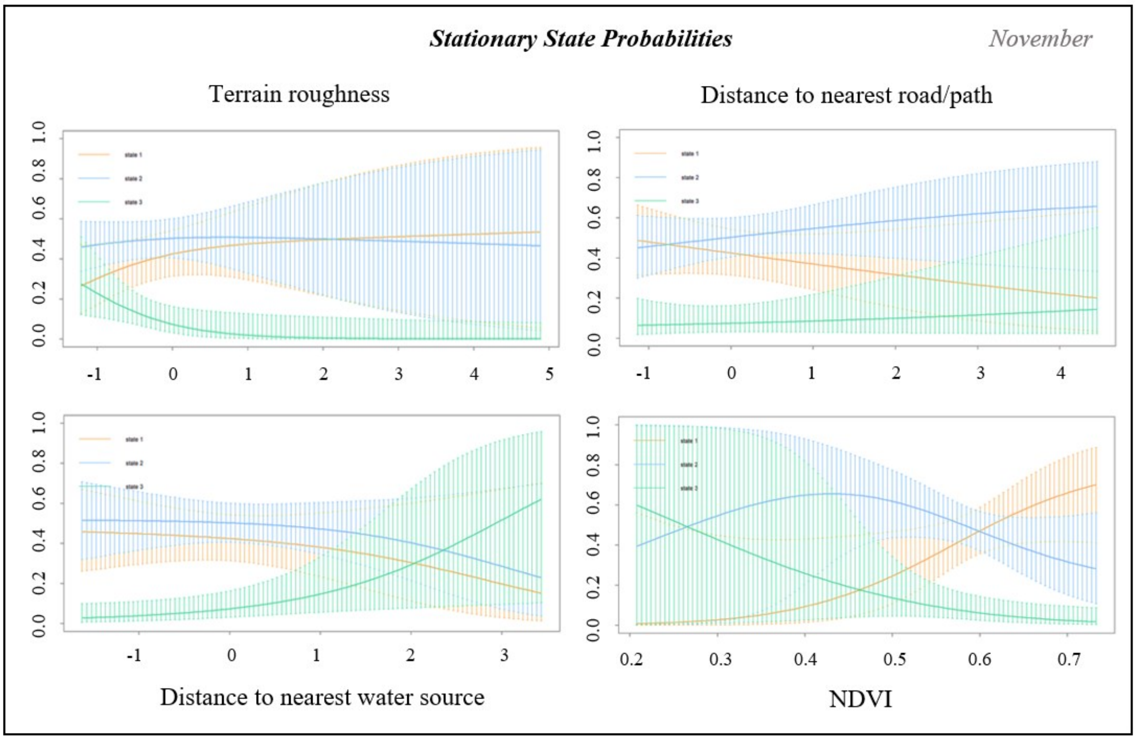

Figure 42. Graph showing stationary state probabilities for each covariate in November.

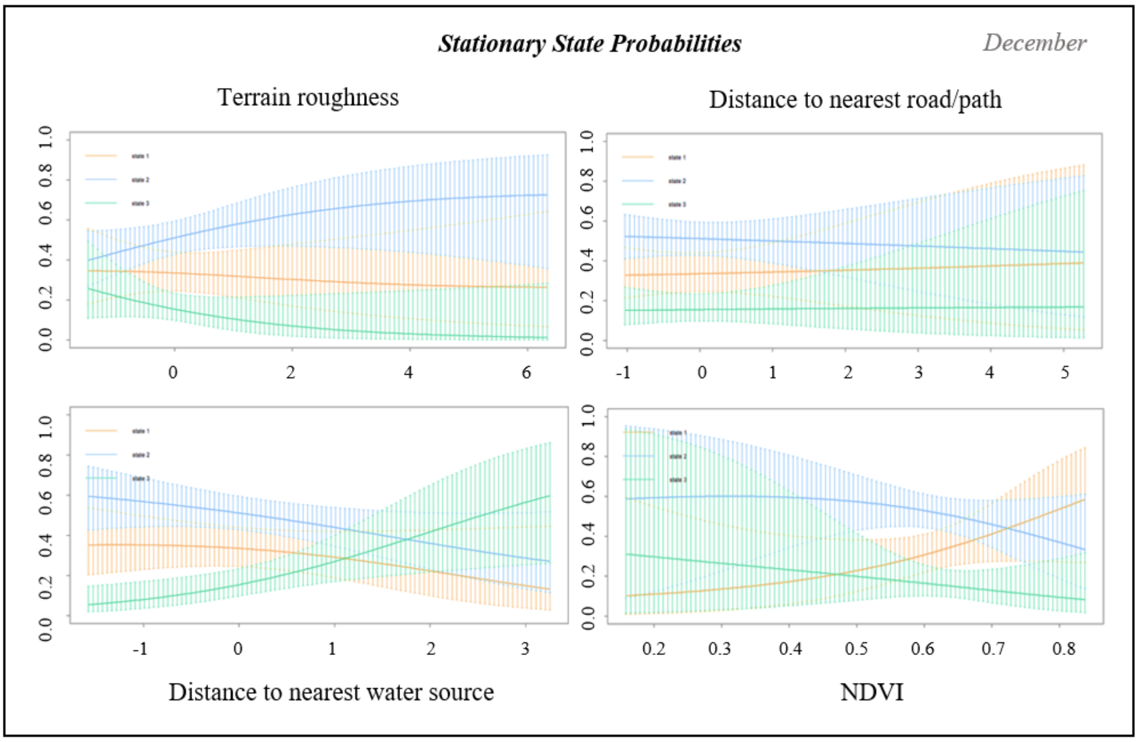

Figure 43. Graph showing stationary state probabilities for each covariate in December.

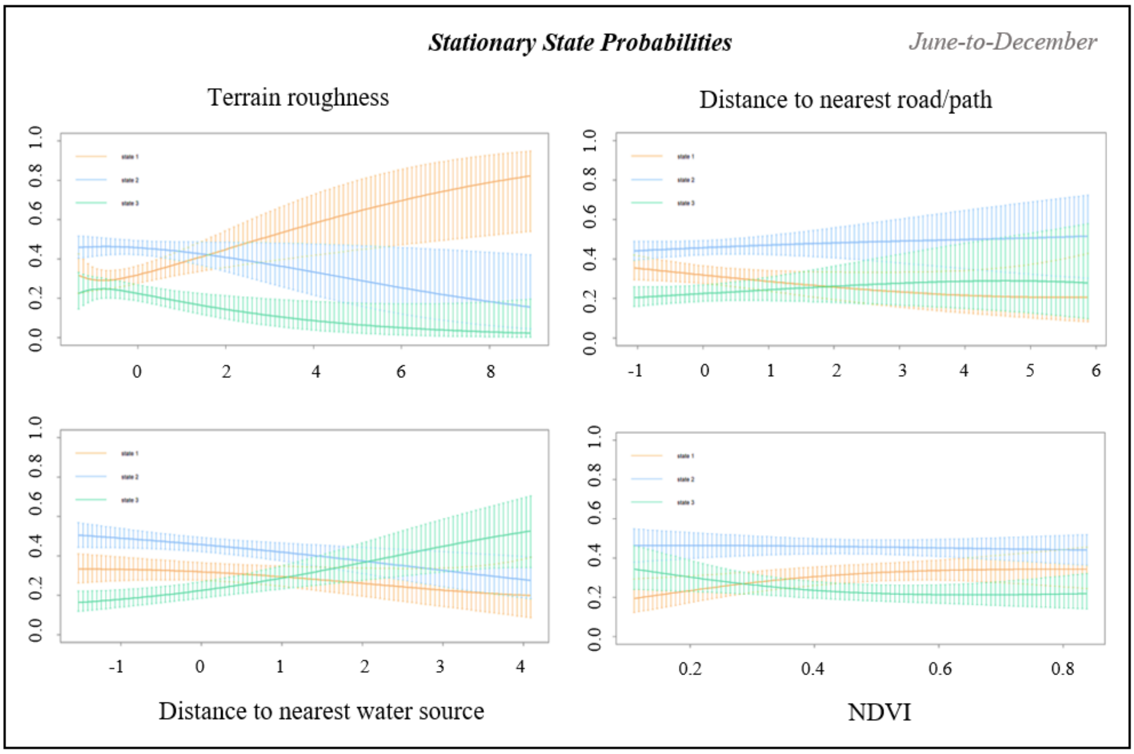

Figure 44. Graph showing stationary state probabilities for each covariate combining all the months.

3.2 Jean

The step length means for each state varied monthly over the 7 months analysed (Table 13). State 1 recorded a minimum of 68 metres in June and a maximum of 129 metres in December; state 2, presented a minimum and a maximum of 333 metres (in August) and 664 metres (in December), respectively; state 3 ranged between 842 metres (in December) as a minimum, and 1769 metres (in October) as a maximum. Taking the 7 months together, the step length mean is 50, 223, and 887 metres for states 1,2, and 3, respectively. The SD results followed the same fluctuation patterns as the mean. For greater accuracy of the model, the turning angle parameters, which include the mean and concentration, were also calculated (Table 14).

Table 13. Step length parameters showing the mean (expressed in km) and standard deviation (SD) for each month and for all the months combined (last row). The step length mean corresponds to the average distance covered in a single step for each state.

Step length parameters						
	Mean			*SD*		
	State 1	*State 2*	*State 3*	*State 1*	*State 2*	*State 3*
June	0.068	0.370	1.476	0.075	0.262	0.701
July	-	-	-	-	-	-
August	0.084	0.333	1.288	0.080	0.183	0.677
September	0.090	0.349	1.225	0.092	0.213	0.555
October	0.100	0.565	1.769	0.108	0.377	0.698
November	-	-	-	-	-	-
December	0.129	0.664	0.842	0.148	0.488	0.633
June-December	**0.050**	**0.223**	**0.887**	**0.056**	**0.146**	**0.580**

Table 14. The turning angle parameters, showing the mean and the concentration for each month and for all the months combined (last row). The turning angle mean corresponds to the average angle performed in a single step for each state.

Turning angle parameters						
	Mean			*Concentration*		
	State 1	*State 2*	*State 3*	*State 1*	*State 2*	*State 3*
June	0.042	-0.103	0.030	0.576	1.461	1.500
July	-	-	-	-	-	-
August	0.045	0.062	0.029	0.969	1.664	1.431
September	-0.108	0.133	-0.074	0.807	1.414	2.413
October	-0.070	0.042	-0.176	0.748	1.675	5.452
November	-	-	-	-	-	-
December	-0.324	-0.013	-0.048	0.374	1.213	7.032
June-December	**-0.243**	**0.045**	**-0.007**	**0.265**	**1.585**	**1.508**

Between June and October, the percentage of time spent in state 1 increasingly rose, reaching 51% occurrence in October, which also recorded the lowest percentage of time spent in state 3 (6%). In an analysis on a monthly scale, Jean recorded a high presence in state 2, with percentages ranging from 39% to 61%. Particularly, the wet season was characterised by elevated values of time spent in state 1 and 2. Considering collectively the months from June to December, Jean spent 42% of the time in state 2, 37% in state 3 and 20% in state 1 (Table 15).

Table 15. Percentage of time spent for each state obtained with the Viterbi algorithm, included in the Viterbi function of the moveHMM package. It provides the most probable sequence of states that generated the observation, based on the fitted model.

	Percentage of time spent on each state		
	State 1	*State 2*	*State 3*
June	0.274	0.613	0.123
July	-	-	-
August	0.381	0.502	0.209
September	0.462	0.391	0.151
October	0.510	0.426	0.069
November	-	-	-
December	0.354	0.502	0.147
June-December	**0.201**	**0.428**	**0.369**

In June (Table 16, Fig.45-48), the baseline probability of *1→2* transitioning was +1.23. When setting the terrain roughness as a predictor variable, the *1→2* value became slightly negative (-0.22), whereas when considering *2→1* transition, the probability was +0.22, indicating a tendency to remain in state 1 as roughness increased. As evidence, the probability of persistence in state 1 was higher when the terrain was rougher (Fig.45). Under the influence of NDVI as a covariate, a great negative transition probability was recorded for the *2→3* transition (-5.29), whilst *3→1* switching probability registered a value of +10.68. As proof, the persistence odds in state 1 increased with increasing NDVI value and, and concurrently, switching probabilities of *1→2* decreased (Fig.48). Considering the influence of the distance to the nearest water source, the *3→2* probability was greater near the water, whereas *3→1* probability was greater away from water points.

The regression coefficients for the *1→3* transition were not taken into account for the analysis of this month's movements, as there was no correspondence in the graphs.

Table 16. Regression coefficients for the transition probabilities referred to the month of June. The table shows the probability of transition between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The first row indicates the baseline probability of transition when all the covariates are set to zero. From the second to the fifth row, 4 different covariates and their influence on the transition probabilities are shown.

	Regression coefficients for the transition probabilities					*June*
	1→2	*1→3*	*2→1*	*2→3*	*3→1*	*3→2*
Intercept	1.238	-577.939	-4.768	0.426	-10.112	-2.011
Terrain roughness	-0.222	82.068	0.222	0.285	-2.465	1.526
Min. road/path distance	0.146	143.762	0.445	-0.059	-0.935	-0.151
Min. water source distance	0.142	-462.273	-0.582	-0.100	2.481	-1.762
NDVI	-3.632	-399.035	5.063	-5.292	10.618	1.354

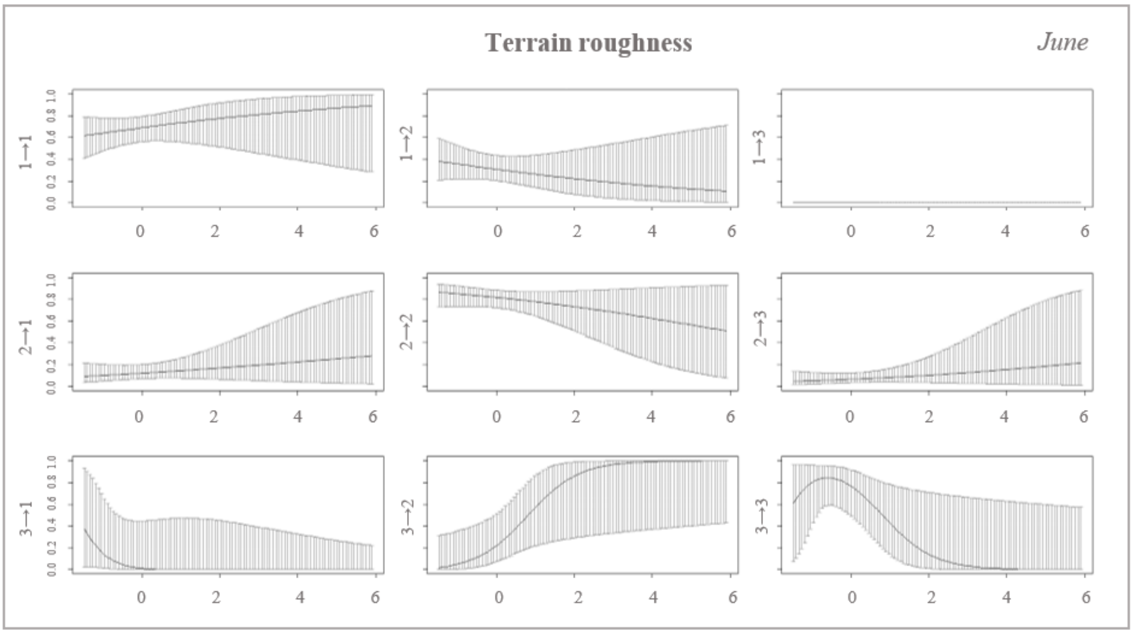

Figure 45. Graph showing transition probabilities under the influence of terrain roughness as a covariate in June, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

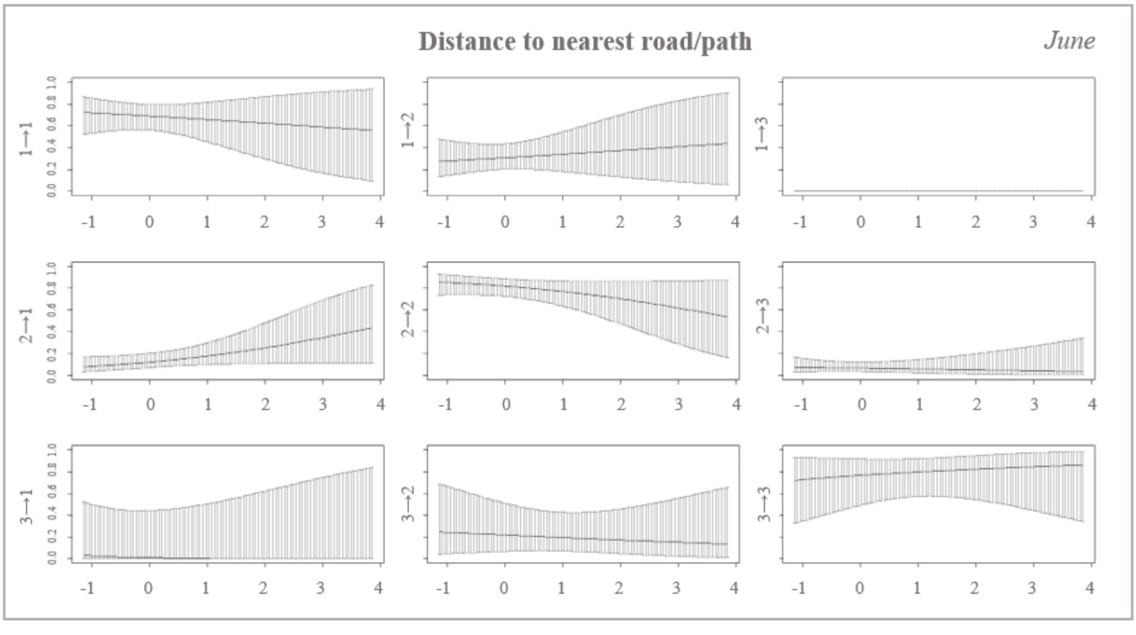

Figure 46. Graph showing transition probabilities under the influence of distance to nearest road/path as a covariate in June, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

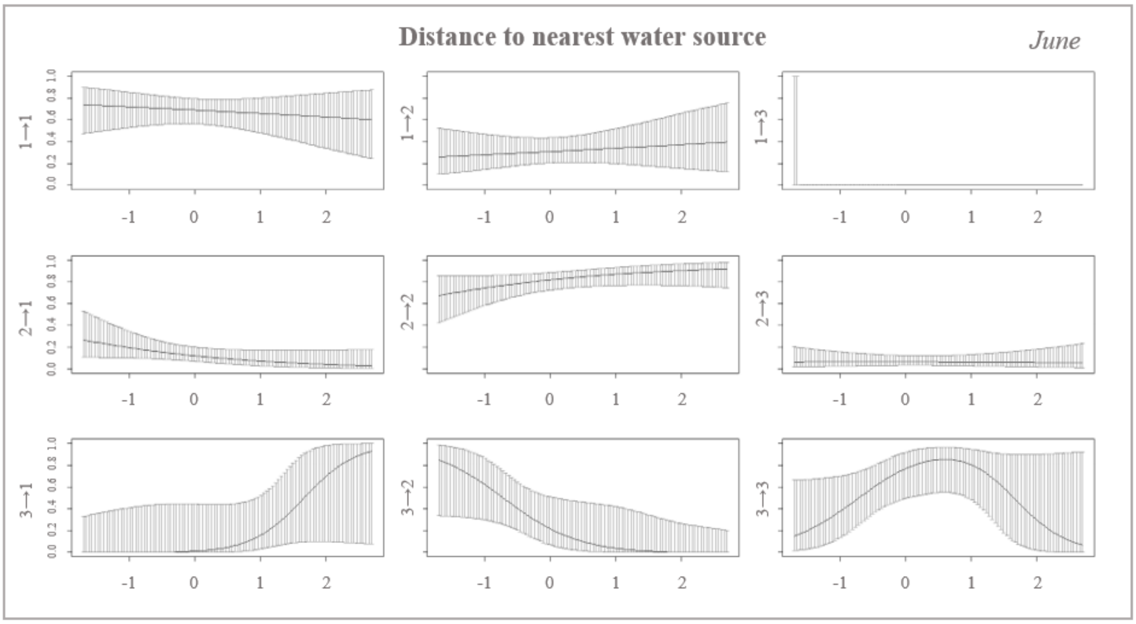

Figure 47. Graph showing transition probabilities under the influence of distance to nearest water source as a covariate in June, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

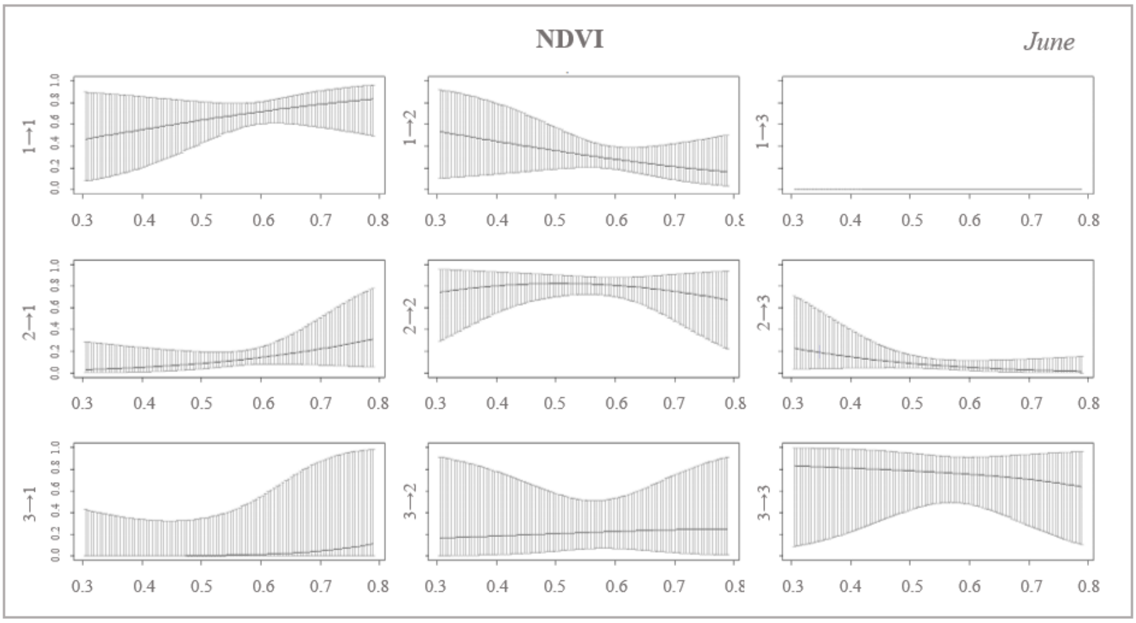

Figure 48. Graph showing transition probabilities under the influence of NDVI as a covariate in June, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

In August (Table 17, Fig.49-52), the NDVI had a great influence on transition probabilities, with a tendency to promote occurrence in state 1 as the covariate value increased (*2→1* = +10.98). In support of this, as the NDVI value augmented, persistence in state 2 decreased remarkably, while persistence in state 1 increased (Fig.52). The distance to nearest road/path did not notably influence the transition probability, recording slightly positive value of *2→1* and *2→3* transition values as the distance augmented (+0.12 and +0.35 respectively), along with a persistence probability in state 2 that decreased as the distance to the road increased (Fig.50). Terrain roughness in this month presented a probability of *2→1* switching when the terrain was rougher, followed by a decreasing value of persistence in state 2 when the roughness was greater (Fig.49).

Table 17. Regression coefficients for the transition probabilities referred to the month of August. The table shows the probability of transition between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The first row indicates the baseline probability of transition when all the covariates are set to zero. From the second to the fifth row, 4 different covariates and their influence on the transition probabilities are shown.

	Regression coefficients for the transition probabilities					*August*
	1→2	*1→3*	*2→1*	*2→3*	*3→1*	*3→2*
Intercept	0.463	-332.935	-4.733	-5.846	-821.089	-2.169
Terrain roughness	-0.235	-32.848	0.552	0.152	68.825	0.084
Min. road/path distance	0.110	38.576	0.121	0.355	-477.328	-0.133
Min. water source distance	-0.027	6.275	-0.303	-0.087	-124.250	0.041
NDVI	-4.395	-103.113	10.983	13.098	463.953	4.159

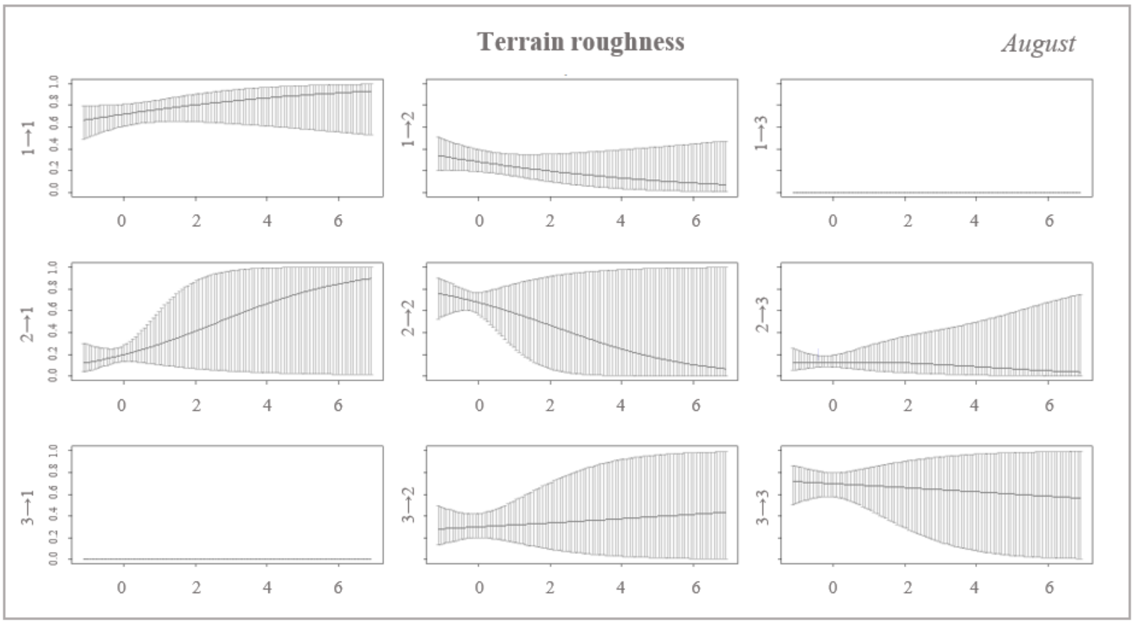

Figure 49. Graph showing transition probabilities under the influence of terrain roughness as a covariate in August, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

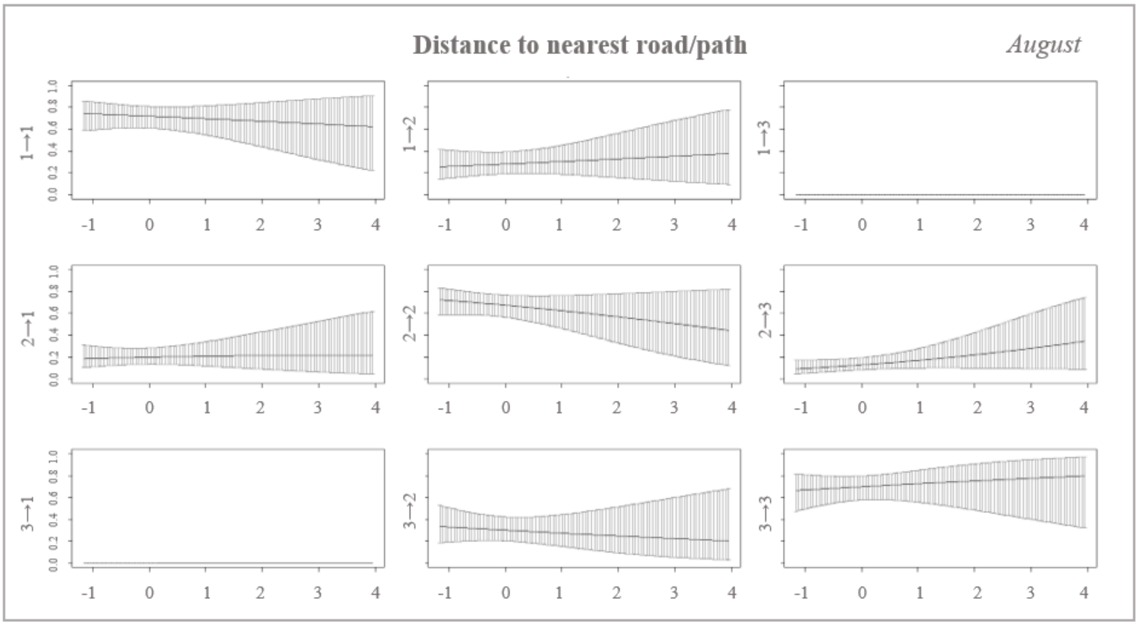

Figure 50. Graph showing transition probabilities under the influence of distance to nearest road/path as a covariate in August, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

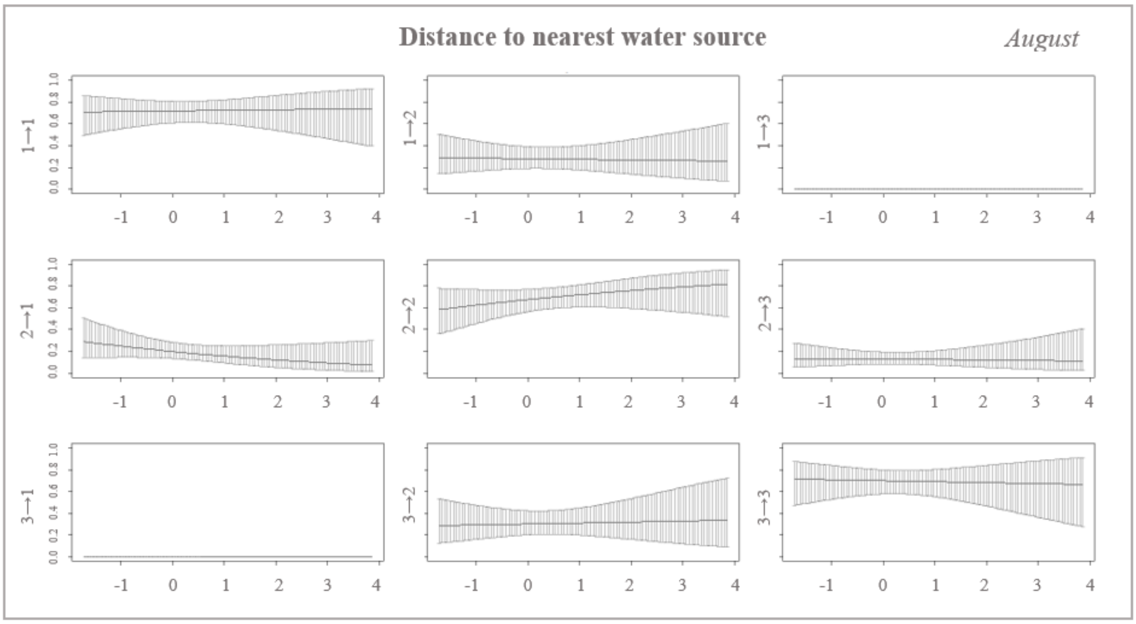

Figure 51. Graph showing transition probabilities under the influence of distance to nearest water source as a covariate in August, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

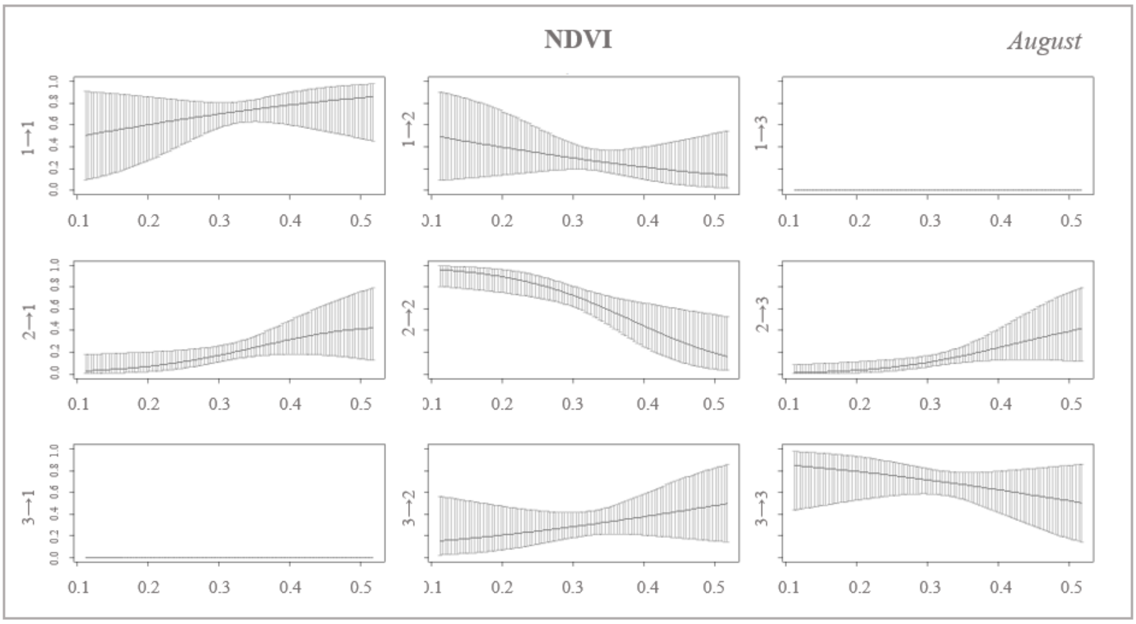

Figure 52. Graph showing transition probabilities under the influence of NDVI as a covariate in August, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

In September (Table 18, Fig.53-56), when the distance to the nearest road/path was set, persistence in state 3 was higher the further away from the road (Fig.54), as well as *3→2* probability of occurrence was higher near the road and lower with the distance (-1.11). Therefore, the increase in distance from the road inhibited the likelihood of moving from state 3 to state 2. Regarding the influence of distance to the nearest water source, the probability of persisting in state 2 was higher near the water (Fig.55), while the *2→1* increased with distance (+0.59). Considering the NDVI as a covariate, the probability of persisting in state 3 was null at the highest NDVI value (Fig.56). Furthermore, *3→1* and *2→1* probabilities were promoted as the NDVI values increased (+66.24 and +3.08, respectively).

Table 18. Regression coefficients for the transition probabilities referred to the month of September. The table shows the probability of transition between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The first row indicates the baseline probability of transition when all the covariates are set to zero. From the second to the fifth row, 4 different covariates and their influence on the transition probabilities are shown.

	Regression coefficients for the transition probabilities					*September*
	1→2	*1→3*	*2→1*	*2→3*	*3→1*	*3→2*
Intercept	-1.466	-1452.85	-2.071	1.077	-26.902	-3.054
Terrain roughness	-0.032	-694.761	0.275	0.152	0.236	-0.470
Min. road/path distance	-0.350	282.184	-0.269	0.152	-1.398	-1.119
Min. water source distance	0.086	437.579	0.595	0.528	1.396	-0.028
NDVI	0.383	-1047.92	3.087	-7.719	66.247	8.161

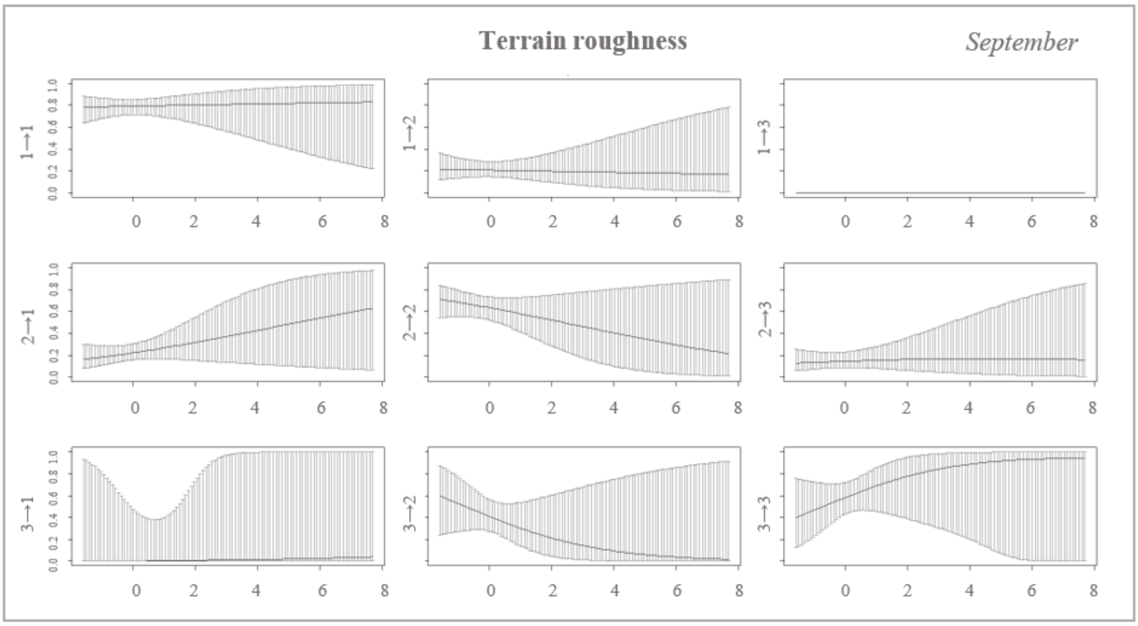

Figure 53. Graph showing transition probabilities under the influence of terrain roughness as a covariate in September, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

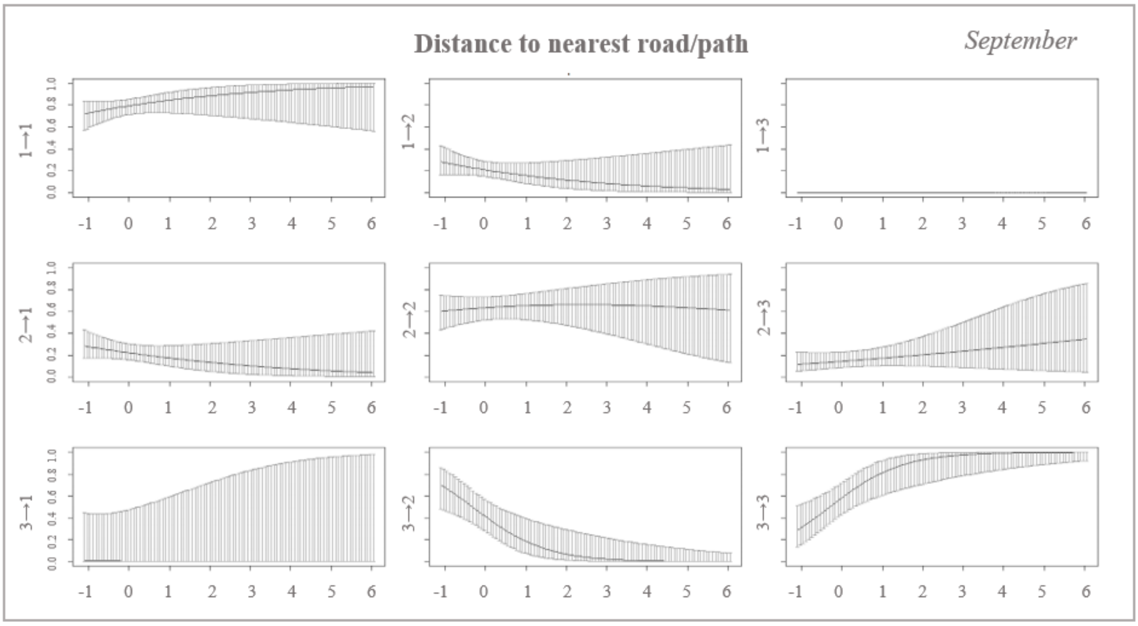

Figure 54. Graph showing transition probabilities under the influence of distance to nearest road/path as a covariate in September, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

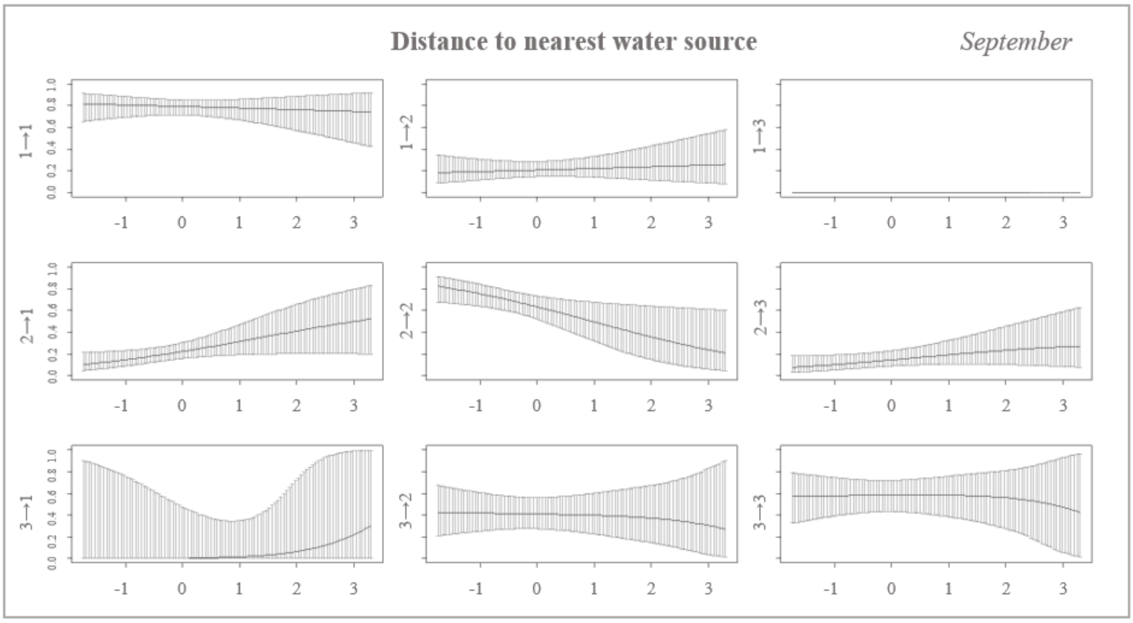

Figure 55. Graph showing transition probabilities under the influence of distance to nearest water source as a covariate in September, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

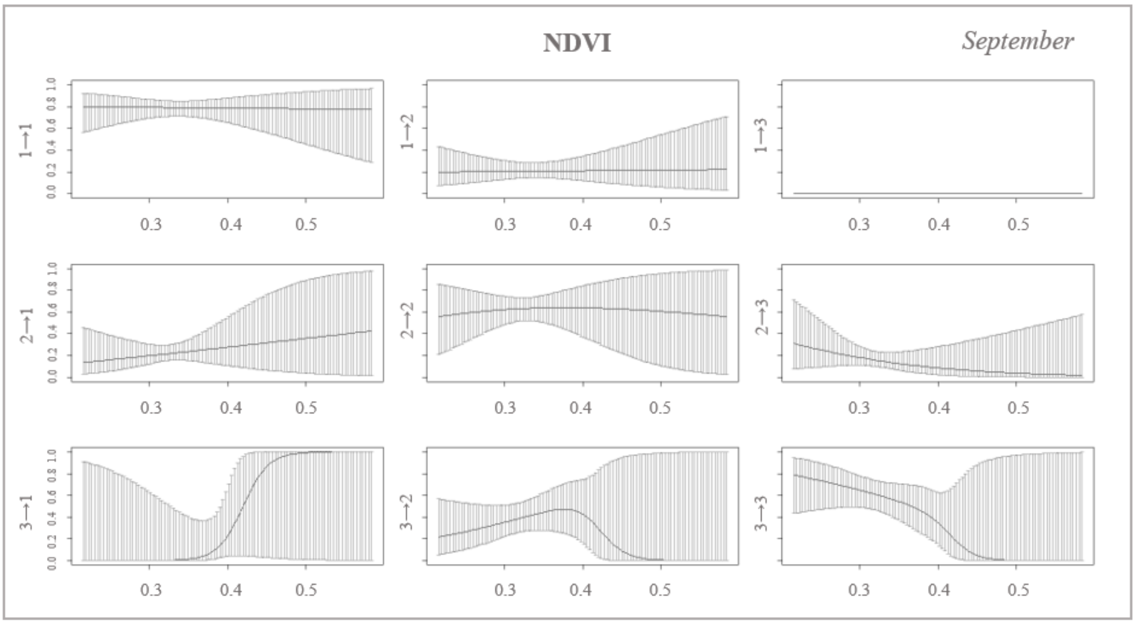

Figure 56. Graph showing transition probabilities under the influence of NDVI as a covariate in September, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

In October (Table 19, Fig.57-60) when setting the distance to the nearest road/path as a covariate, a persistence in state 1 was greater near the road, increasingly becoming prone to zero as moving away from the road (Fig.58). In support of this, when distance increased, the *1→2* probability was promoted (+0.39) and the *2→1* transition probability was inhibited (-0.22). When considering the influence of the distance to the water source, there was a tendency to transition to state 3 (*1→3*= 0.91, *2→3*= 0.56) as the distance from the water increased, which was also confirmed by the probability of persisting in state 3, which was higher the further away from the water (Fig.59). Under the influence of the NDVI, the probabilities to move from state 3 to state 2 and then to state 1 were the greatest (*3→2* = +65.08 and *2→1*= +15.70) (Fig.60). Persistence in state 1 was higher as the terrain was rougher (Fig.57).

Table 19. Regression coefficients for the transition probabilities referred to the month of October. The table shows the probability of transition between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The first row indicates the baseline probability of transition when all the covariates are set to zero. From the second to the fifth row, 4 different covariates and their influence on the transition probabilities are shown.

	Regression coefficients for the transition probabilities					*October*
	1→2	*1→3*	*2→1*	*2→3*	*3→1*	*3→2*
Intercept	0.134	-9.979	-6.438	1.188	-0.212	-19.627
Terrain roughness	-0.476	0.372	0.306	-0.522	-0.626	0.043
Min. road/path distance	0.392	-4.882	-0.222	-0.055	0.108	-0.369
Min. water source distance	0.023	0.918	0.124	0.566	0.047	-1.110
NDVI	-4.771	3.236	15.707	-11.945	-3.544	65.083

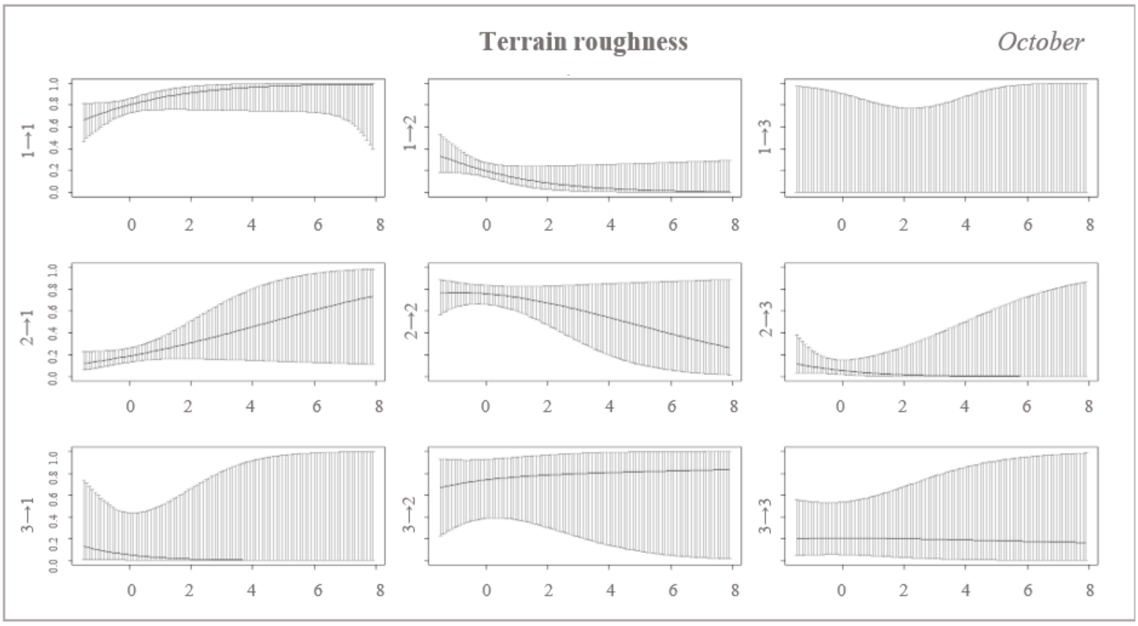

Figure 57. Graph showing transition probabilities under the influence of terrain roughness as a covariate in October, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

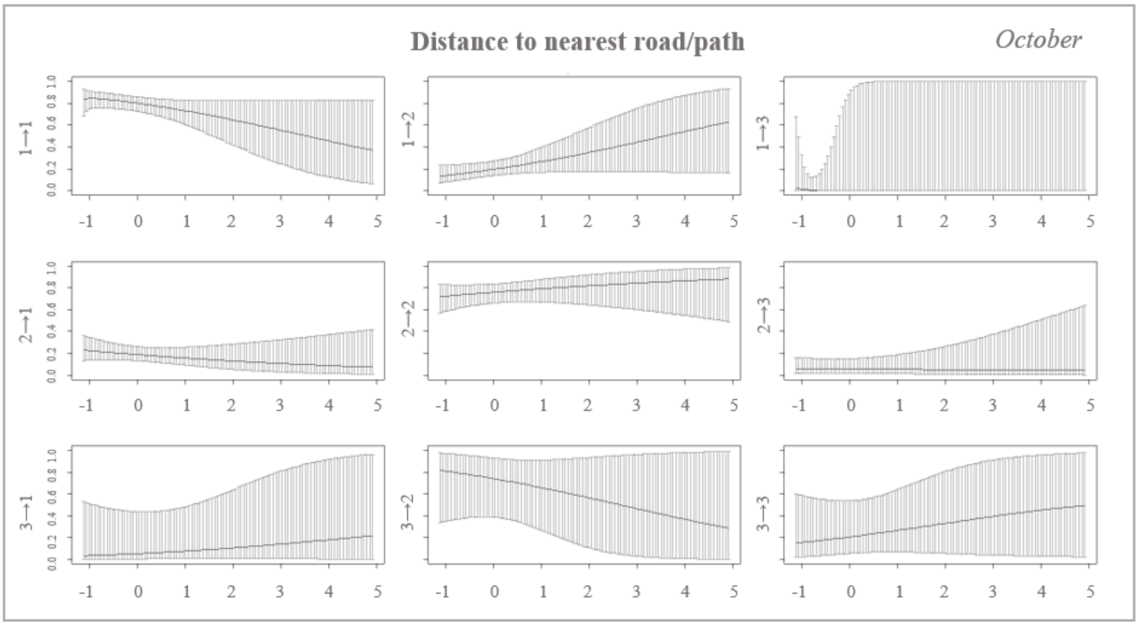

Figure 58. Graph showing transition probabilities under the influence of distance to nearest road/path as a covariate in October, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

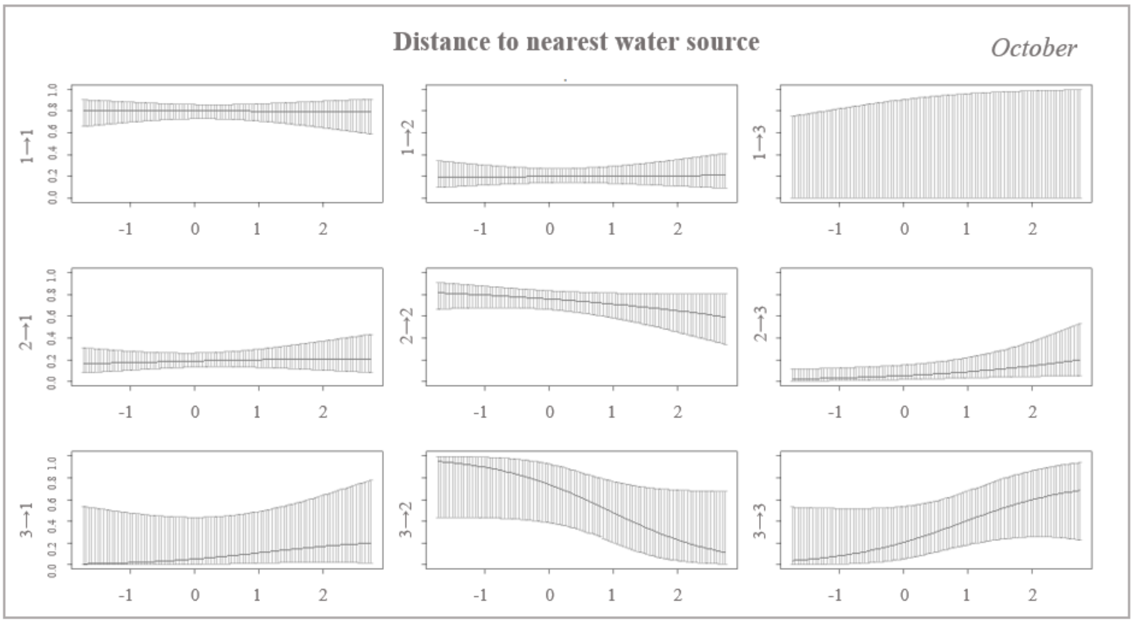

Figure 59. Graph showing transition probabilities under the influence of distance to nearest water source as a covariate in October, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

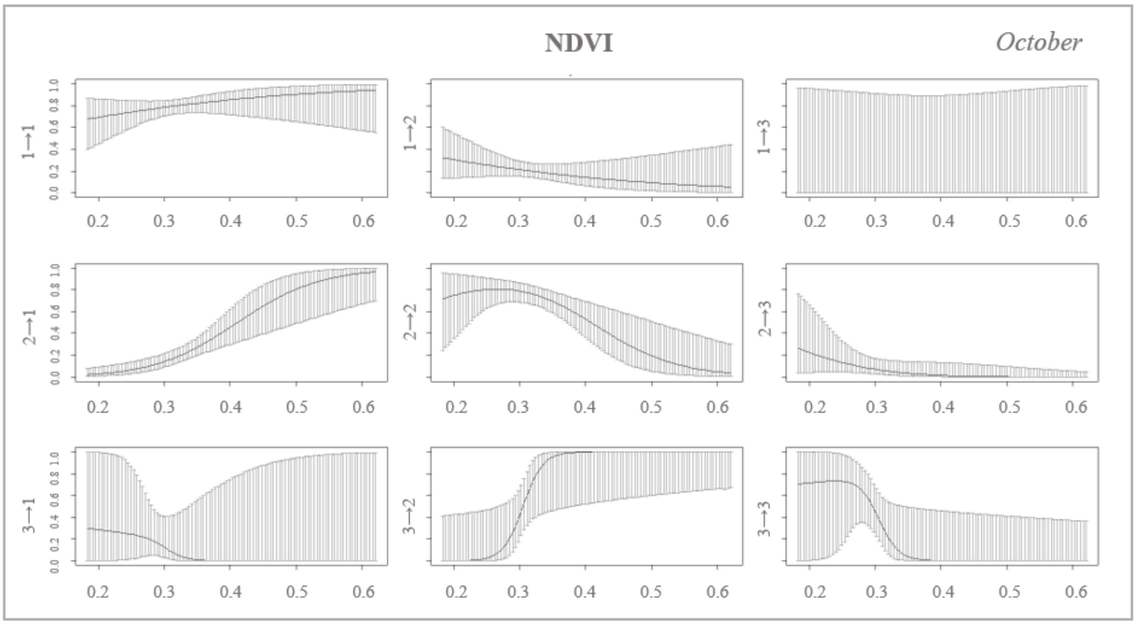

Figure 60. Graph showing transition probabilities under the influence of NDVI as a covariate in October, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

December (Table 20, Fig.61-64) recorded a high probability of persistence in state 2 in the vicinity of the water source (Fig.63), while as the distance increased, the *2→3* transition probability also increased (+1.23). Under the influence of NDVI as a covariate, an increasingly higher probability of switching to state 1 was showed when the NDVI value was higher (*2→1*= +28.02) (Fig.64). When considering distance to road, the probability of persisting in state 3 was more elevated when the distance increased, with a maximum peak at the greatest distance (Fig.62). Persistence in state 1 was higher as the rougher was the terrain.

Table 20. Regression coefficients for the transition probabilities referred to the month of December. The table shows the probability of transition between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The first row indicates the baseline probability of transition when all the covariates are set to zero. From the second to the fifth row, 4 different covariates and their influence on the transition probabilities are shown.

	Regression coefficients for the transition probabilities					*December*
	1→2	*1→3*	*2→1*	*2→3*	*3→1*	*3→2*
Intercept	-3.446	-29.723	-22.761	0.471	1.213	-41.165
Terrain roughness	-0.438	3.503	-2.136	0.342	-0.086	-0.400
Min. road/path distance	-0.091	4.780	-0.397	-4.129	-0.927	-8.763
Min. water source distance	0.278	0.831	0.060	1.238	0.108	2.140
NDVI	3.446	-16.286	28.029	-6.504	-2.399	54.843

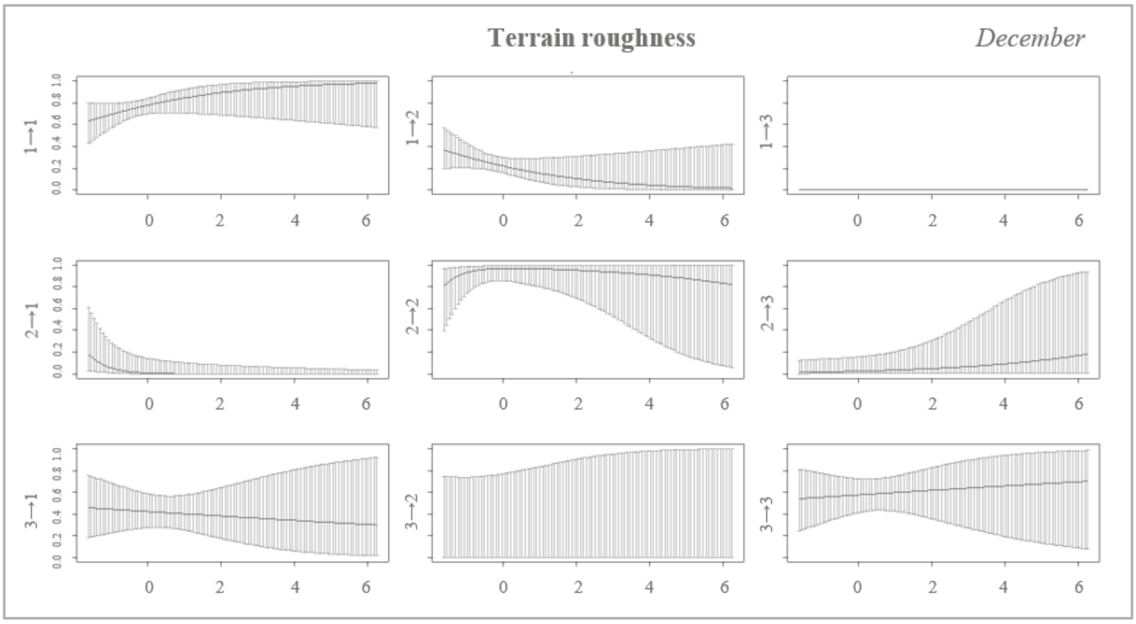

Figure 61. Graph showing transition probabilities under the influence of terrain roughness as a covariate in December, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

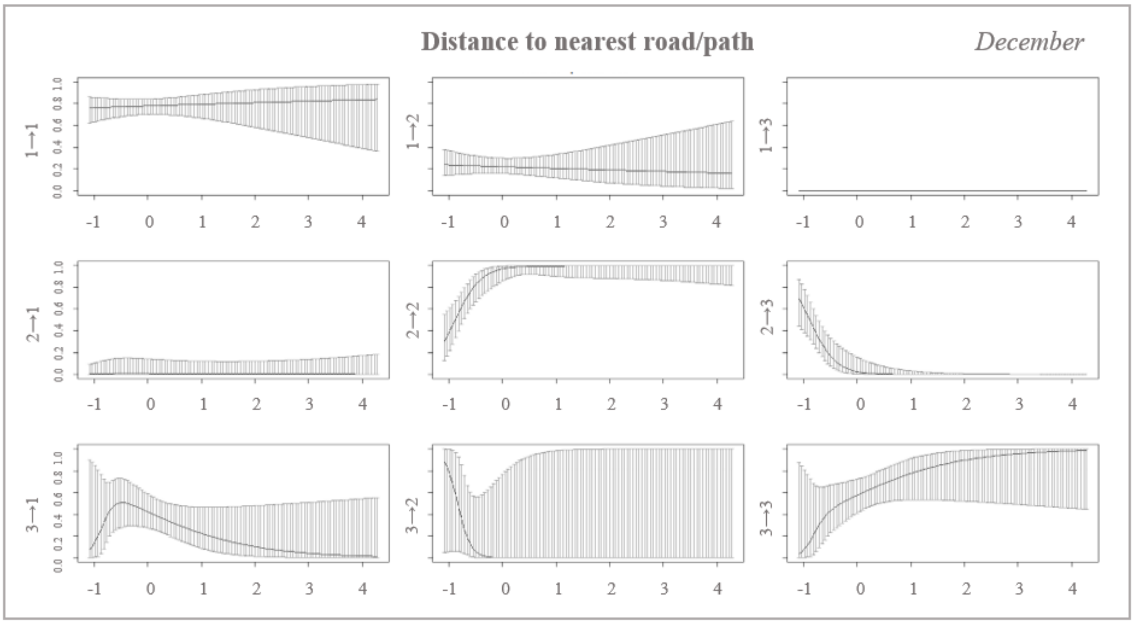

Figure 62. Graph showing transition probabilities under the influence of distance to nearest road/path as a covariate in December, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

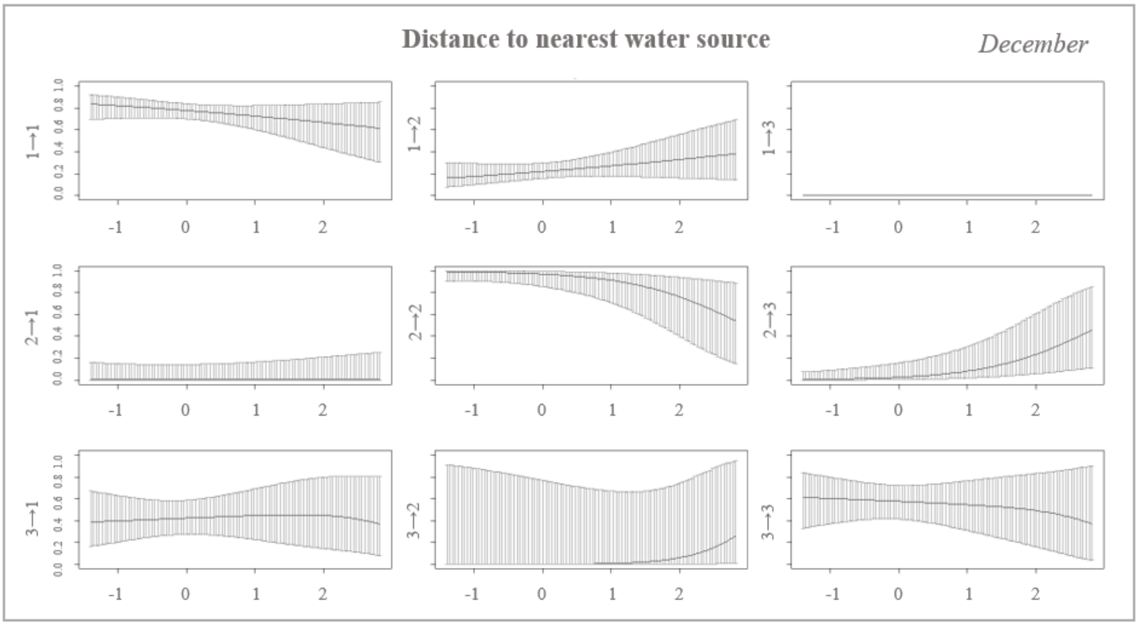

Figure 63. Graph showing transition probabilities under the influence of distance to nearest water source as a covariate in December, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

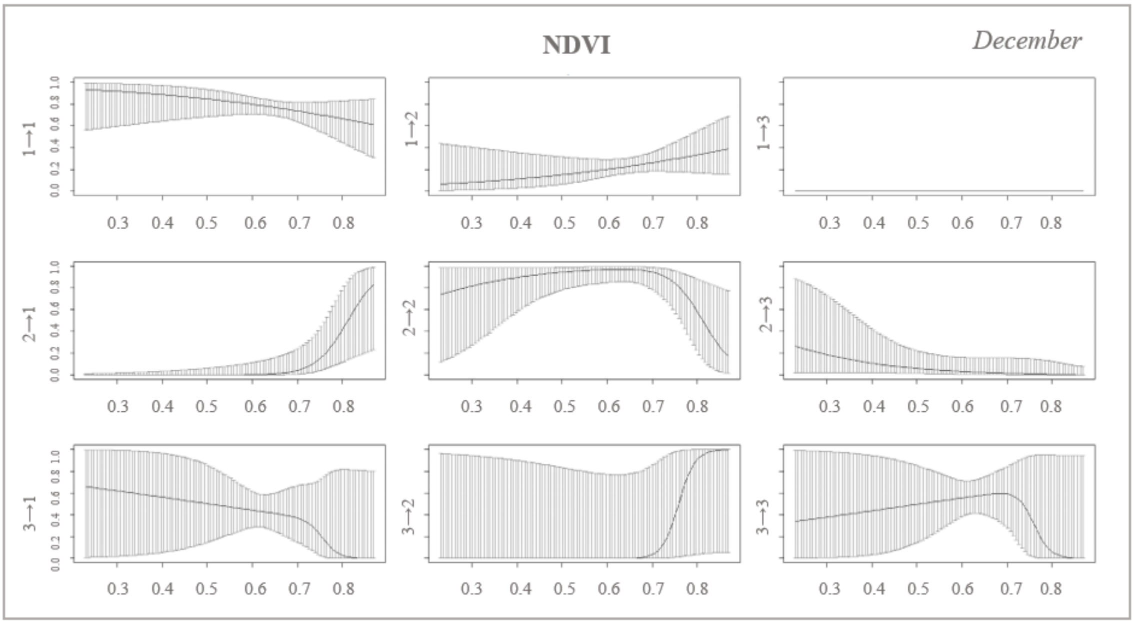

Figure 64. Graph showing transition probabilities under the influence of NDVI as a covariate in December, between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

The overall analysis of transition probabilities considering all 7 months as a whole showed trends that mirrored the analysis on a monthly scale (Table 21, Fig.65-68): terrain roughness as a covariate influenced the transition probability by favouring the transition to state 1 the rougher the terrain was (*3→2*= +0.10, *2→1*= +0.18, and *1→2*= -0.20) (Fig.65); considering the distance to the nearest road/path as a predictor variable, the transition probabilities were in favour of moving to state 3 the further away from the road (*1→2*=+0.10 and *2→3*=+0.24) and persisting in such state at the greatest distance from the road (Fig.66); when distance from the water source was considered, a prevalence of occurrence in state 2 was recorded (Fig.67); when the NDVI was set as a covariate, state 1 was the most probable as the NDVI value increased (*2→1*= +1.47 and *3→1*=+2.69) (Fig.68).

Table 21. Regression coefficients for the transition probabilities referred to the month from June to December combined as a whole. The table shows the probability of transition between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The first row indicates the baseline probability of transition when all the covariates are set to zero. From the second to the fifth row, 4 different covariates and their influence on the transition probabilities are shown.

Regression coefficients for the transition probabilities					*June-to-December*	
	1→2	*1→3*	*2→1*	*2→3*	*3→1*	*3→2*
Intercept	0.255	-2.420	-1.978	-2.566	-5.136	-1.608
Terrain roughness	-0.020	-0.575	0.180	0.036	-1.084	0.103
Min. road/path distance	0.103	0.032	0.079	0.241	-0.234	-0.151
Min. water source distance	-0.109	-0.071	0.050	0.266	0.367	-0.061
NDVI	-2.235	1.530	1.477	1.914	2.692	0.325

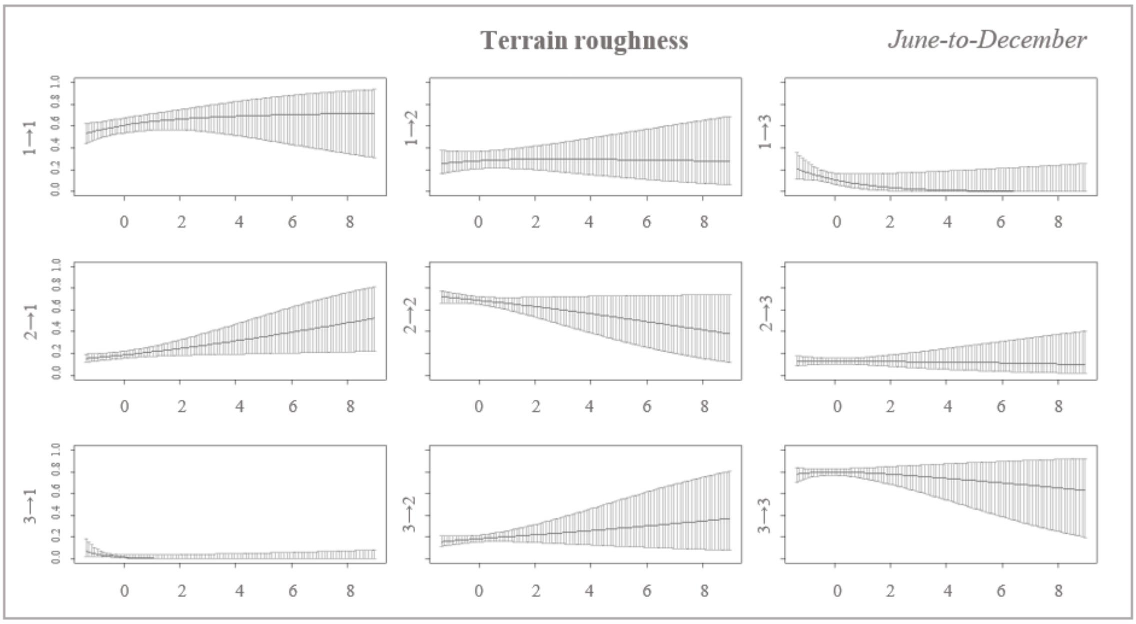

Figure 65. Graph showing transition probabilities under the influence of terrain roughness as a covariate for the 7-month period (June to December), between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

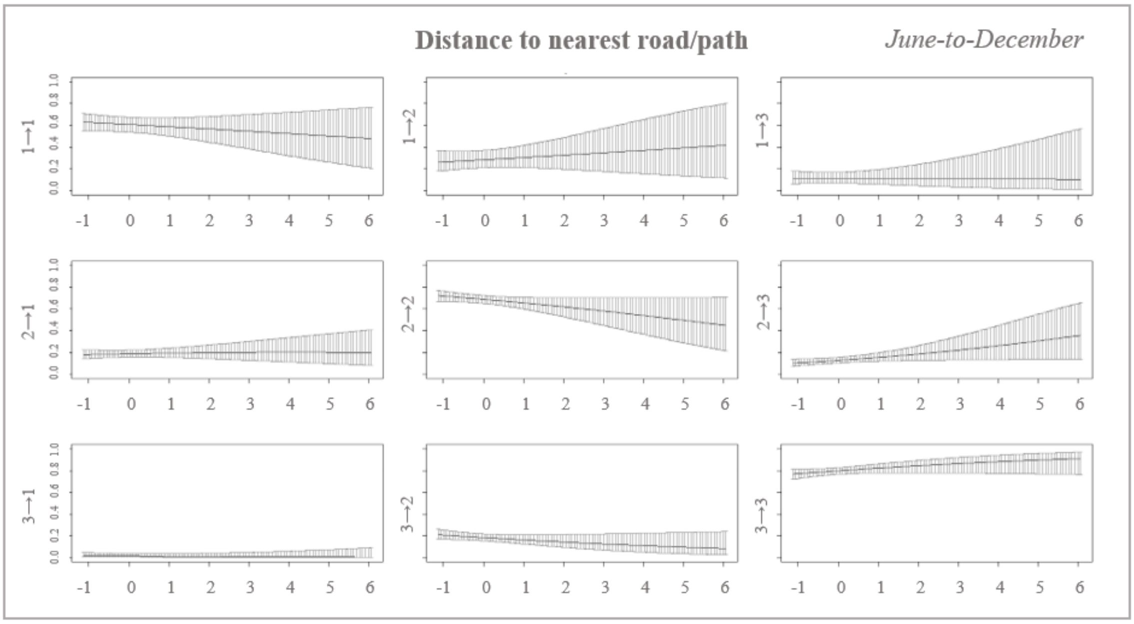

Figure 66. Graph showing transition probabilities under the influence of distance to nearest road/path as a covariate for the 7-month period (June to December), between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

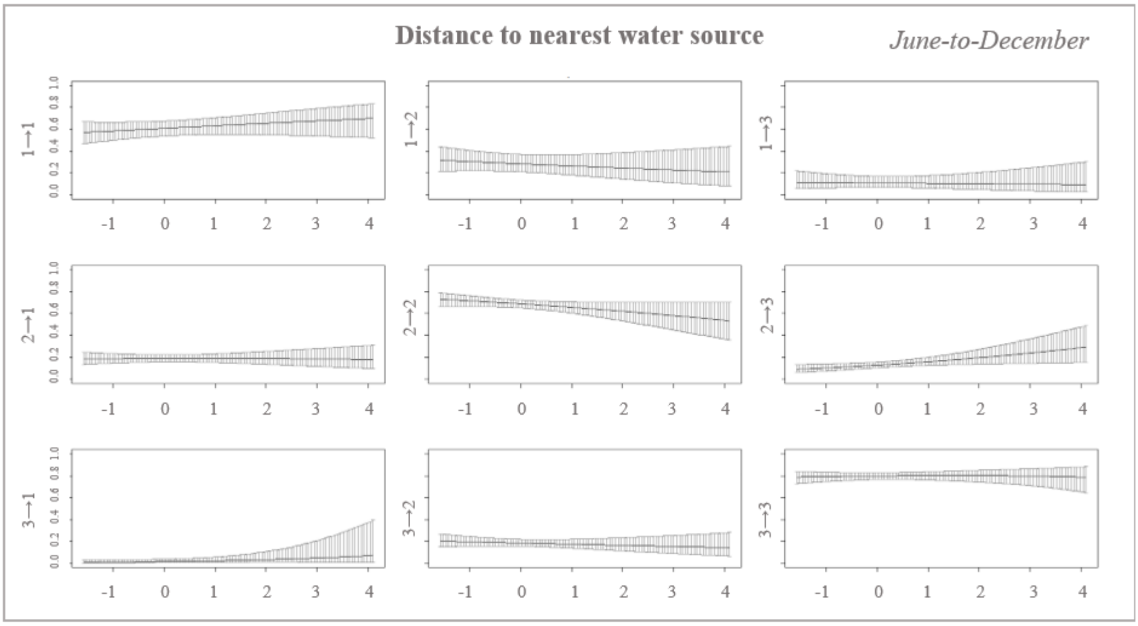

Figure 67. Graph showing transition probabilities under the influence of distance to nearest water source as a covariate for the 7-month period (June to December), between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

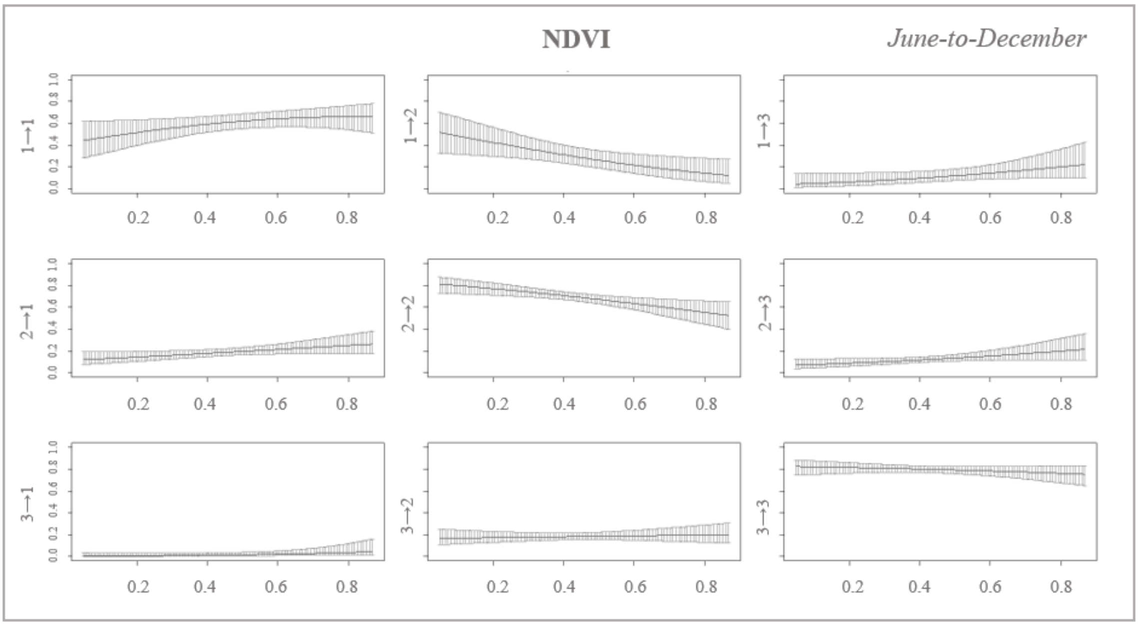

Figure 68. Graph showing transition probabilities under the influence of NDVI as a covariate for the 7-month period (June to December), between state 1 and 2 (1→2), state 1 and 3 (1→3), state 2 and 1 (2→1), state 2 and 3 (2→3), state 3 and 1 (3→1), and state 3 and 2 (3→2). The graph also shows persistence probabilities in state 1 (1→1), state 2 (2→2) and in state 3 (3→3).

The results regarding the stationary state probabilities were analysed covariate by covariate (Fig.69-74).

Considering the terrain roughness as a covariate, the stationary state probabilities reflected the same results across all the months analysed (Fig.69-73), with a higher probability of lying in state 1 as the roughness value increased and lying in state 2 at the lowest roughness value. This trend was also confirmed by the 7-month period analysis (Fig.74).

When setting the distance to the nearest road/path, the result differed between months. While June showed a stationary state probability of being in state 1 and 2 at the greatest distance from the road (Fig.69), August indicated a higher probability of staying in state 3 (Fig.70). In September, it was recorded an extremely high prevalence of state 3 as distance from the road augmented (Fig.71), while state 2 prevailed in October under the same conditions (Fig.72). The latter was also found in December (Fig.73), with a remarkably elevated probability. However, combining all months together, the occurrence in state 3 was the highest as distance from the road increased (Fig.74).

Under the influence of distance to the nearest water source as a predictor variable, in June at the nearest distance there was a higher probability of lying in state 1, whereas, at the maximum distance, state 2 was prevalent (Fig.69), as in August (Fig.70). September and October showed similar trends (Fig.71-72), with higher probabilities of lying in state 2 near water and state 1 far from water. December recorded a remarkably high value of being in state 2 in the proximity of water (Fig.73). However, although with very similar values between states, state 3 was the most likely when away from water (Fig.74).

The influence of the NDVI as a covariate was consistent across all the months. Even if with different grades of probability, lying in state 1 was the most probable at the highest values of NDVI throughout the analysed months (Fig.69-74).

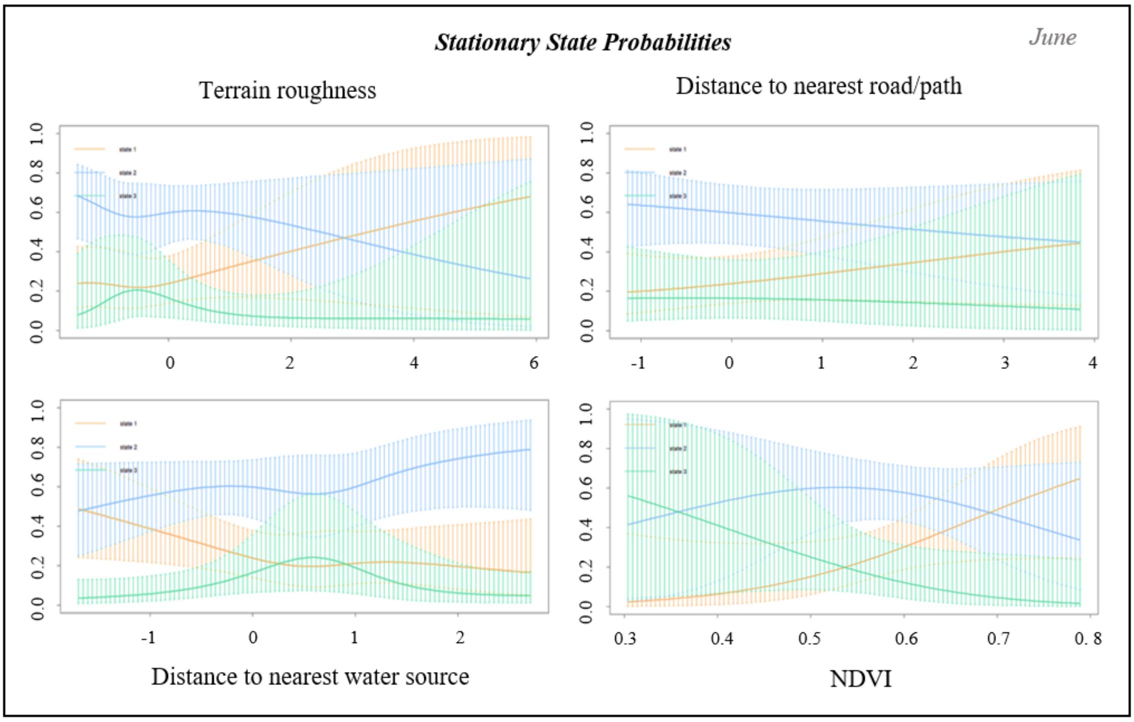

Figure 69. Graph showing stationary state probabilities for each covariate in June.

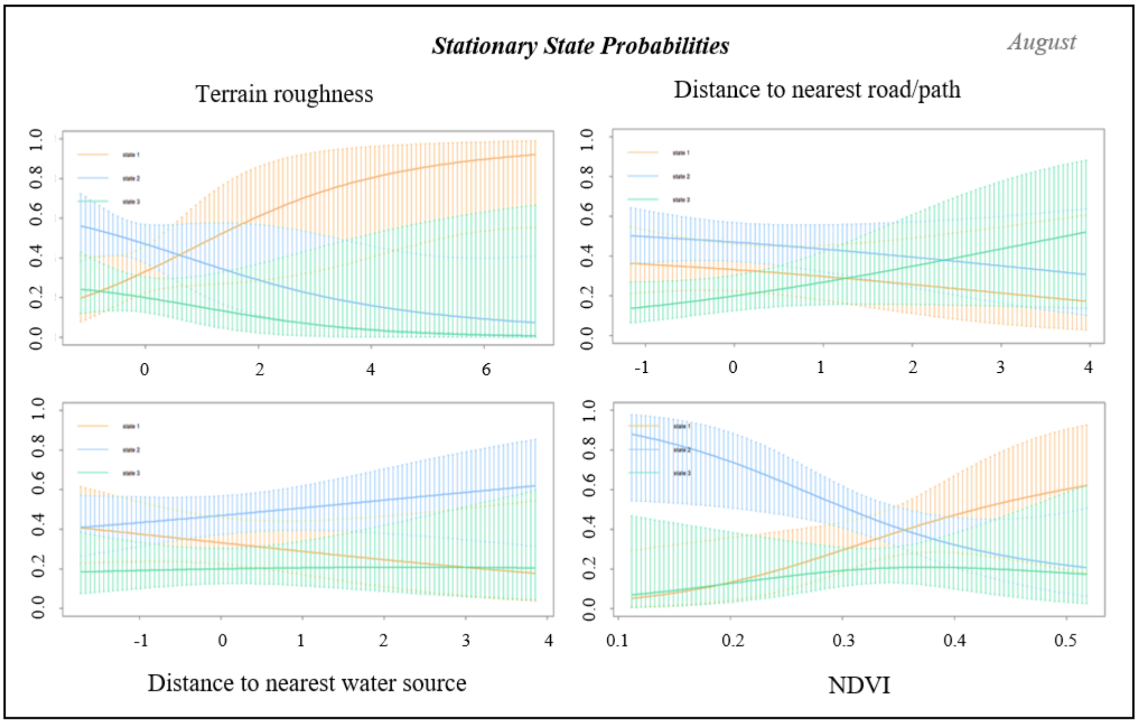

Figure 70. Graph showing stationary state probabilities for each covariate in August.

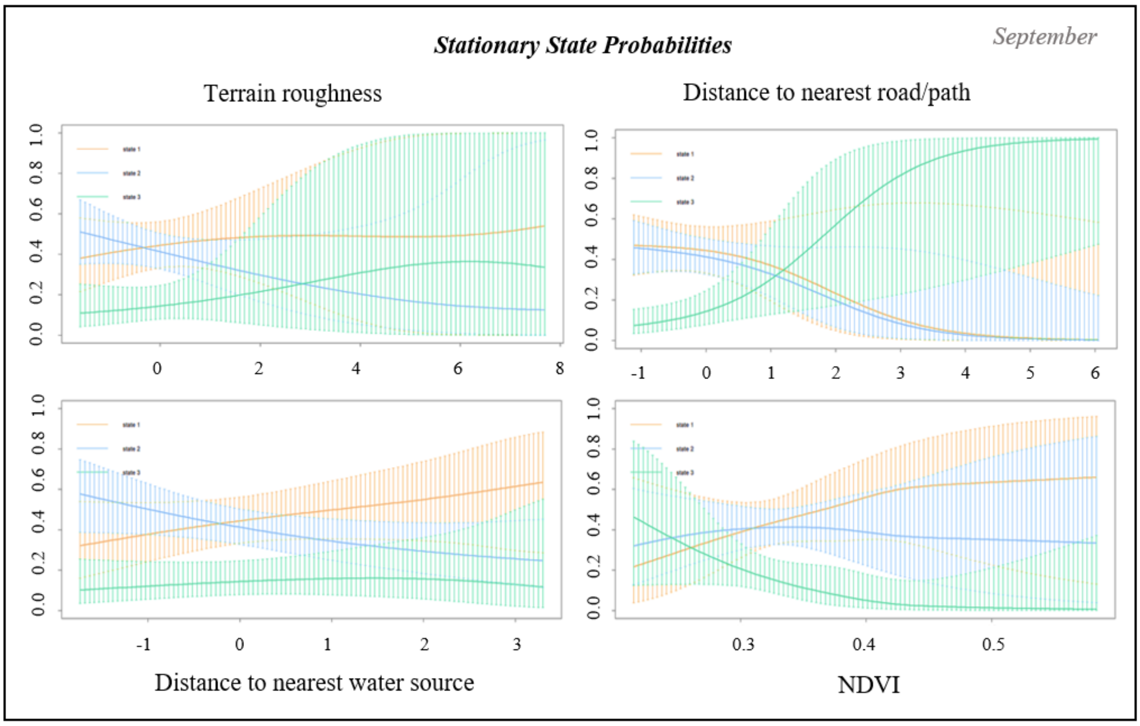

Figure 71. Graph showing stationary state probabilities for each covariate in September.

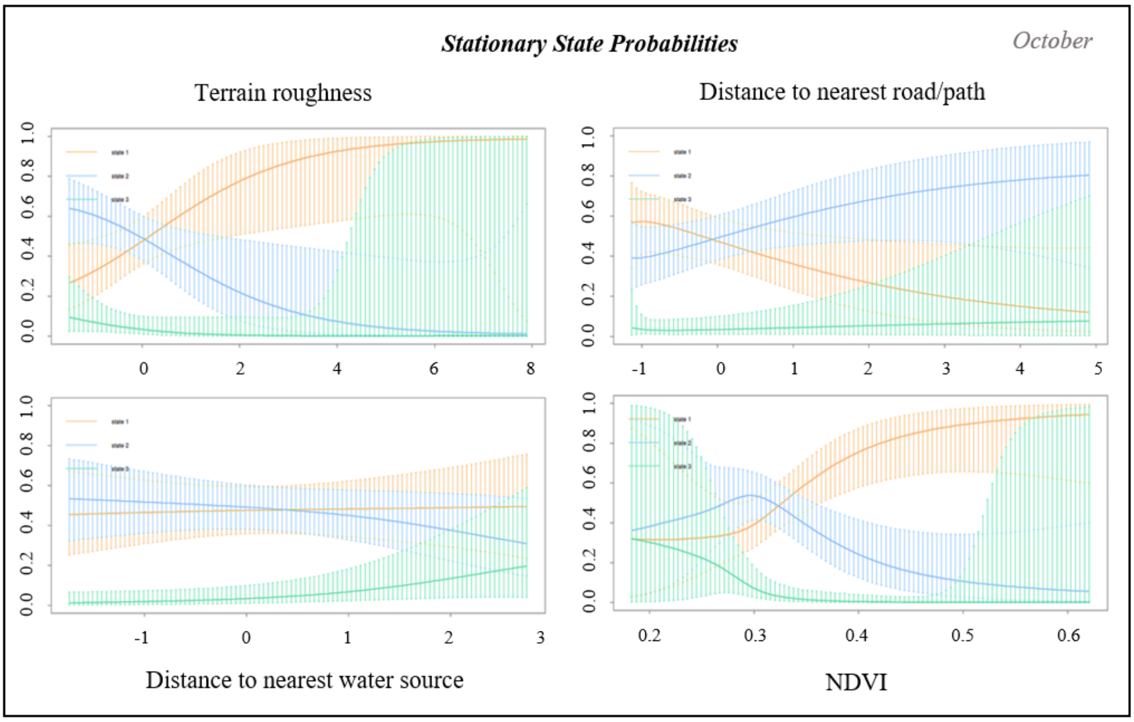

Figure 72. Graph showing stationary state probabilities for each covariate in October.

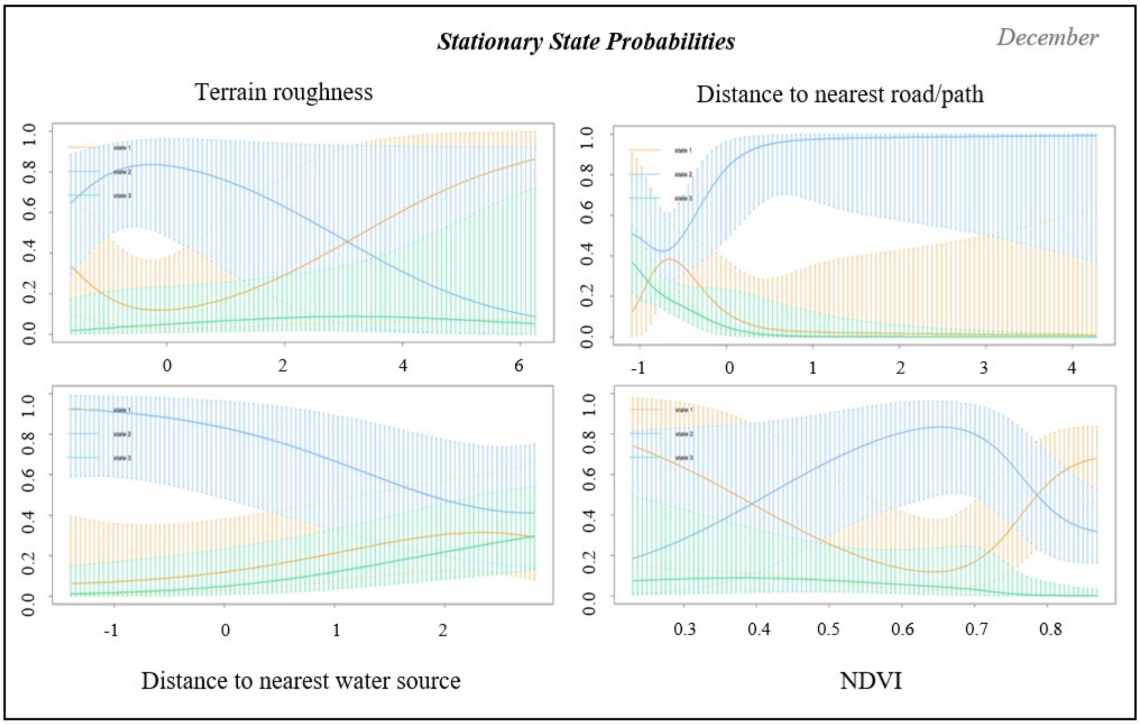

Figure 73. Graph showing stationary state probabilities for each covariate in December.

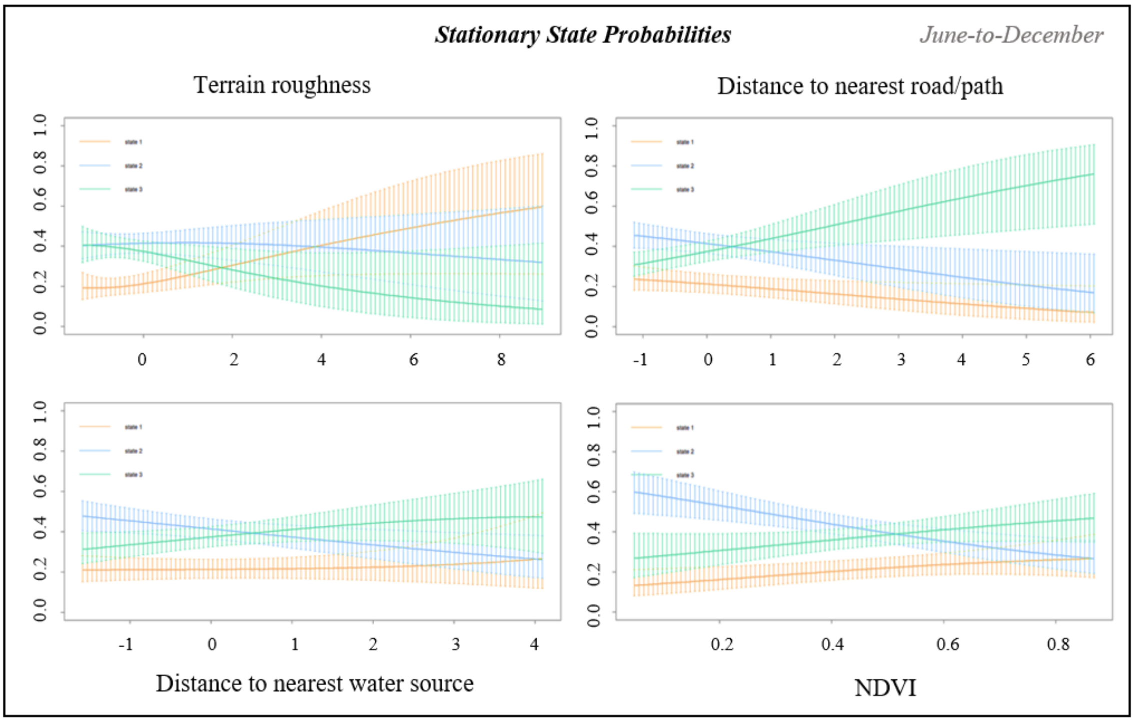

Figure 74. Graph showing stationary state probabilities for each covariate combining all the months.

4 DISCUSSION

Although elephant movements are complex and season-dependent (Young *et al.*, 2009a; Young *et al.*, 2009b; de Beer and van Aarde, 2008; Leggett, 2006; Cushman *et al.*, 2005; Douglas-Hamilton *et al.*, 2005), this study succeeded in delineating the movement patterns of two matriarchs within the SGR, a fenced reserve in South Africa. Furthermore, it demonstrated how external variables -namely in this study terrain roughness, distance to nearest road/path, distance to nearest water source, and NDVI- exerted a significant influence on movement patterns, as well as on the prediction of movements. Indeed, consistent results were found for each predictor variable throughout the analysed period, on a monthly scale and between different individuals.

From the analysis of the seven months combined, the step length mean for each state of the two matriarchs was consistent between the two individuals. Additionally, consistency was also found with a previous study, which analysed 155 elephants over 21 years (Berti *et al.*, 2023). This concordance with the latter indicated a great accuracy of the model used to study matriarchs' movements, denoting how well the chosen parameters fit the data. Nonetheless, on a monthly scale, the second matriarch, Jean, showed a longer average step length of 30.5%, 76% and 37% in states 1, 2 and 3, respectively, compared to the step length mean of the first matriarch, Elza. A valid hypothesis to explain this difference, which was particularly pronounced only in certain months, could be the presence of more calves in Elza's herd than in Jean's during the evaluated period. This theory could explain why Elza's pace was found to be slower than Jean's. It was verified that during the aerial census of September 2022, four calves under one year old were found in different herds. However, it could not be determined whether one of these herds was Elza's. Nonetheless, studying the influence of calves on herd's pace, Taylor *et al.* (2022) concluded that adult elephants may not need to adapt their speed because of the presence of calves. However, it should be noted that this research was the first on this topic, thus further analyses may be necessary to confirm or refute these results. Evaluating overall rather than on a monthly scale, the difference between the average step length of the two matriarchs has narrowed considerably; therefore, it is conceivable that as the months passed, the calves grew up and influenced the rhythm of the herds less.

A prevalence of time spent in state 1 was found, especially for Elza, during the wet months included in this study (i.e., November and December). The analysis revealed that Jean commenced to increase its time spent in state 1 from October onwards. This slight discrepancy between the two individuals can be explained by the fact that October is generally classified as a transition month between the two seasons, it is therefore plausible that different matriarchs change their movement behaviour with a gap of few weeks. In contrast, during the months belonging to the dry season analysed in this study (i.e., from June to September-October), both individuals spent more time mainly in states 2 and 3, with a peak in August. This may reflect the need to move more within the reserve when resource availability decreased, in order to reach areas with still available forage sources. On the contrary, with the transition to the wet season, they exhibited an important shift to short steps. This shift likely occurred because the flourishing of food availability, after months of scarcity, led them to dedicate more time foraging and feeding than before. These results are in contrast to some previous papers (Vogel *et al.*, 2020; Birkett *et al.*, 2012; Loarie *et al.*, 2009), which found a lower movement velocity during the dry season and an increase in speed during the wet season. However, it is essential to note that the matriarchs' movements analysed in this study were constrained by fences. In contrast, the previously mentioned studies encompassed open systems of vast extent, such as KNP (Birkett *et al.*, 2012), the Okavango Delta (Vogel *et al.*, 2020), and transboundary areas spanning different countries (Loarie *et al.*, 2009). Therefore, the seemingly contrasting results must be contextualised within the difference in available space for elephants. In light of this, the findings may be plausible and consistent with the extent of the fenced reserve considered, in which these matriarchs have lived for several years, and of which they have developed a great knowledge of where each resource is available and at what time of year. As the dry season reached its peak, there was an observable increase in the time spent in states 2 and 3 by the matriarchs. Their movements during this period appeared to be direct and precise, suggesting their intent to reach specific areas of the reserve. These areas were likely chosen based on their past experiences with the presence of foraging resources during that time of year. Furthermore, the main constraint that justified the results of the cited articles was the low availability of water during the dry season in such open systems, which forced the elephants to a smaller home range than during the wet season (Vogel *et al.*, 2020; Birkett *et al.*, 2012; Loarie *et al.*, 2009). This major limitation may have been overcome within the SGR due to the large number of artificial water points operating throughout the dry season. Therefore, not having such constraint in a relatively small closed system, conceivably matriarchs decided to move more during the dry season in order to exploit areas with more availability of food supply. Likewise, having limited possibilities for large migrations, they probably decided to settle for longer periods in highly productive areas during the wet season.

4.1 Terrain roughness

In previous studies on elephant movements, changes in elevation or energy landscapes were included as a covariate for large areas (Berti *et al.*, 2023; Evans *et al.*, 2020; Songhrust *et al.*, 2016; Bohrer *et al.*, 2014). Williams *et al.* (2018) also included terrain roughness as a covariate to assess the correlation with movement pattern, within a 40,000 km^2 corridor area in south-eastern Kenya. However, they stated that no major influence of terrain roughness on elephant movement was found, whereas elevation played a key role in elephant movement. Notwithstanding, within the SGR, a fenced reserve of 258 km^2, relatively small compared with the areas considered in such studies, the elevation seemed to not play a notable role, due to the geographical and topographical characteristics of the reserve itself. The latter, instead, comprises a great diversity in terrain roughness, due to mixed soil composition, and topography. Therefore, it seemed more logical to include it as covariate, since hills, valleys, drainages, changes in soil composition, slope, and ruggedness may have been important drivers on movement patterns. Therefore, Elza and Jean movements were analysed under the influence of the terrain roughness as a predictor variable. At the lowest values of roughness, Elza showed a higher probability of being in state 2, whereas Jean an equal probability of occurring in state 2 or 3. At the highest values of roughness, both Elza and Jean showed a higher probability of occurrence in state 1, generally. While Jean showed the exact same results across each month, Elza, instead, exhibited a weaker influence of such covariate on its movements as closer to the wet period. Overall, a strong occurrence in state 1 as the terrain became rougher was found in both matriarchs when combining the seven months together. These results indicated that when Elza's and Jean's herds had to travel long distances (i.e., they persisted in state 3), they preferred flatter areas to facilitate their movements. Furthermore, they switched to state 1 whenever they crossed areas with high roughness values because rough terrain can present obstacles that the elephants must circumvent. Steep slopes or drainages, for example, may limit their speed and movement in certain directions, forcing them to slow down and, hence, to switch to state 1. In particular, seasonal drainages can be classified as rough terrain not only when they are full, but also when they are empty, as they often present irregular and rough terrain characteristics. These features may include rocky surfaces, debris, uneven terrain and even small cliffs or embankments. These terrain variations can make the elephants' movement more challenging. Hence, this phenomenon may elucidate why, when matriarchs selected a path necessitating the crossing of one of these soil types, they displayed a tendency to transition to state 1 upon approaching that particular soil type. Consequently, they remained in that state for as long as the soil roughness value remained elevated.

4.2 Distance to nearest road/path

The influence of distance to the nearest road/path was estimated using the road/path network of the reserve as a covariate. Previous research has estimated the most likely route of elephants based on their movements (Duffy *et al.*, 2011; Cushman and Huettmann 2010; Shannon *et al.*, 2009). In contrast, this study aimed to assess the influence of the existing road/path network within the reserve, which is also regularly used by rangers' and ecotourism guides' vehicles. In particular, the aim was to assess whether elephants used such paths as corridors or game path, and in what way. The findings regarding the influence of this predictor variable were consistent between the two matriarchs Elza and Jean. Combining the results of the transition probabilities and stationary state probabilities, it is worth noting that both matriarchs exhibited a limited influence of the nearest road or path on a particular state between June and August. In general, during this period, they displayed a stronger tendency to persist in states 1 and 2 when located farther away from the road. However, when in proximity to the closest road, they displayed a preference for transitioning to state 2-3. On the contrary, between September and December, persistence in state 2-3 was consistently found further away from the road, whereas at the nearest distance from it, occurrence in state 1 was the most likely. The period between June and August corresponded to the driest months of that year, when the vegetation was rapidly drying up. Thus, the results may explain the matriarchs' need to move more rapidly within the reserve in order to reach areas where food was still available as soon as possible. Consequently, the persistence of medium-to-long steps when on roads/paths may represent their use of these roads as corridors. This explanation is consistent with the study conducted by Vogel *et al.* (2020), which discovered that elephants use corridors when they want to move quickly and directionally trough vegetation and the environment. Additionally, the study conducted by Tsalyuk *et al.* (2019) discovered that when elephants needed to traverse the landscape, they exhibited a preference for utilizing roads, as these pathways enabled them to lower their energy consumption.

The period of the year between September and December was characterised by the end of the dry season, a slow transition to the wet season and the first part of the wet season proper. In the light of this, the results outlined in these months may represent the likelihood of a greater exploitation of roadside and pathway vegetation, which was easier to access due to its proximity to roads. This interpretation is in agreement with what has been empirically observed by reserve managers in recent years, who have noticed a greater impact of elephants on vegetation on both sides of the reserve's road network. Moreover, this tendency to more easily and frequently impact vegetation on the edges of paths is also well documented in the literature (Russo *et al.*, 2023; Blanché, 2021; Brodie *et al.*, 2015; Porensky *et al.*, 2013; Fernando and Leimgruber, 2011; Vanak *et al.*, 2010; Young *et al.*, 1995). In addition, Berger (2007), and Trombulak and Frissell (2000) pointed out that elephants may prefer roads during the wet season due to the greater availability of greener vegetation on the sides of the paths, as a result of the increased exposure to sunlight. Therefore, the fact that roads and paths provided easier travel routes for elephants may have led to an increased utilization of vegetation along their edges during the wet season. Additionally, these pathways likely facilitated more efficient navigation through the reserve during the dry season.

4.3 Distance to nearest water source

It is well known that elephant movements are driven by access to vital resources (Vogel *et al.*, 2020), with water being the most important for their survival. As evidence, several papers have portrayed water points as the most impactful environmental factor in the ecology of elephant movements, both for the direct use (MacFadyen *et al.*, 2019; de Knegt *et al.*, 2011; de Beer and van Aarde, 2008; Chamaillé-Jammes *et al.*, 2007) and indirect use, for example for thermoregulation, shade, and mud bathing (Henley and Cook, 2019; Marshal *et al.*, 2011; Smit *et al.*, 2007; Stokke and du Toit, 2002). In this context, several authors have recognised the water as a driver for elephant choices and preferences (Chibeya *et al.*, 2021; Sach *et al.*, 2019; Taher *et al.*, 2021; Talukdar *et al.*, 2020; Wall *et* *al.*, 2013). Therefore, this study aimed to evaluate the influence of water sources on the movement patterns of the two matriarchs, using the distance to the nearest water source as a predictor variable. Considering mainly the results of the stationary state probabilities plots, they showed consistency between the two matriarchs in terms of persistence in certain states near the water source. Indeed, both Elza and Jean were in states 1 or 2 when closer to the water. However, although Elza was almost equally likely to be in state 1 and 2 during the months considered, Jean showed a strong prevalence of being only in state 2 when near water points during December. This latter peculiarity can be explained by what was discovered by Bastille-Rousseau *et al.* (2020), according to whom elephants did not show a marked interest in necessarily staying close to water during the wet season, a preference instead pronounced during the dry season. Overall, the same probability of lying in states 1 and 2 when in the vicinity of water may be the consequence of an elevated number of water points throughout the reserve. Although some of these are seasonal, thus empty during the dry season, the amount of artificial and semi-artificial water sources remains high in relation to the size of the reserve. Therefore, it is plausible that the herds of the two matriarchs alternated between prolonged and brief stops whenever they were near a water point, preferring, however, more short stops. In support of this, previous research has found that elephants' movements to access water are generally frequent but of short duration (Polansky *et al.*, 2015; Chamaillé-Jammes *et al.*, 2013). Another hypothesis that may explain the high probability of being in state 2 in the proximity of the water may be that the matriarch briefly accelerated as it approached the water points, and then spent time in state 1 in close proximity to the water. Although the differences in speed between the different states were not calculated in this study, it is evident that the step length means of state 2 was greater than that one of state 1, therefore it can consequently be assumed that the average speed was higher in state 2. Furthermore, Chamaillé-Jammes *et al.* (2013) found out that elephants increased their speed when moving closer to water points, hence the previous assumption may be valid.

In contrast, at the greatest distance from the water, Elza and Jean showed two different movement patterns. Particularly, Elza was always found in state 3, with an extremely high probability from September onwards. In contrast, Jean predominantly occupied state 2 when farthest from the water in most months, except for September and October when state 1 at maximum distance from the water prevailed, albeit without a significant dominance over the other two states. Nonetheless, combining the seven months into a single analysis, Elza remained consistent with the results on a monthly scale, while

Jean showed a prevalence of state 3 away from water, again consistent with the other matriarch. The disparity in Jean's results could be attributed to the impact of two months, July and November, within the combined analysis of seven months. However, it's important to note that the individual analysis of these specific months was not conducted, leading to a gap in our understanding of how these months may have influenced the overall assessment of movement patterns in relation to this covariate. Since water is a major determinant of elephant movement patterns, it is conceivable that the two matriarchs were in state 3 for most months when they were away from water, while they tended to stay as close to water as possible when in the other two states. It is therefore likely that they moved quickly from one water source to the other in order to spend as little time as possible at maximum distance from the water and reach another water source as quickly as possible. In support of this, previous articles have highlighted how water-orientated elephant movements can commence from tens of km away (Polansky *et al.*, 2015).

4.4 NDVI

The importance of NDVI as a mean for comprehending the ecology of elephants has already been documented by several authors (Loarie *et al.*, 2009; Wittemyer *et al.*, 2007; Chamaillé-Jammes *et al.*, 2007). The exceptional temporal precision of NDVI proved invaluable for examining elephant movements, as it enabled the correlation of vegetation productivity data with the simultaneous tracking of individual locations (Pettorelli *et al.*, 2011). On a monthly scale, both Elza and Jean showed the same relationship between NDVI and their movements. Particularly, not only the transition probabilities, but also the stationary state probabilities, indicated a constant and persistent presence in state 1 at the highest NDVI values, and in state 3 at the lowest values. This trend was highly consistent between the two matriarchs and across all the months considered. It is therefore clear that the movements of the matriarchs were strongly influenced by the presence or absence of high vegetation availability. The strong correlation observed between high NDVI values and presence in state 1 throughout the analysed period suggested that Elza and Jean exhibited a preference for consistently foraging in the most productive areas of the reserve. This preference may be attributed to the greater diversity in vegetation types and nutrient concentrations in the chosen area, which differ between different times of the year. Loarie *et al.* (2009) drew similar conclusions because in all seasons of their study, elephants showed a constant selection of the greenest vegetation, taking advantage of phenologically diverse vegetation. Thus, the elephants purposely chose the areas in which to feed, denoting a high knowledge of the places where they could find the most qualitative available food, not only in the wet season but also and especially in the dry season. Consequently, these two matriarchs showed a preference for quality over quantity even in the dry season, an uncommon behaviour in open systems, where quantity is generally chosen over quality in the dry season (Tsalyuk *et al.*, 2019; Young *et al.*, 2009a). Nevertheless, Young *et al.* (2009a) found a high presence of elephants in grid-cells with elevated NDVI values during the dry season, which is in agreement with what was found in this study.

In several months, particularly during the dry season, the transition probability values showed a higher probability of moving from state 3 to state 1 rather than from state 2 to state 1 as the NDVI value increased. This peculiarity may be further evidence of the matriarchs' great knowledge of the reserve itself and where they could find the most productive patches throughout the reserve. Therefore, their movements were fast, direct and precise (state 3) towards a specific spot that, once reached, represented the final destination for feeding and foraging (state 1). In support of this, Boettiger *et al.* (2011) and Loarie *et al.* (2009) pointed out that elephants' optimal foraging strategies involved actively seeking out regions with high NDVI values. Furthermore, Wittemeyer *et al.* (2008) indicated that non-random movements are generally associated with feeding strategies, particularly when food and water supplies are scarce or heterogeneously distributed.

5 CONCLUSION AND RECOMMENDATIONS

This research explored elephant movements under the influence of four different probable drivers (i.e., terrain roughness, distance to nearest road/path, distance to nearest water source, NDVI) in a fenced reserve in South Africa, to better understand movement patterns of such megaherbivores limited by fences. Particularly, it showed that movement states derived from step length and turning angle from hourly GPS positions of elephants with HMMs can be extremely effective in the analysis of elephant movement patterns per se and under the influence of different predictor variables. The findings of this study emphasised the importance of including terrain roughness, distance to nearest road/path, distance to nearest water source, and NDVI as a key driver of elephant movement patterns.

In summary, using terrain roughness as a covariant contributed to the assessment that increased roughness led to a change in the movement pattern, resulting in elephants slowing down. Such results aided to evaluate whether elephants showed preferences for certain types of terrain, how terrain influences their movements, and how they navigate the landscape to meet their ecological needs. Moreover, understanding which roads or paths were frequently used by elephants can inform resource management decisions. Elephants showed to use the road network to navigate the landscape faster during the dry season, and to exploit roadside vegetation during the wet season. Therefore, managers could focus vegetation restoration efforts or water source maintenance along these routes to ensure Therefore, managers could concentrate their efforts on restoring vegetation or maintaining water sources along these routes to ensure that the needs of elephants and other wild animals are met. Additionally, persistence in state 3, the farthest from water sources, was found with direct and accurate movement patterns. Hence, the knowledge that elephants' movements are driven by water points with specific movement patterns has profound implications for conservation management within a fenced reserve. For instance, conservation manager can use this information to plan a rotation on water points available in order to avoid a repeated impact on the same patches of vegetation near water sources, giving vegetation time to recover. Finally, matriarchs consistently occurred in state 1, when NDVI values were highest, and in state 3, when NDVI values were lowest. Such strong correlation between elephant movements and high NDVI values can have several important conservation management implications within a fenced reserve: conservation managers can focus their habitat management efforts on areas with high NDVI values, as these areas are likely critical for elephant foraging and nutrition. This may involve protecting and restoring key habitats that contribute to high NDVI values. All these strategies therefore have the common goal of promoting the conservation and welfare of elephants, maintaining an ecosystem balance that indirectly benefits the rest of the wildlife in the reserve.

In terrestrial ecosystems where megaherbivores such as elephants serve as critical ecosystem engineers (Vanak *et al.*, 2012; Shannon *et al.*, 2011; Owen-Smith *et al.*, 2006), it becomes imperative to not only understand the spatial distribution of individuals but also to discern the timing of behavioural changes and identify the pivotal factors driving these shifts (Birkett *et al.*, 2012). Such understanding enables the development of more efficient conservation management strategies for the preservation of the species. Hence, future research could investigate elephant movement patterns across various temporal scales, including finer scales like daily or weekly observations, as well as broader scales such as seasonal or annual trends. This approach can aim to gain a comprehensive understanding of the underlying mechanisms and influences guiding their choices and preferences. Ultimately, these insights can inform initiatives aimed at enhancing conservation management plans for elephants.

In conclusion, delving into the spatial ecology of elephants provides information that is of significant and, especially in the context of fenced reserves, even critical importance for the successful and efficient management and conservation not only of this species' habitat but also of the species itself (Chui, 2021).

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7 APPENDIX I

This appendix shows some photographs of the two matriarchs studied in this paper: Elza (Fig. 1-7) and Jean (Fig.8-10).

Figure 1. Close-up of Elza in Selati Game Reserve (Provided by: Selati Game Reserve).

Figure 2. Photography shot by a camera trap. Date and time are shown in the photo (Provided by Selati Game Reserve).

Figure 3. Photography shot by a camera trap. Date and time are shown in the photo (Provided by Selati Game Reserve).

Figure 4. Elza with other elephants of its herd (Provided by Selati Game Reserve).

Figure 5. Elza walking with its herd (Provided by Selati Game Reserve).

Figure 6. Elza walking with its herd (Provided by Selati Game Reserve).

Figure 7. Elza walking with its herd (Provided by Selati Game Reserve).

Figurre 8. Close-up of Jean (Provided by Selati Game Reserve).

Figure 9. Jean (Provided by Selati Game Reserve).

Figure 10. Jean eating mopane leaves (Provided by Selati Game Reserve).

8 APPENDIX II

This Appendix contains all the relevant maps about the covariates used in this study. Particularly, the road network (Fig.1), the distribution of water points, divided into natural and artificial, as well as into perennial and seasonal (Fig.2), and the graphical outputs of NDVI calculation for each month (Fig. 3-9).

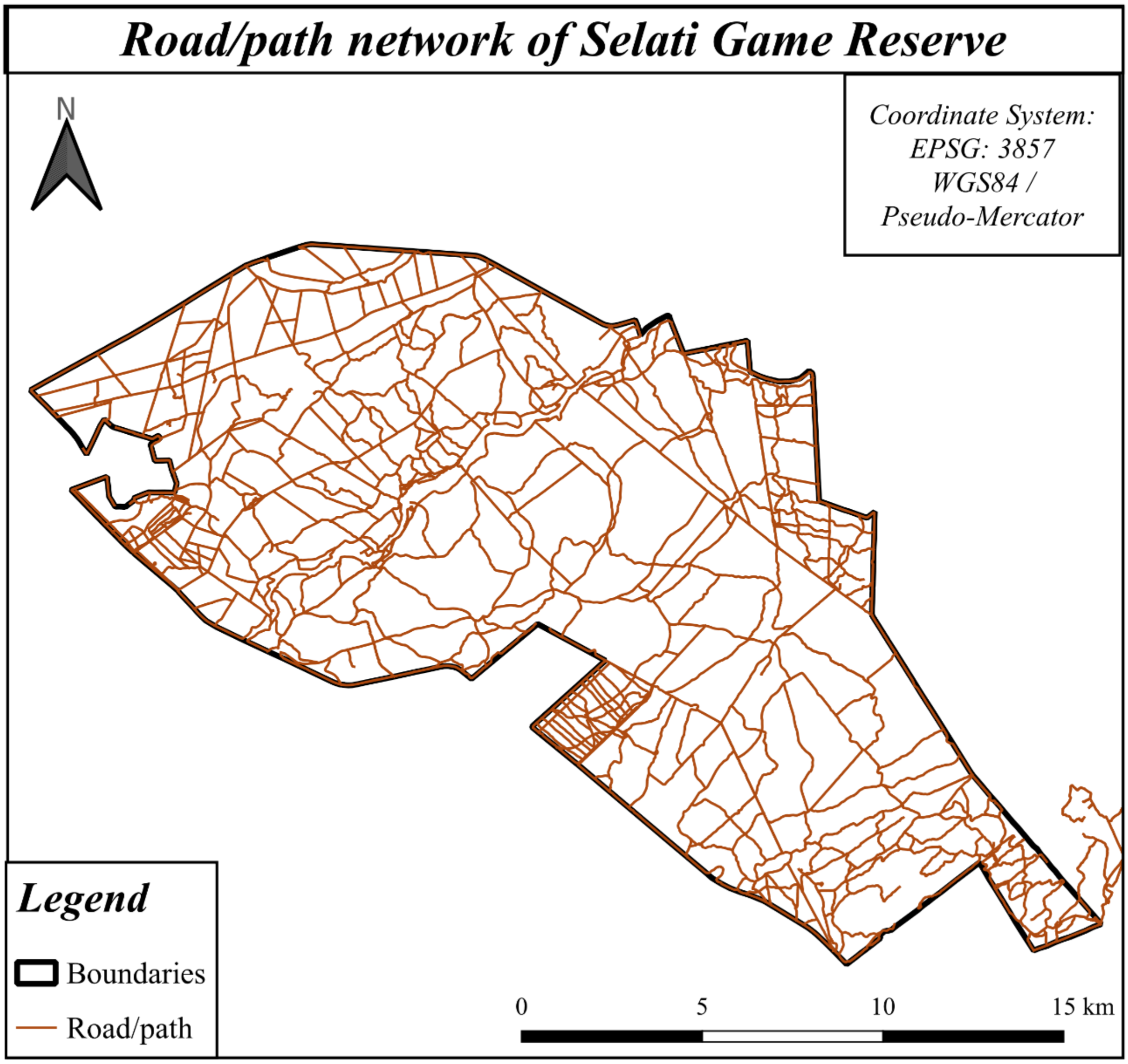

Figure 1. Road/path network of Selati Game Reserve (Created with QGIS Desktop by Zelia Romano).

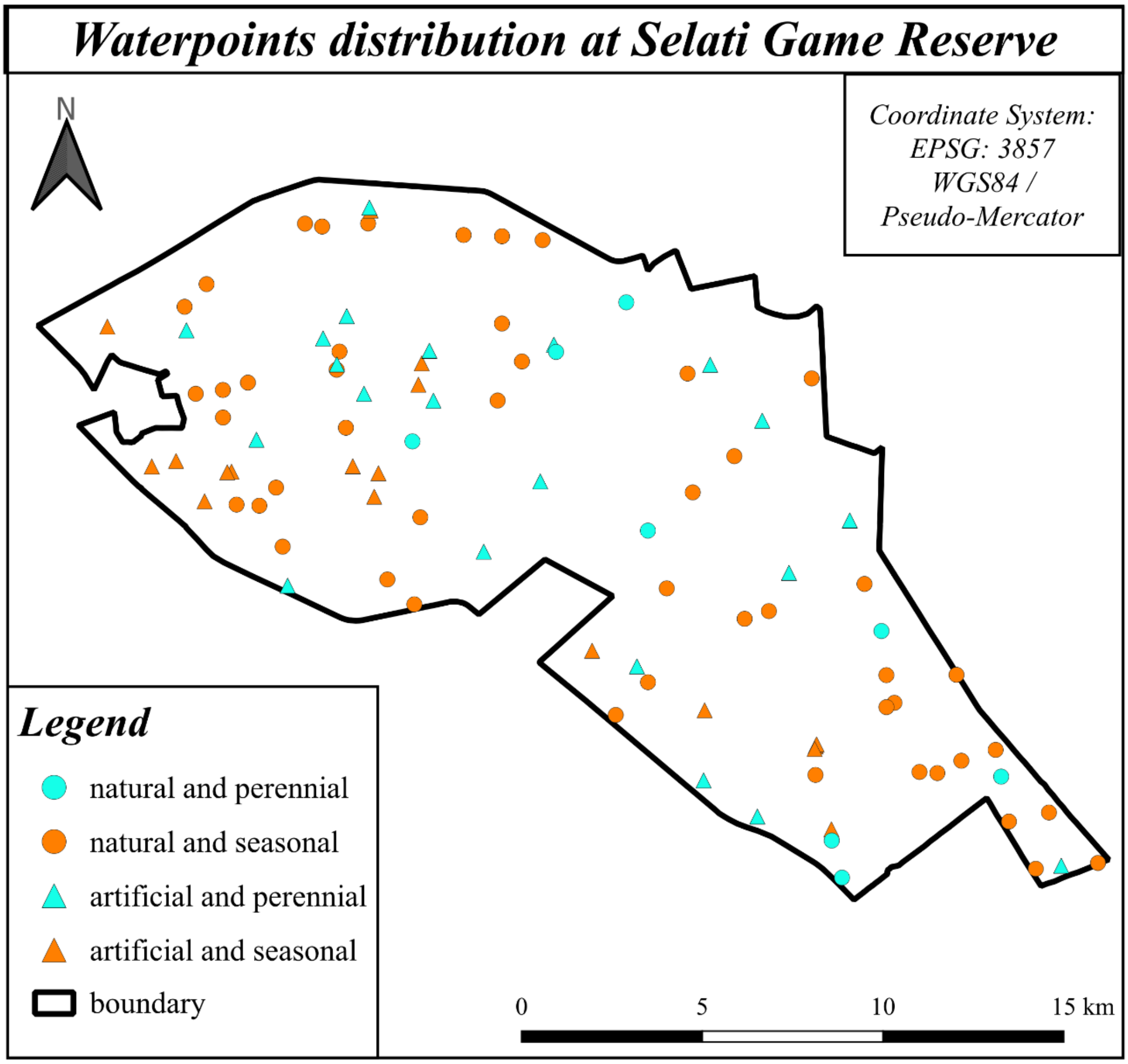

Figure 2. Distribution of all water points present at Selati Game Reserve (Created with QGIS Desktop by Zelia Romano).

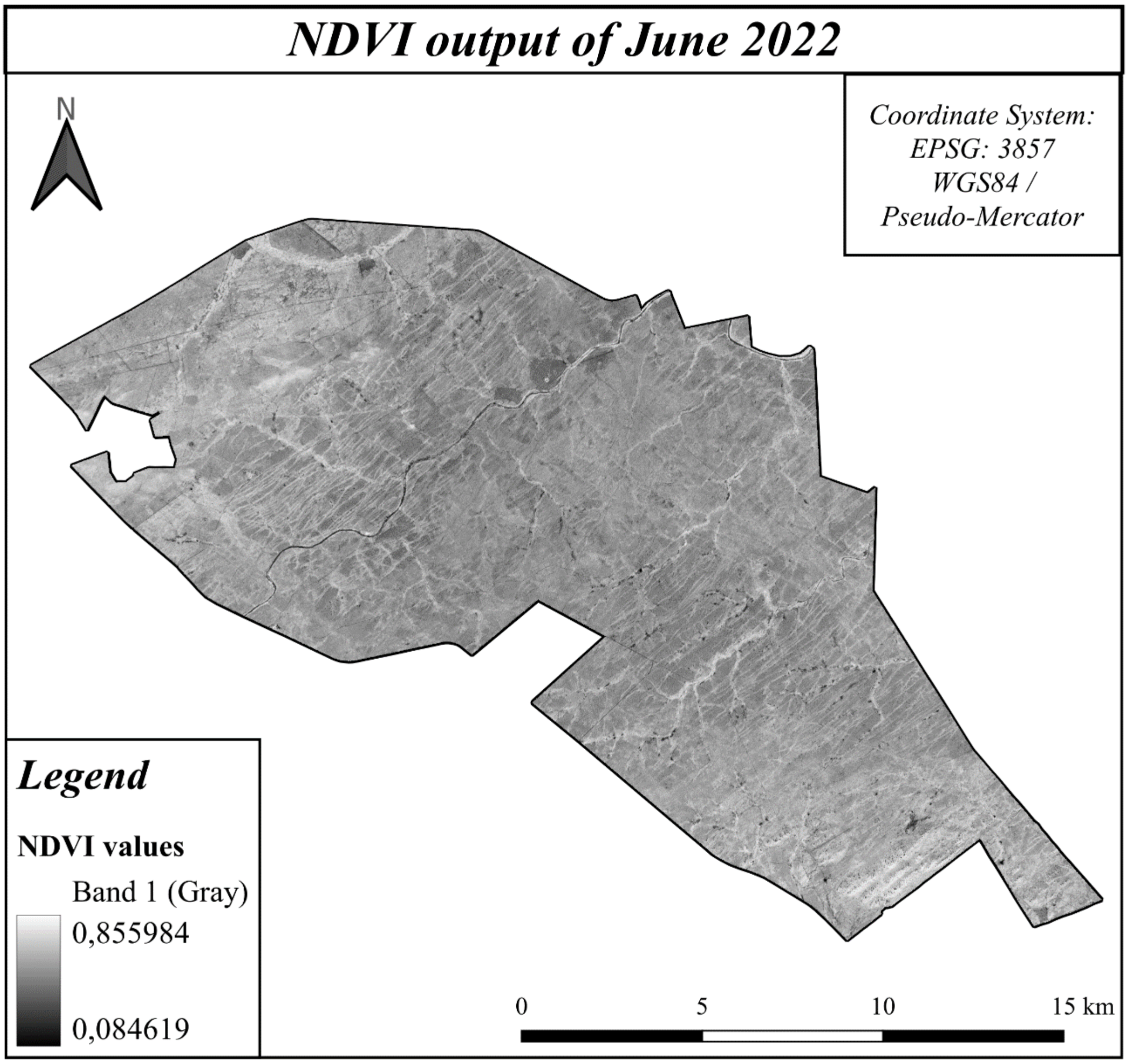

Figure 3. NDVI output for the month of June 2022 (Created with QGIS Desktop by Zelia Romano).

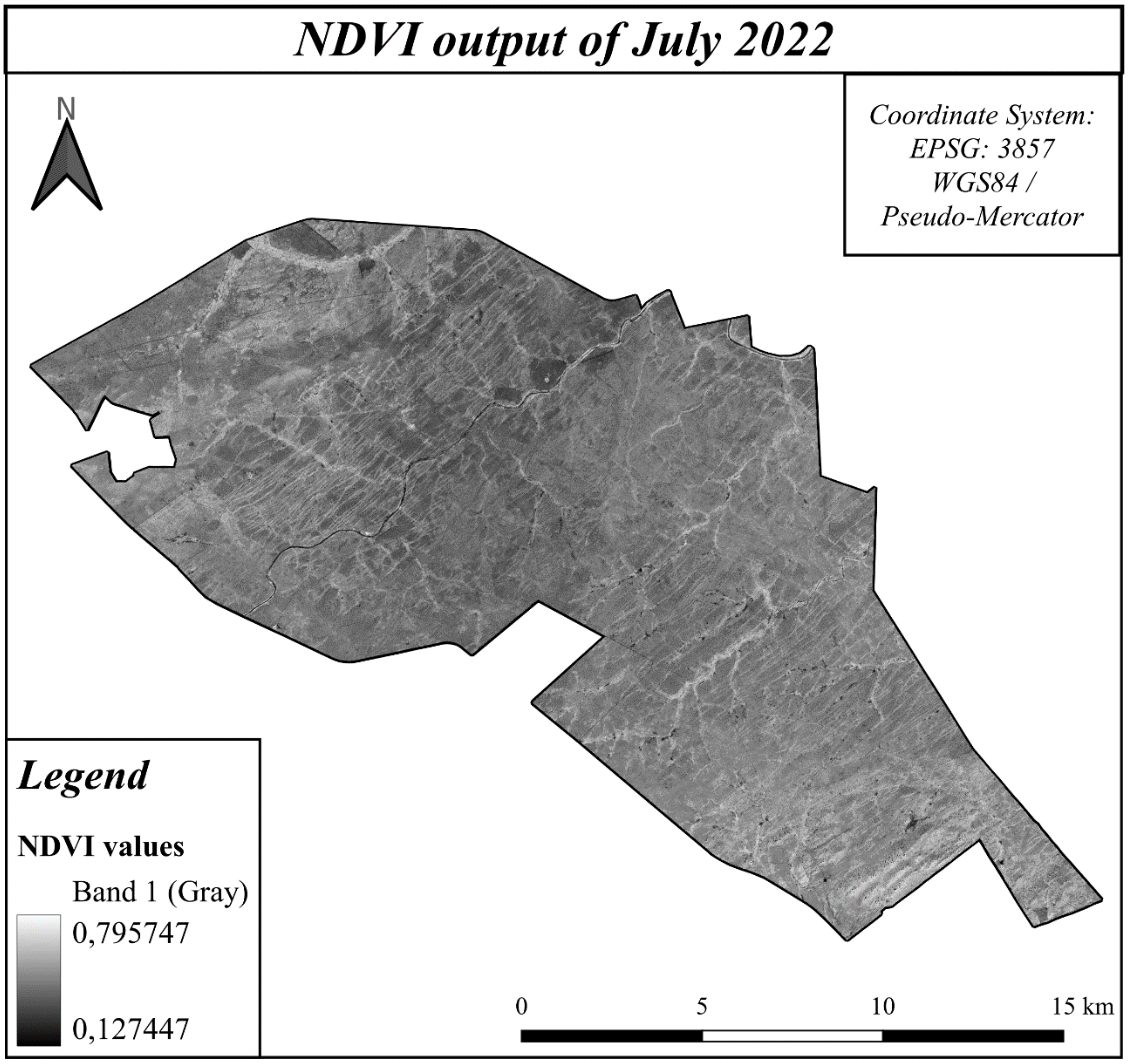

Figure 4. NDVI output for the month of July 2022 (Created with QGIS Desktop by Zelia Romano).

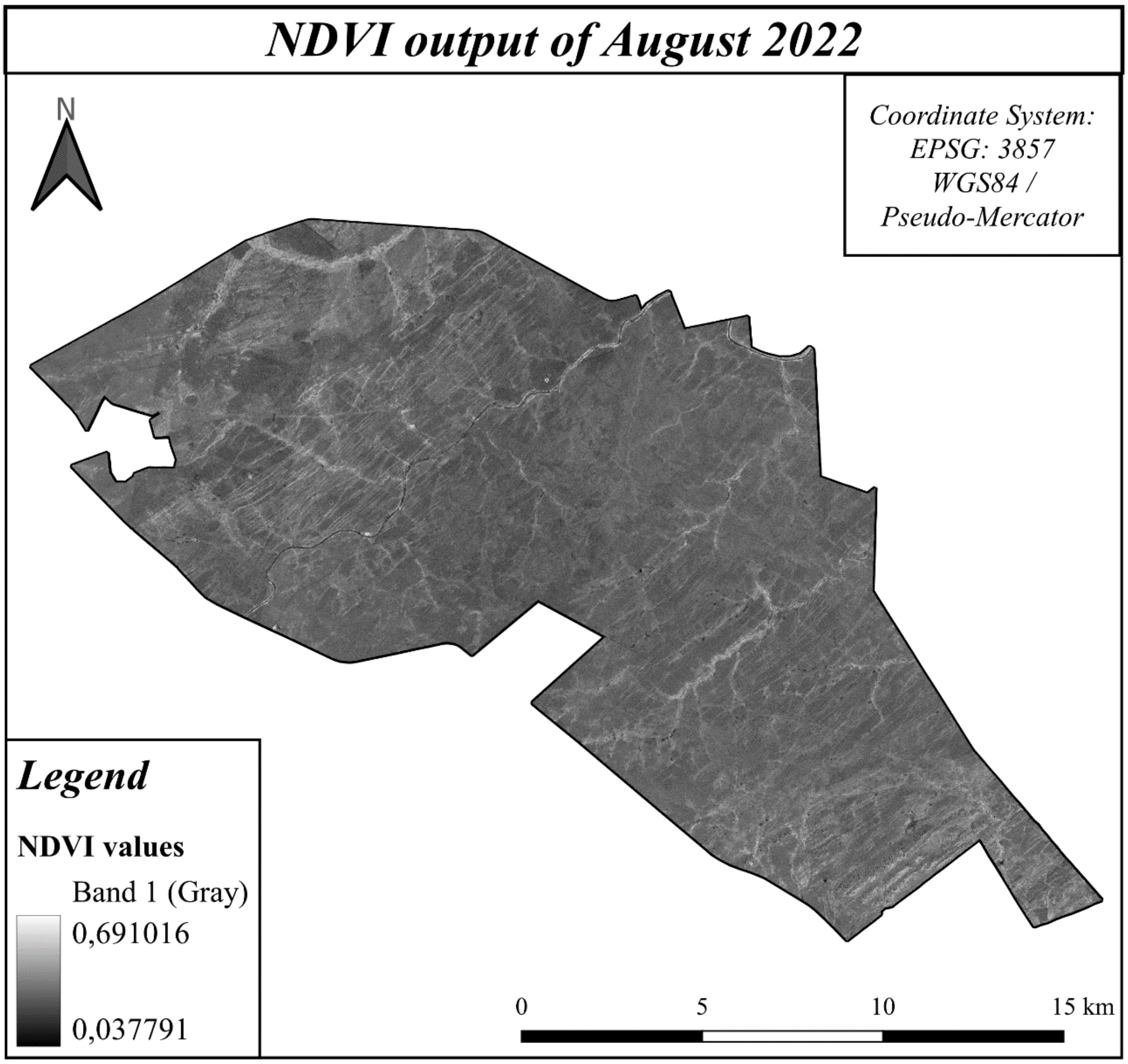

Figure 5. NDVI output for the month of August 2022 (Created with QGIS Desktop by Zelia Romano).

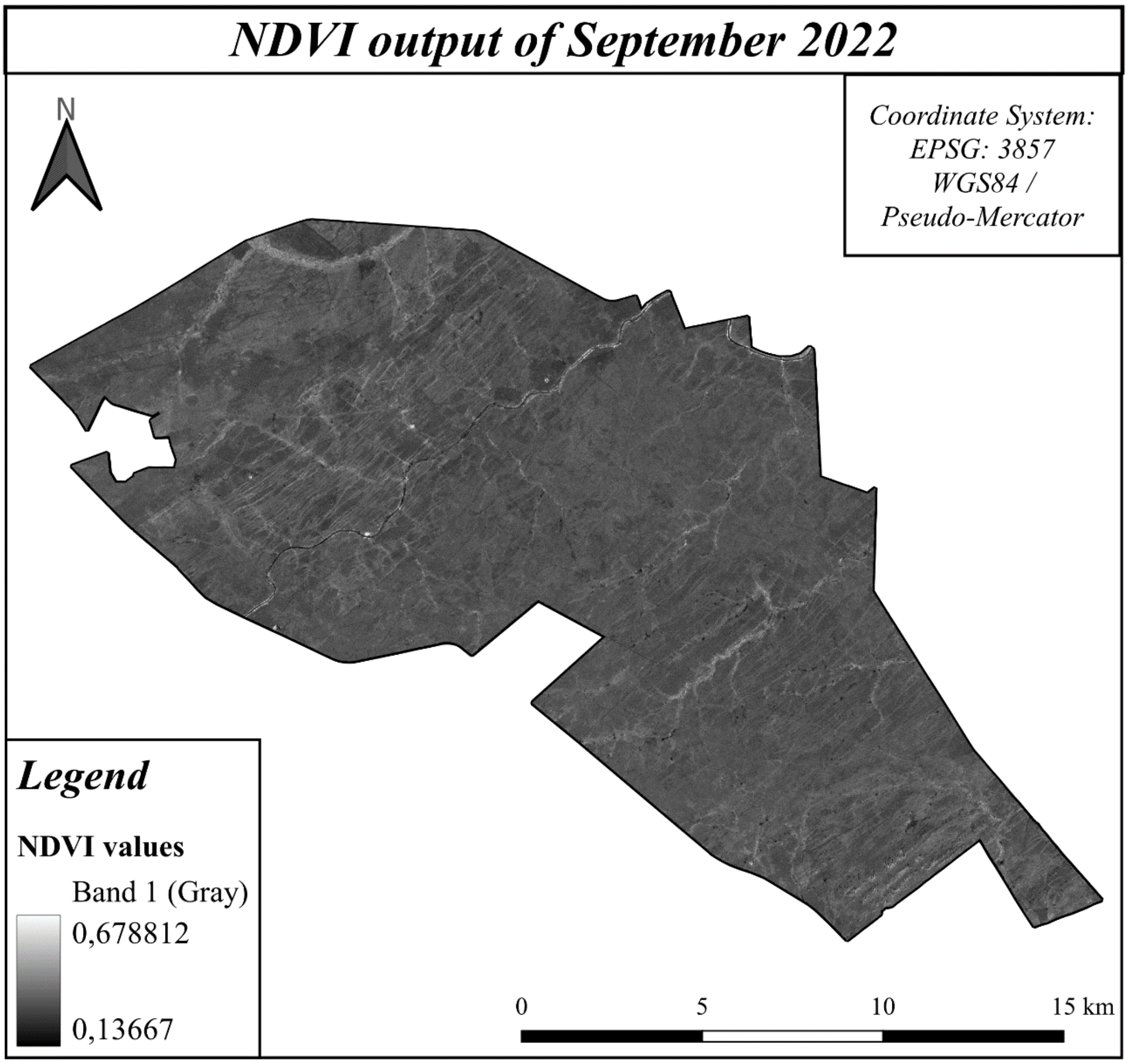

Figure 6. NDVI output for the month of September 2022 (Created with QGIS Desktop by Zelia Romano).

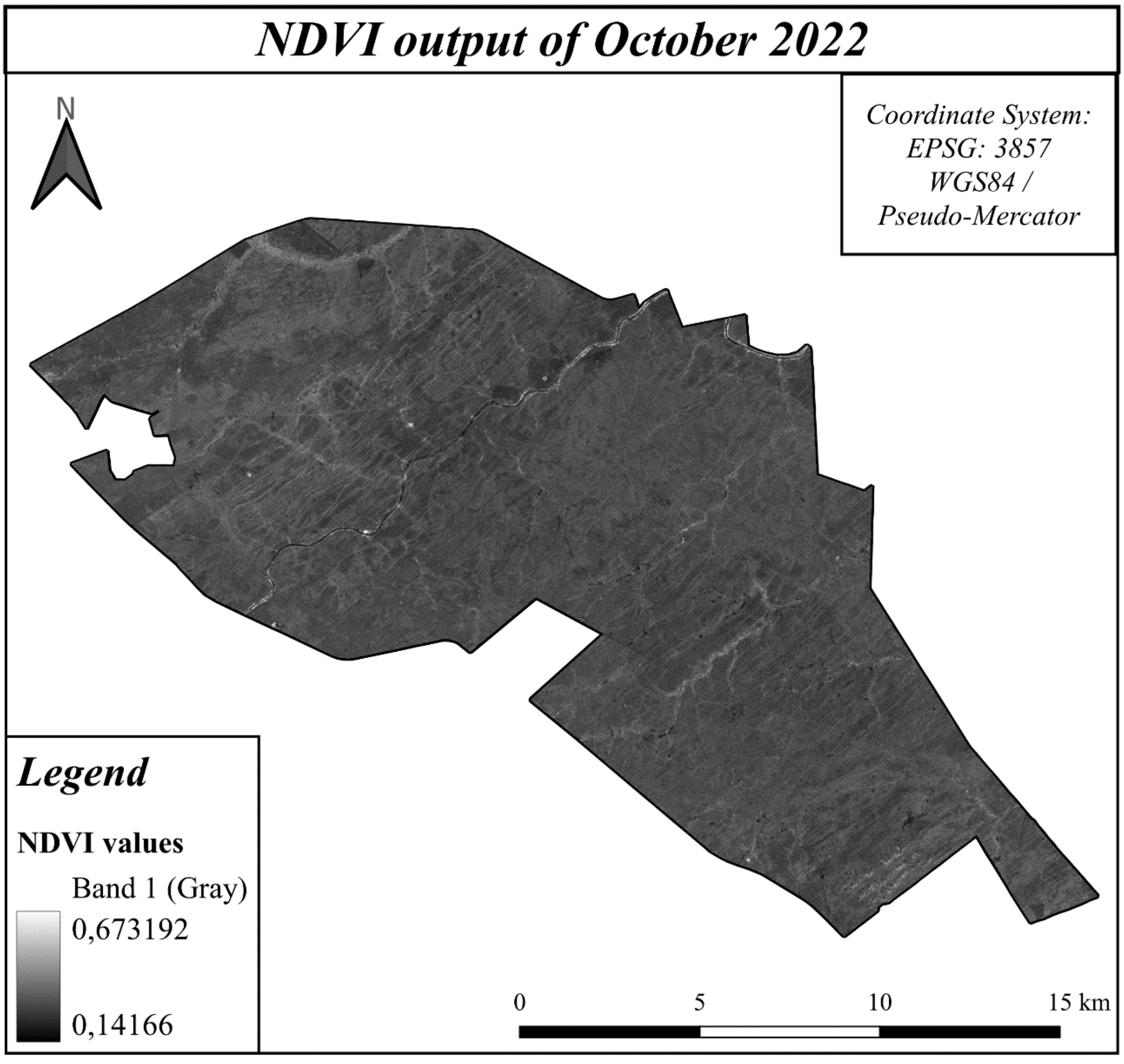

Figure 7. NDVI output for the month of October 2022 (Created with QGIS Desktop by Zelia Romano).

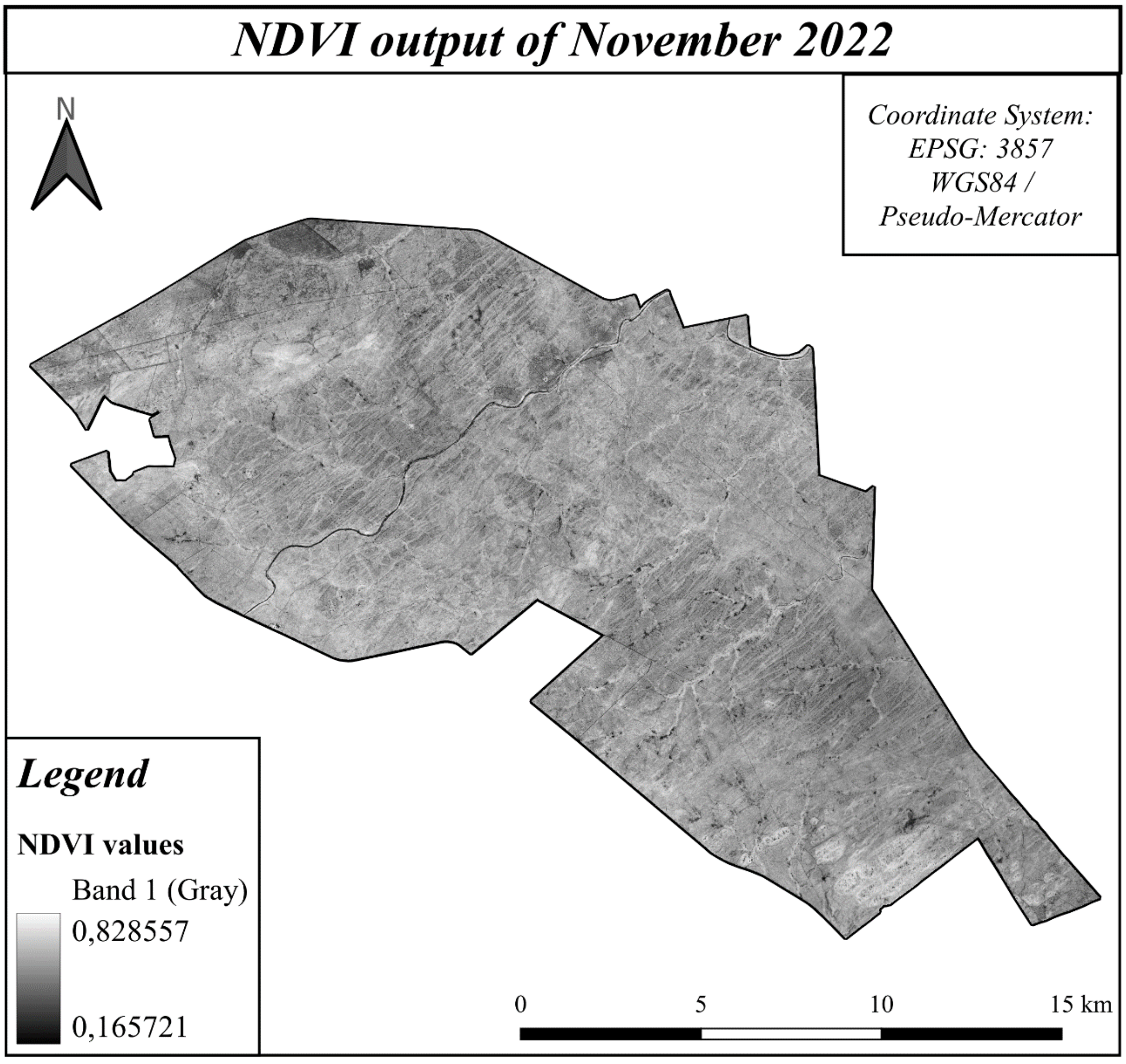

Figure 8. NDVI output for the month of November 2022 (Created with QGIS Desktop by Zelia Romano).

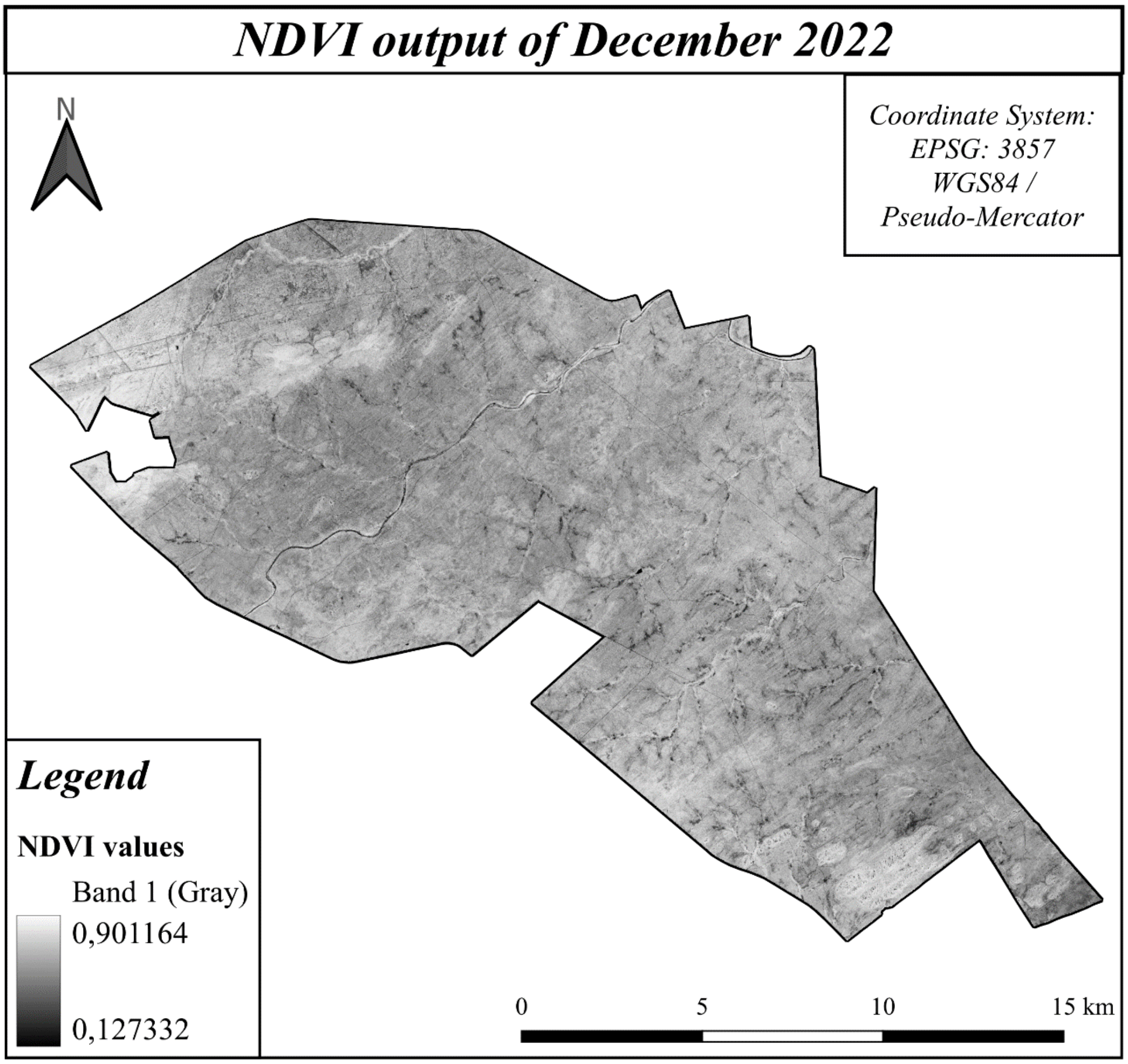

Figure 9. NDVI output for the month of December 2022 (Created with QGIS Desktop by Zelia Romano).

9 APPENDIX III

Here are reported the details of all the satellite images used for performing the NDVI calculation.

Table 1. ID (i.e., tile number), acquisition date, and acquisition time (in UTC) of the satellite images used in this study are reported for each month.

	ID	Acquisition date dd-mm-yyyy	Acquisition time hh:mm:ss
June	3227b58e-eb8f-4390-9d70-f5baf7b3ec5b	17-06-2022	07:43:37 / 07:43:39 07:43:41 / 07:43:43
July	c79f6424-73a3-4685-87a7-39b489900769	14-07-2022	07:26:46 / 07:26:48 07:57:54 / 07:57:56
August	58a06dbb-319c-494d-b3e0-89d86c94a969	18-08-2022	07:11:43 / 07:11:46 07:57:05 / 07:57:07
September	347489d1-722f-42c5-9b0c-708a7675dca9	16-09-2022	07:42:16 / 07:42:19 07:42:21/ 07:43:59 07:44:01
October	e0e2792a-4ec3-4458-b881-245886b2f102	04-10-2022	07:07:26 / 07:07:28 07:30:08 / 07:30:10 07:52:39 / 07:52:41 07:52:43
November	e03daeaf-eeda-461a-8a95-e99f8bfac69b	17-11-2022	07:09:17 / 07:09:19 07:11:52 / 07:11:54 07:40:45 / 07:40:47
December	e2fbc078-3e0d-4ec1-a031-acd44302ddb2	24-12-2022	07:08:29 / 07:08:31 07:09:32 / 07:41:27 07:41:29

Table 2. Satellite ID, Satellite orbit number, Product level, Product type, Asset type are showed for each month in this table.

	Satellite ID	Satellite orbit number	Product level	Product type	Asset type
June	248f 2484	34, 65 37	3B	Analytic MS	ortho_analytic_4b_sr ortho_analytic_4b_xml ortho_udm2
July	2262 240c	45, 73 09, 38	3B	Analytic MS	ortho_analytic_4b_sr ortho_analytic_4b_xml ortho_udm2
August	2432 240a	83, 13 29, 50	3B	Analytic MS	ortho_analytic_4b_sr ortho_analytic_4b_xml ortho_udm2
September	249a 2483	88, 16, 44 50, 79	3B	Analytic MS	ortho_analytic_4b_sr ortho_analytic_4b_xml ortho_udm2
October	2447 2251 2424	42, 70 07, 35 17, 46, 75	3B	Analytic MS	ortho_analytic_4b_sr ortho_analytic_4b_xml ortho_udm2
November	245c 241f 2461	47, 62 48, 81 09, 44	3B	Analytic MS	ortho_analytic_4b_sr ortho_analytic_4b_xml ortho_udm2
December	2451 241e 2480	30, 62 24 27, 41	3B	Analytic MS	ortho_analytic_4b_sr ortho_analytic_4b_xml ortho_udm2

10 APPENDIX IV

Maps of Elza's (Fig. 1-8) and Jean's (Fig. 9-14) tracks are showed below, each map referring to a different month.

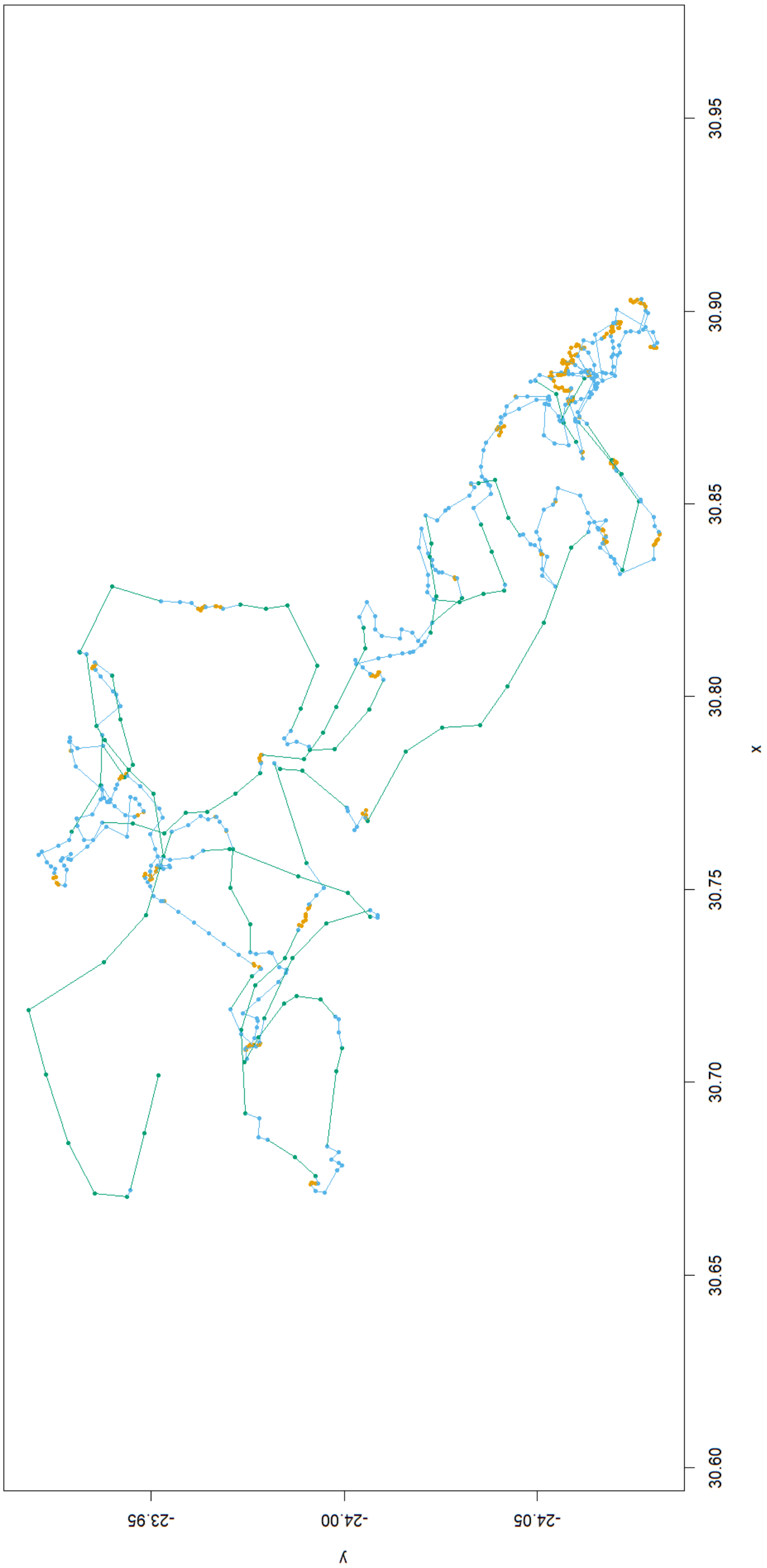

Figure 1. Elza's tracks in June 2022. State 1 = orange; state 2= blue; state 3= green.

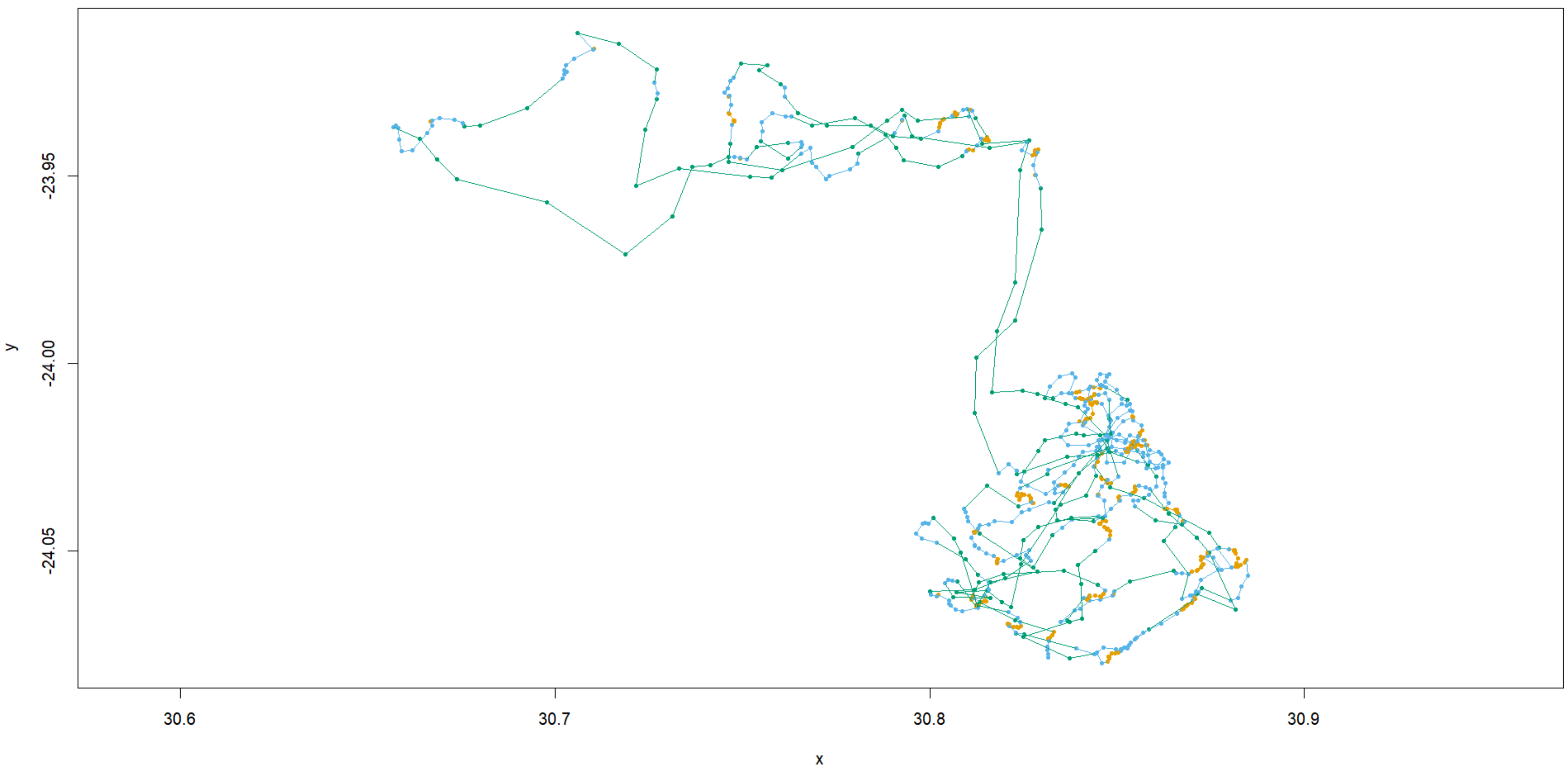

Figure 2. Elza’s tracks in July 2022. State 1 = orange; state 2= blue; state 3= green.

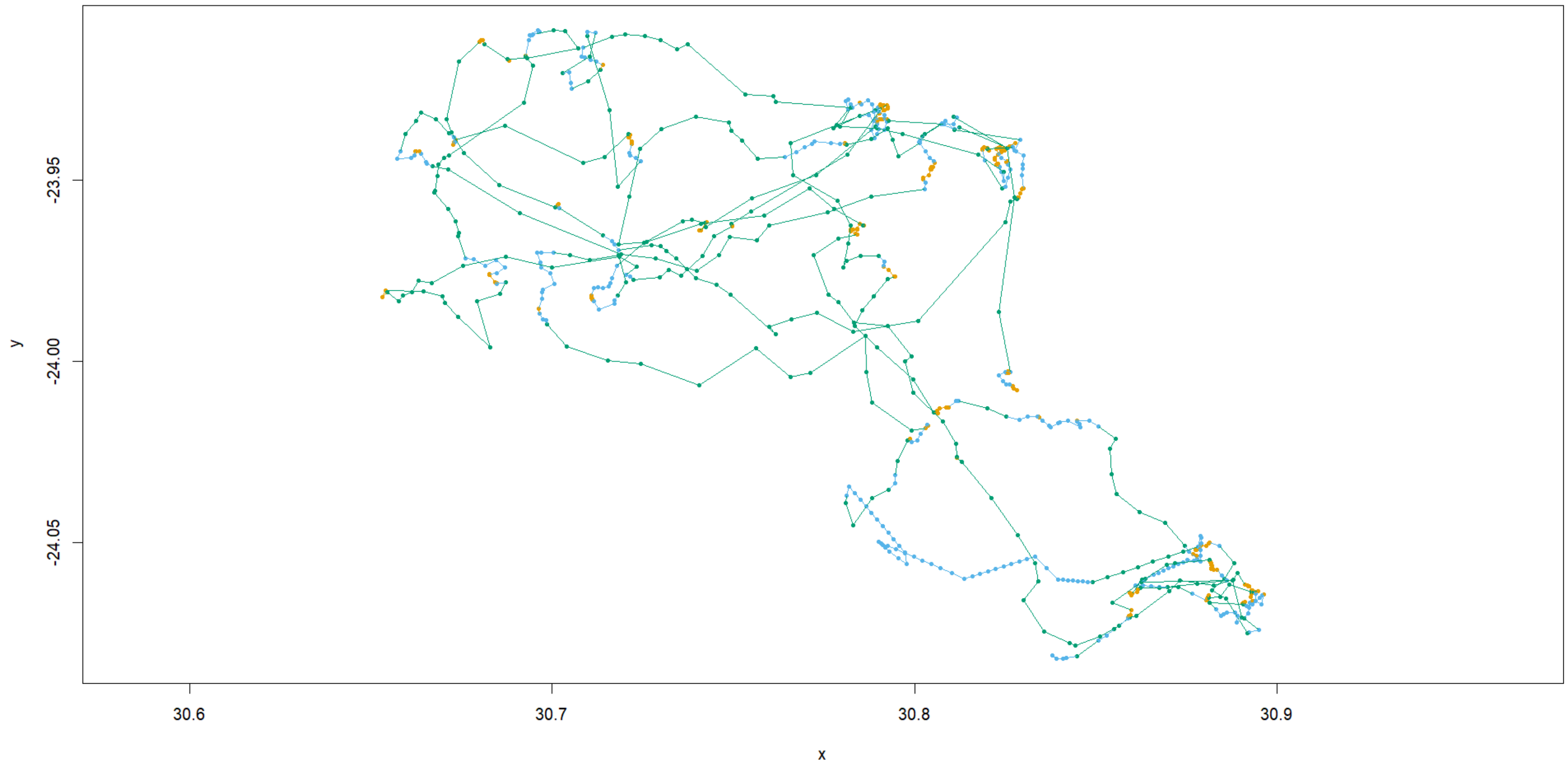

Figure 3. Elza's tracks in August 2022. State 1 = orange; state 2= blue; state 3= green.

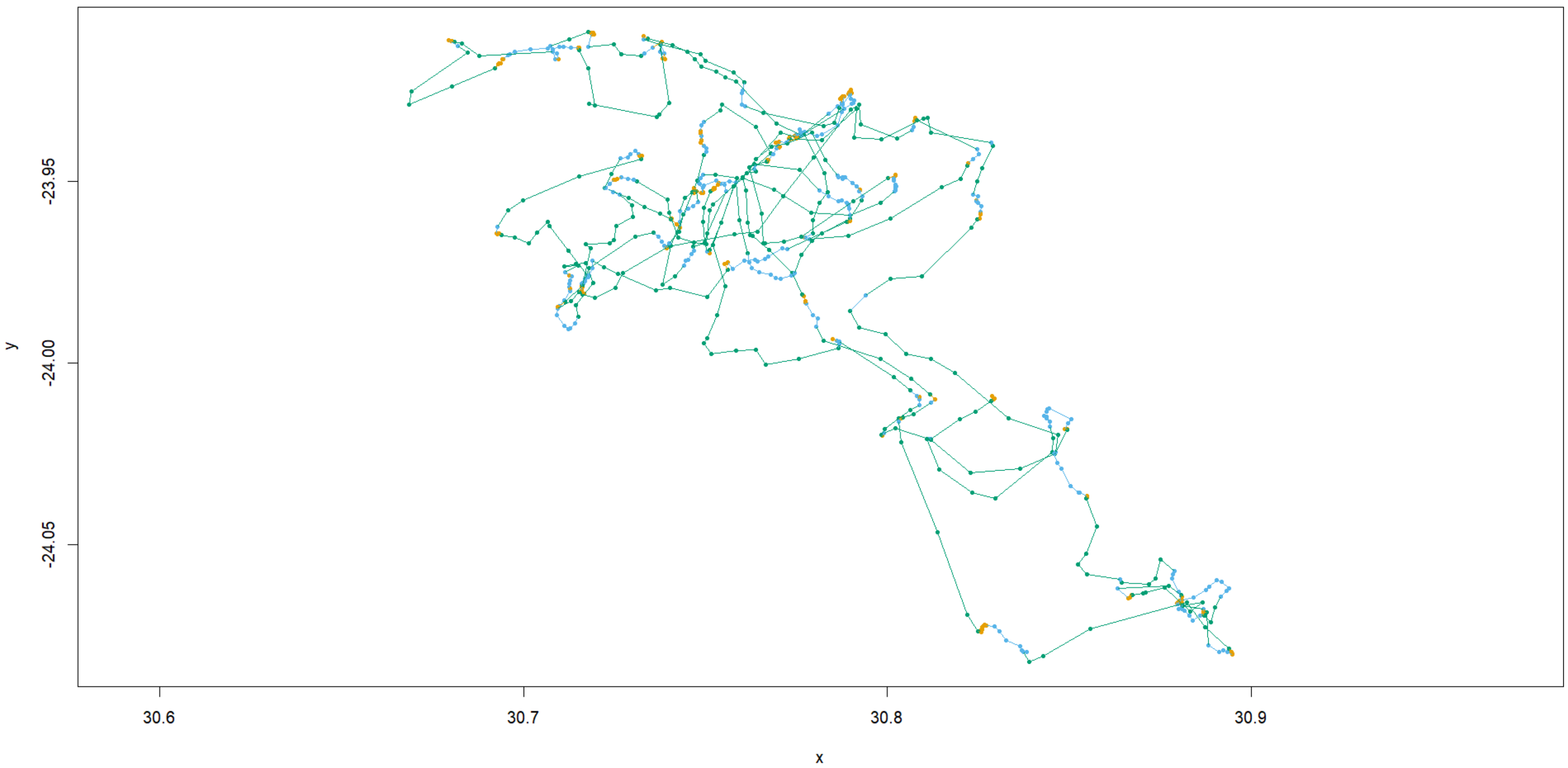

Figure 4. Elza’s tracks in September 2022. State 1 = orange; state 2= blue; state 3= green.

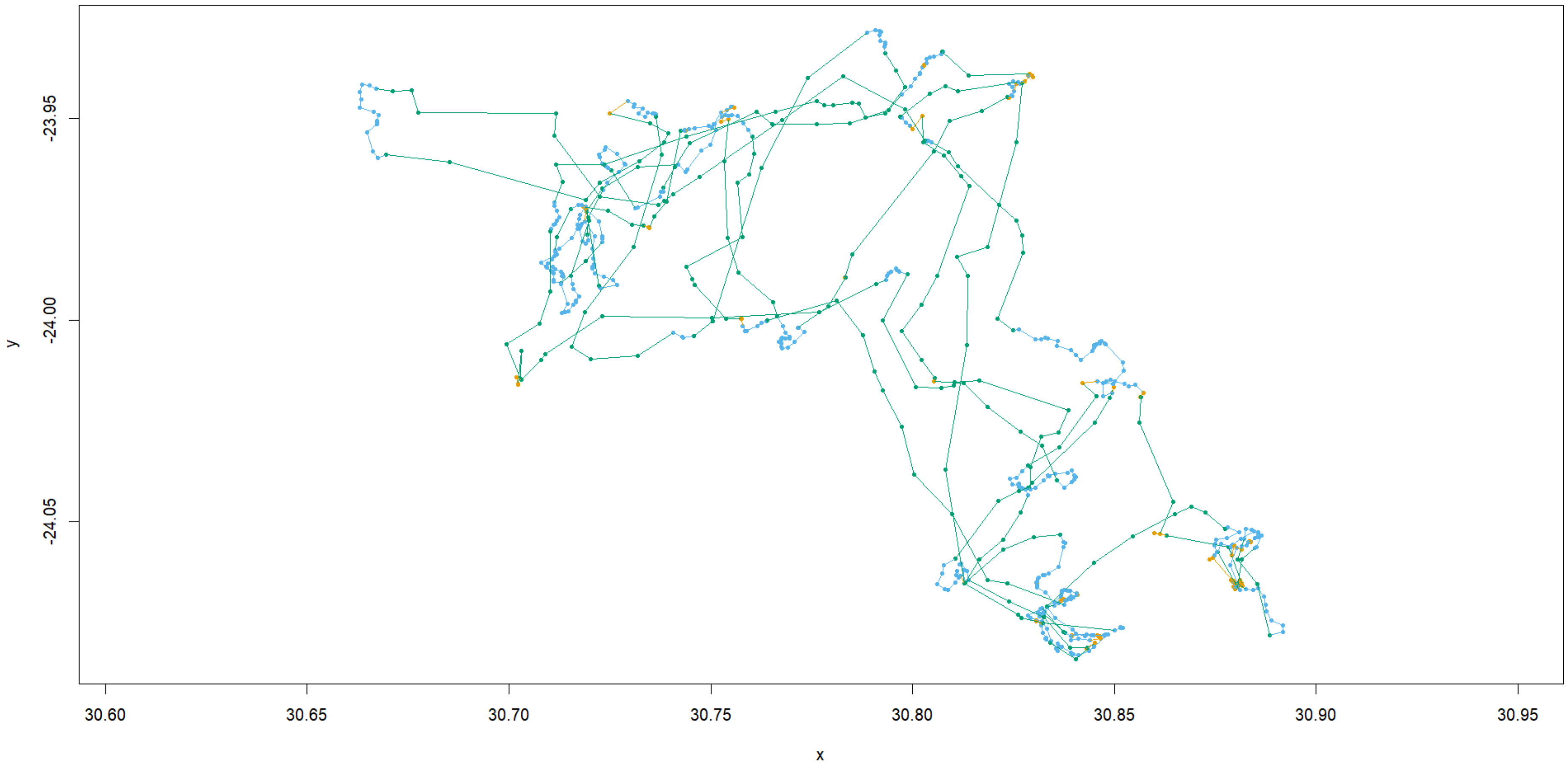

Figure 5. Elza's tracks in October 2022. State 1 = orange; state 2= blue; state 3= green.

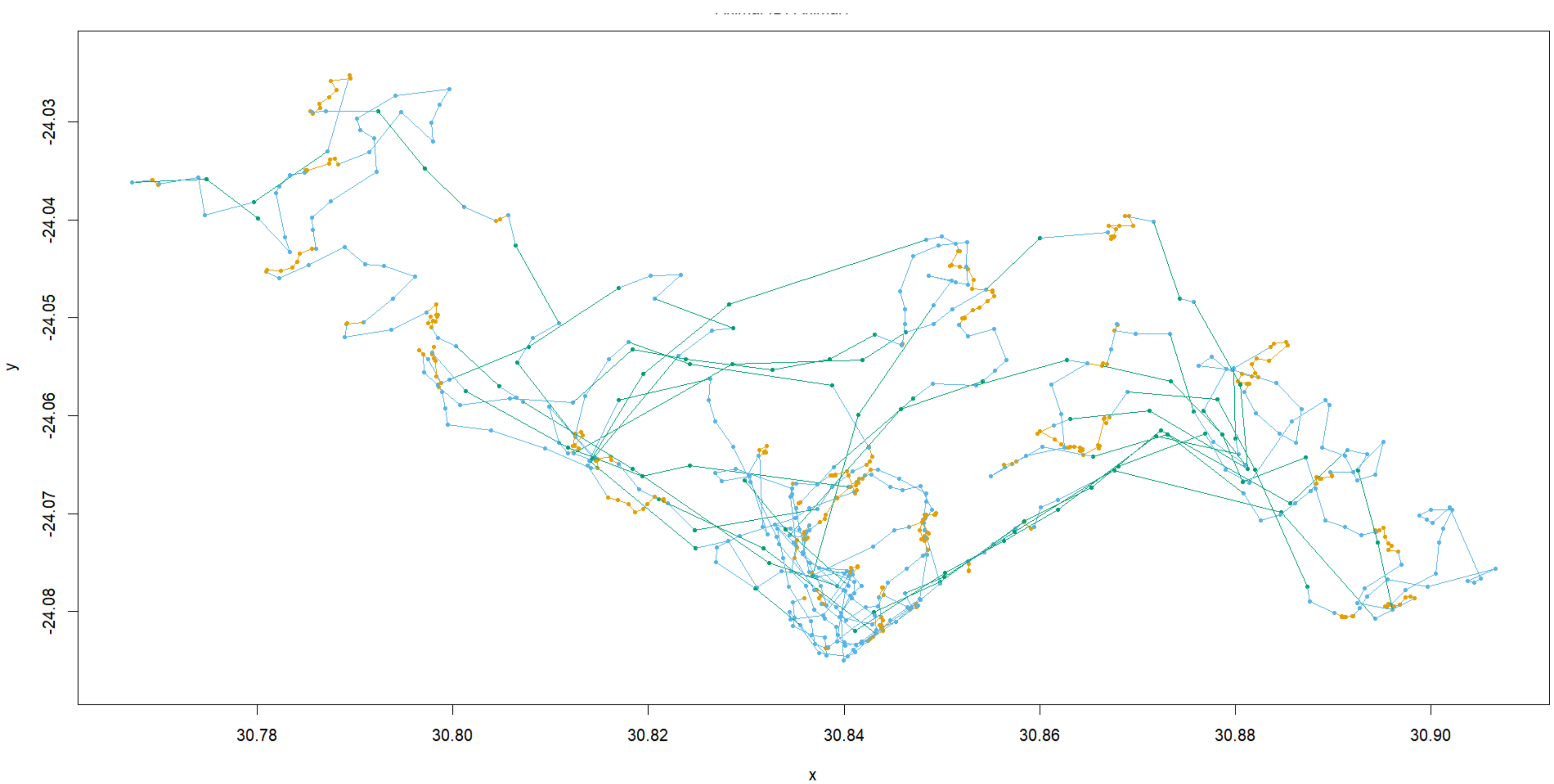

Figure 6. Elza’s tracks in November 2022. State 1 = orange; state 2= blue; state 3= green.

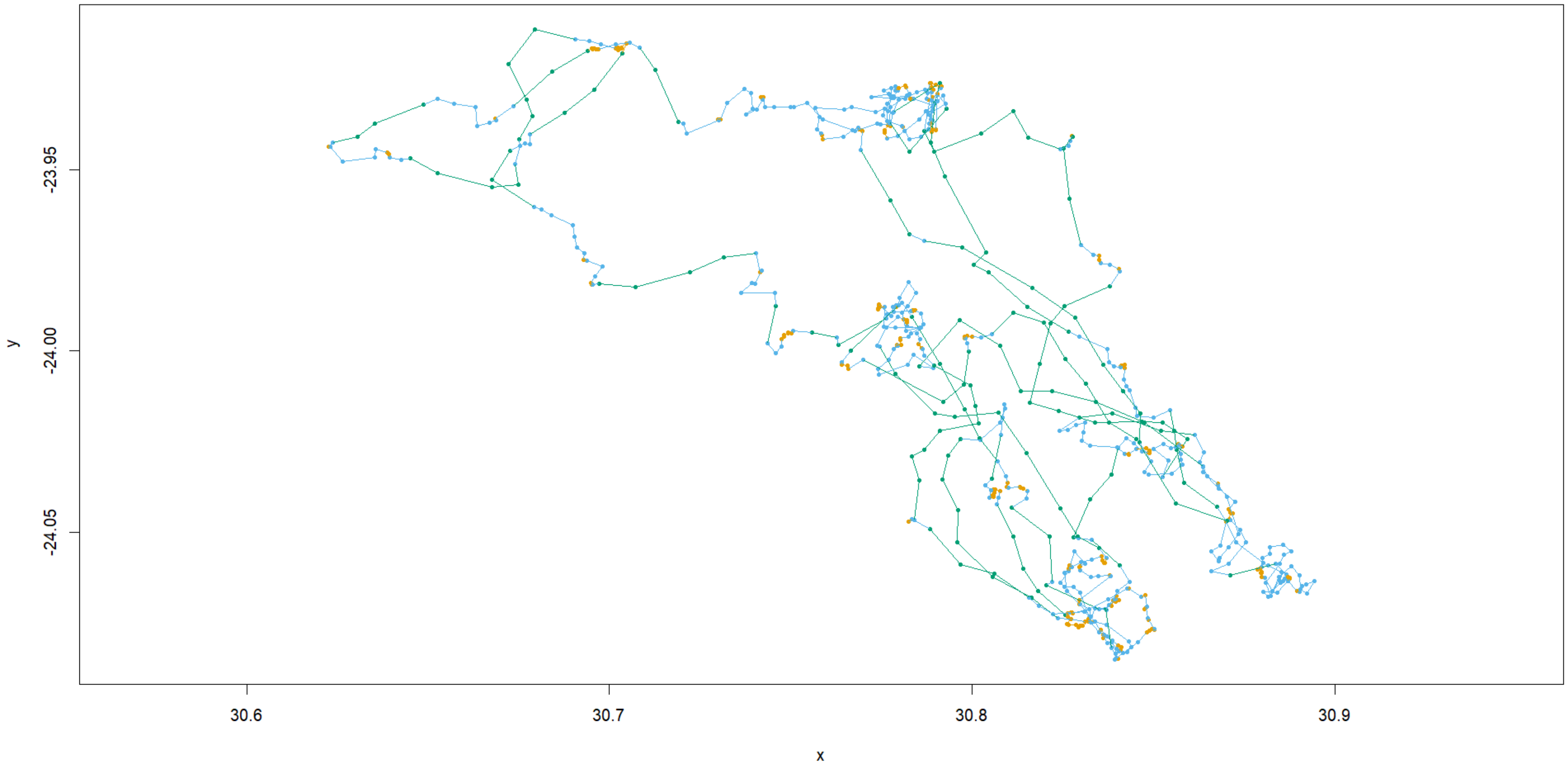

Figure 7. Elza's tracks in December 2022. State 1 = orange; state 2= blue; state 3= green.

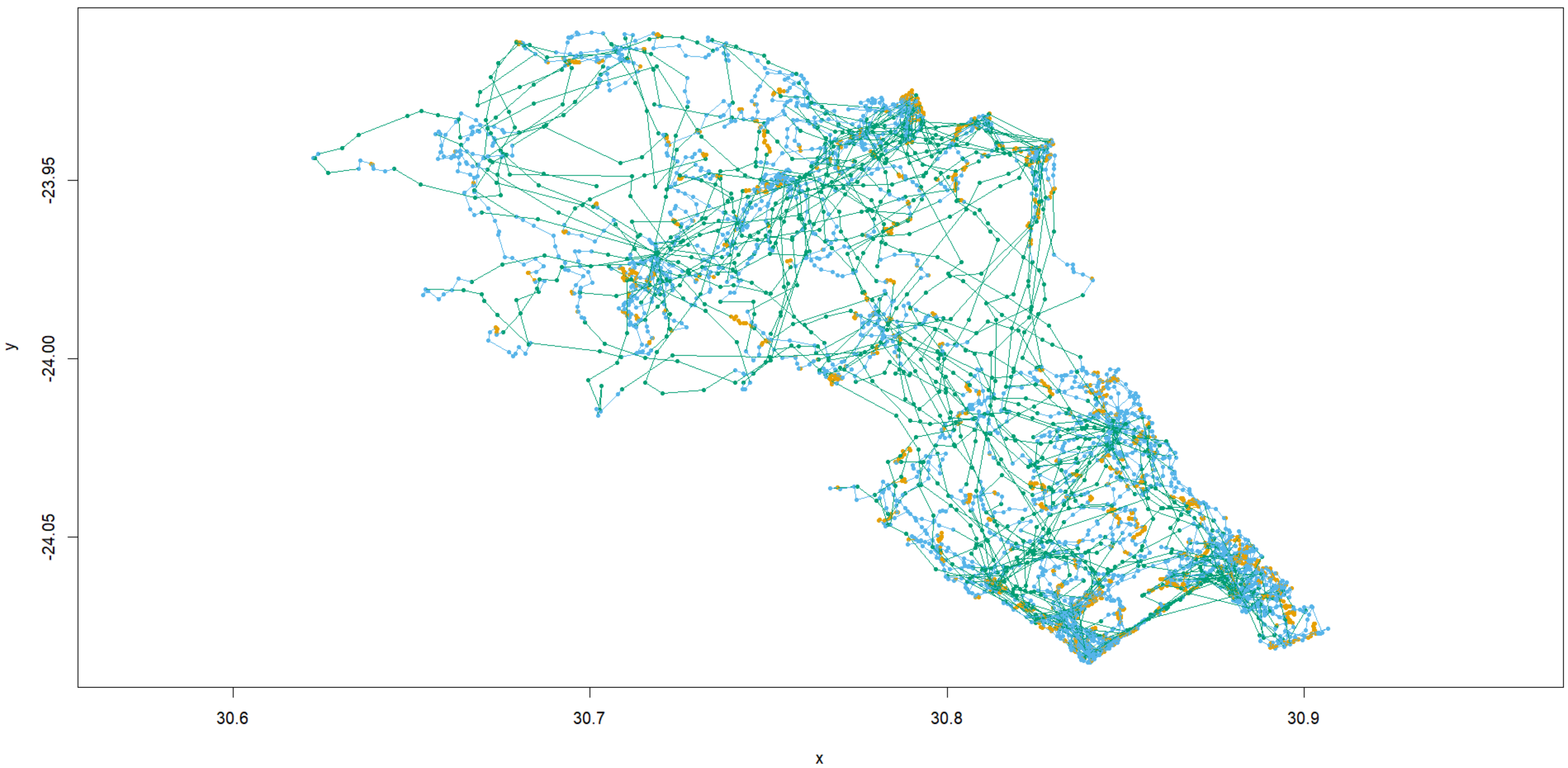

Figure 8. Elza's tracks from the 1st of June to the 31st of December 2022. State 1 = orange; state 2= blue; state 3= green.

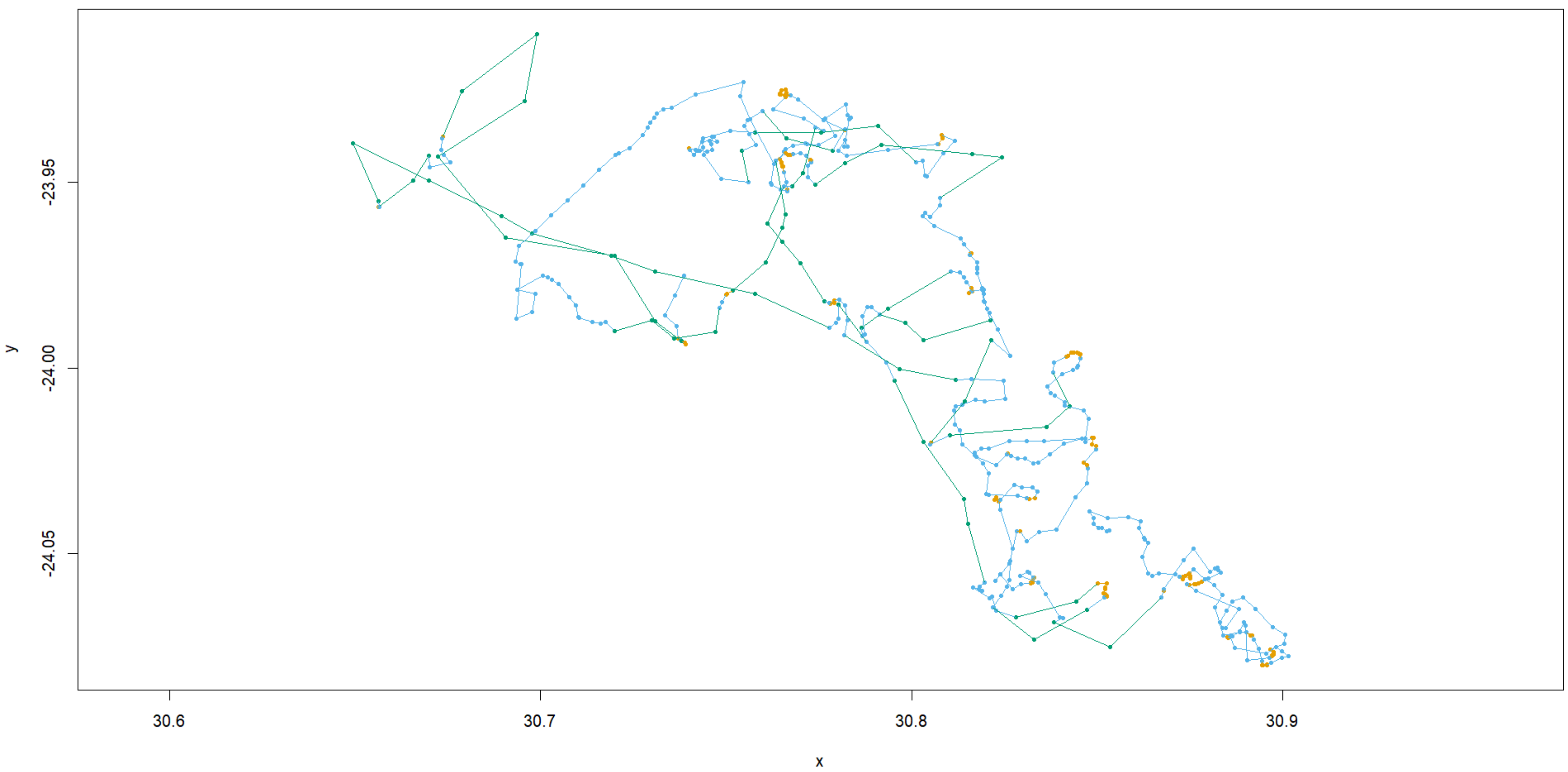

Figure 9. Jean's tracks in June 2022. State 1 = orange; state 2= blue; state 3= green.

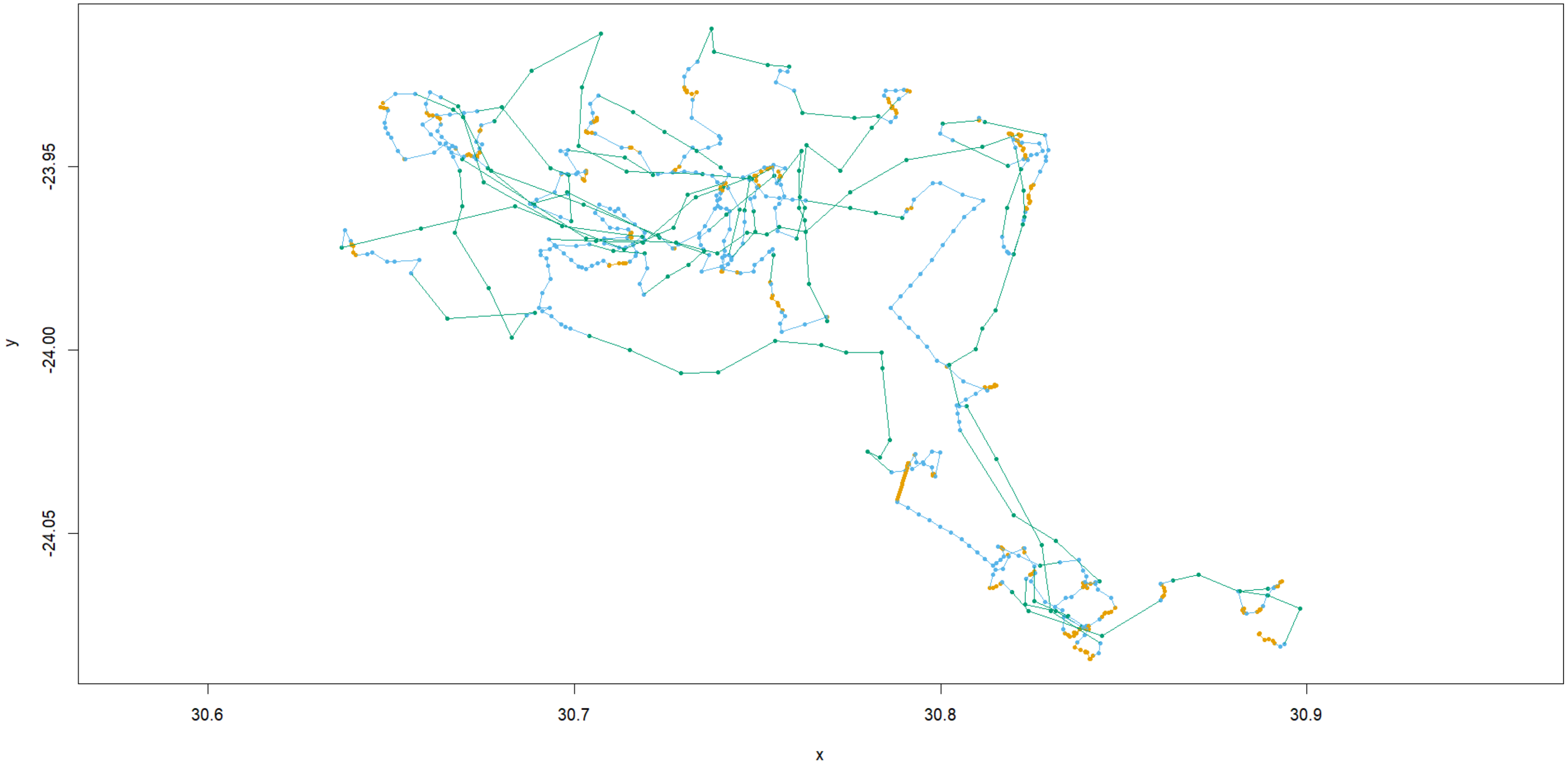

Figure 10. Jean’s tracks in August 2022. State 1 = orange; state 2= blue; state 3= green.

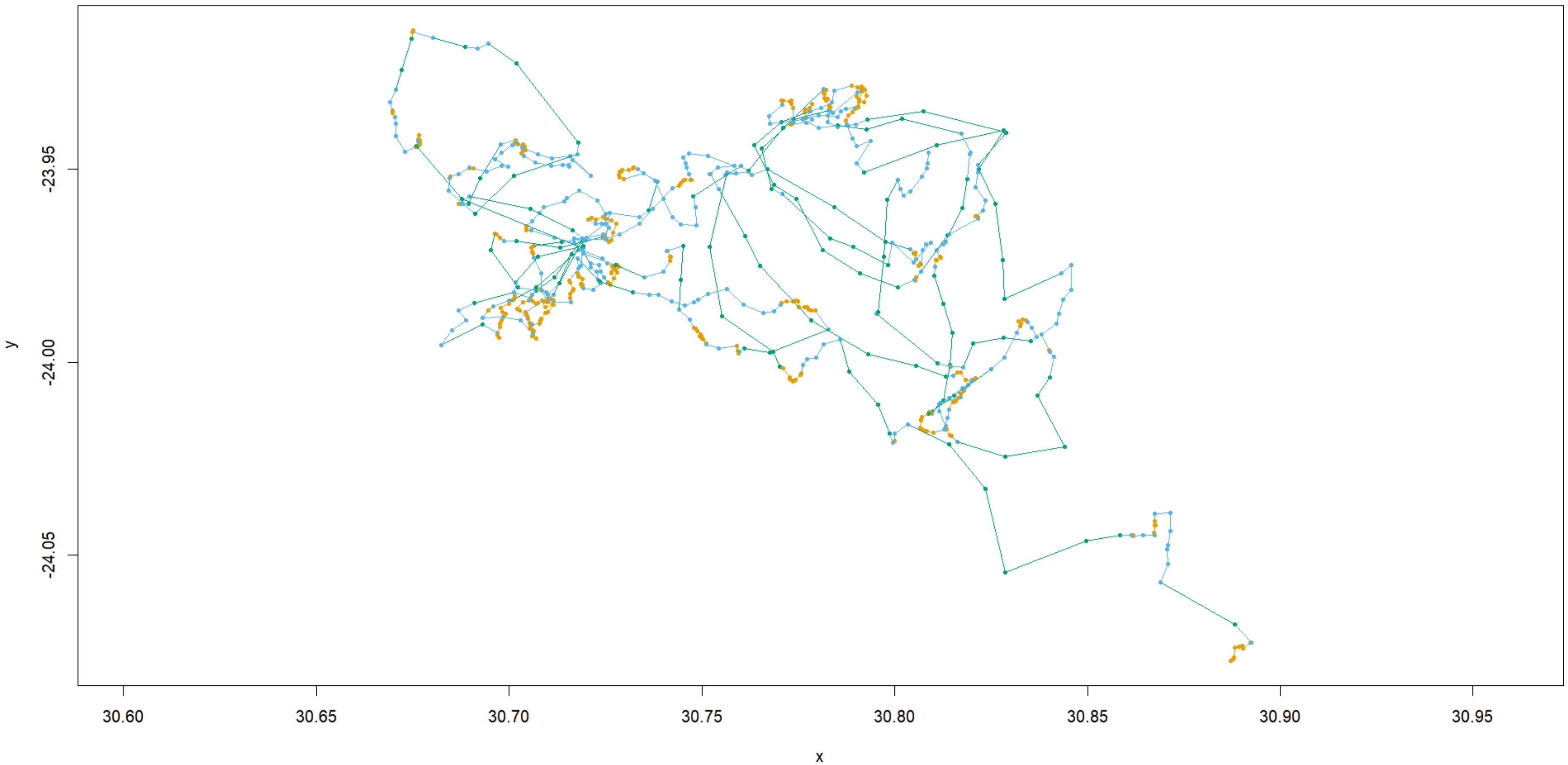

Figure 11. Jean’s tracks in September 2022. State 1 = orange; state 2= blue; state 3= green.

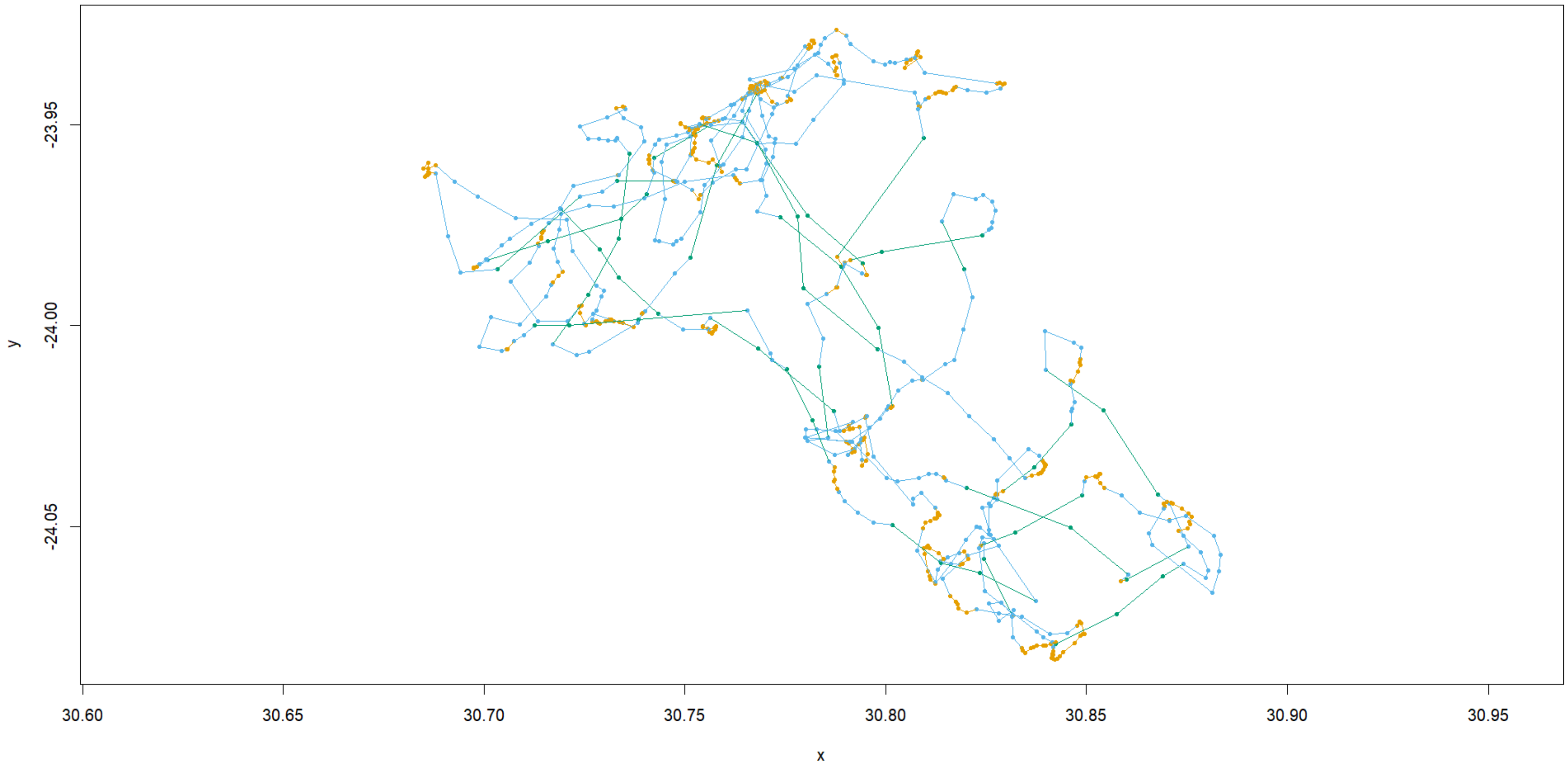

Figure 12. Jean's tracks in October 2022. State 1 = orange; state 2= blue; state 3= green.

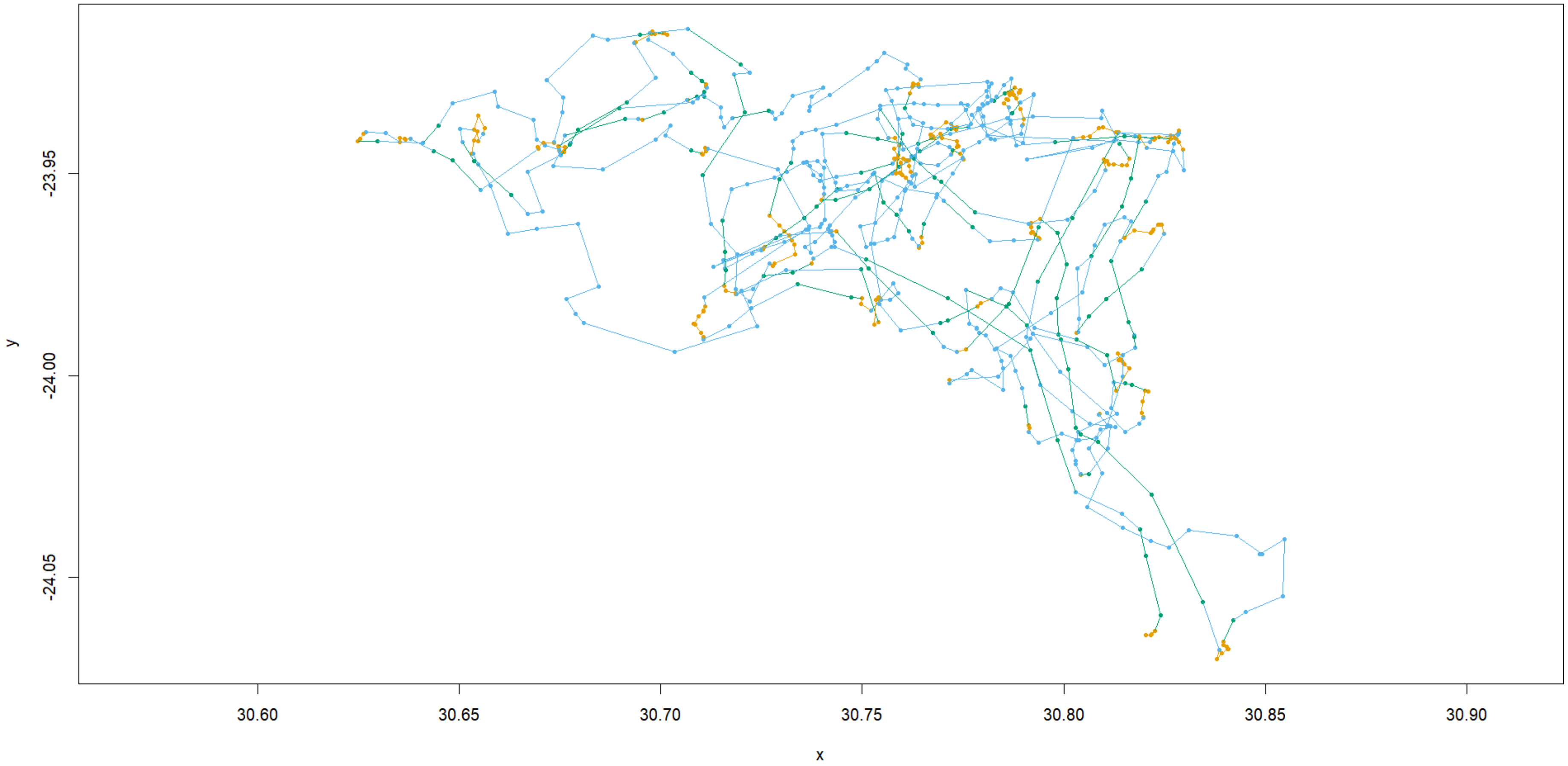

Figure 13. Jean’s tracks in December 2022. State 1 = orange; state 2= blue; state 3= green.

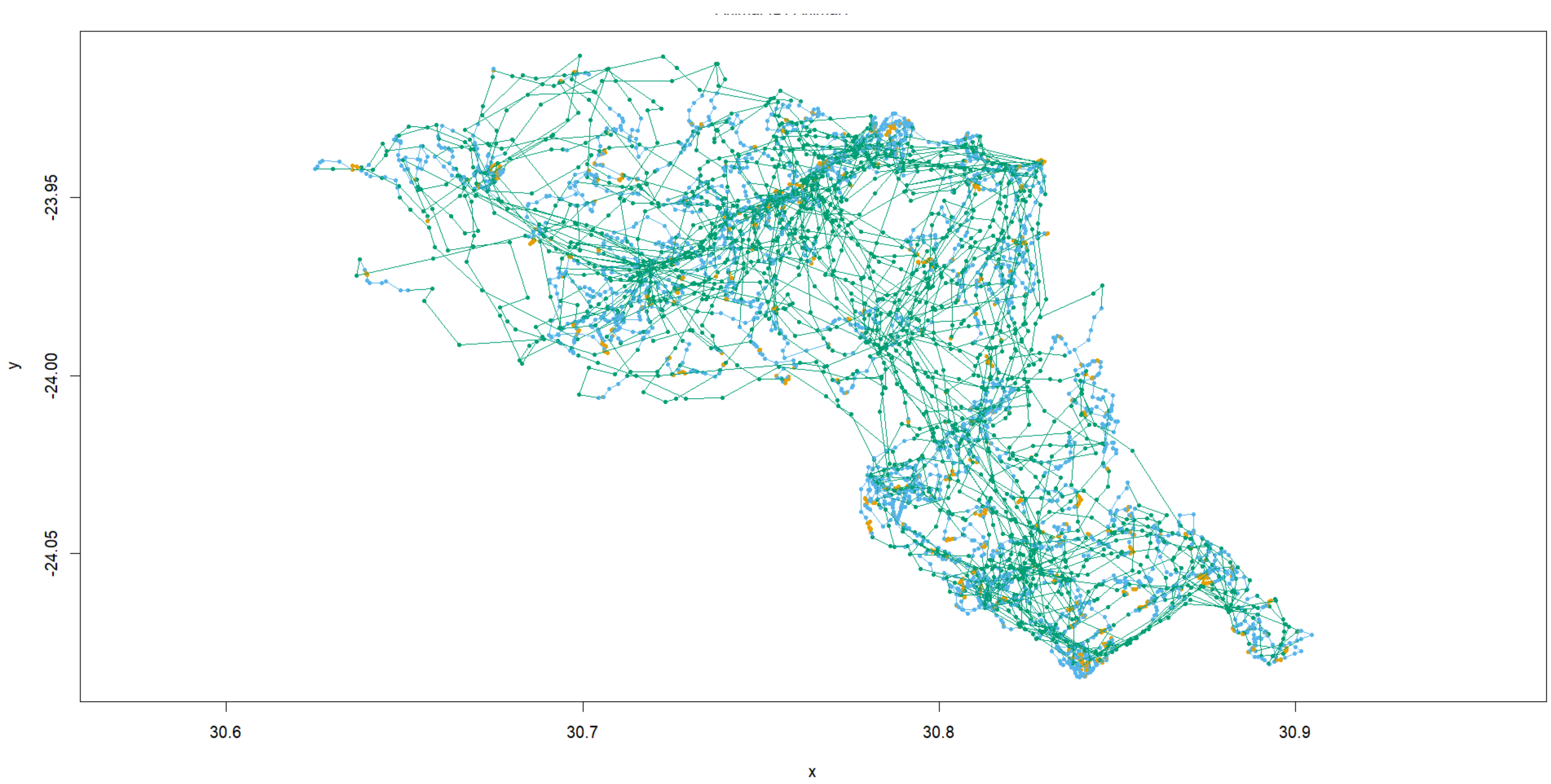

Figure 14. Jean's tracks from the 8th of June to the 31st of December 2022. State 1 = orange; state 2= blue; state 3= green.