What Causes a Locust Swarm: A Hierarchical Patch Dynamics Approach

by

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ABSTRACT

Ecological phenomena act on various spatial and temporal scales. To understand what causes animal populations to build and decline depends heavily on abiotic and biotic conditions which vary spatiotemporally throughout the biosphere. One excellent example of animal populations dynamics is with locusts. Locusts are a subset of grasshoppers that undergo periodical upsurges called swarms. Locust swarms have plagued human history by posing significant threats to global food security. For example, the 2003-2005 desert locust (*Schistocerca gregaria*) swarm destroyed 80%-100% of crops in the impacted areas and cost over US $500 million in mitigation as estimated by the Food and Agriculture Organization of the United Nations. An integrative multi-scale approach must be taken to effectively predict and manage locust swarms. For my dissertation, I looked at the ecological causes of locust swarms on multiple scales using both the Australian plague locust (*Chortoicetes terminifera*) and desert locust as focal species. At the microhabitat scale, I demonstrated how shifts in the nutritional landscape can influence locust gregarization. At the field level, I show that locust populations avoid woody vegetation likely due to the interactive effect of plant nutrients, temperature, and predators. At the landscape level, I show that adaptations to available nutrient variation depends on life history strategies, such as migratory capabilities. A strong metapopulation structure may aid in the persistence of locust species at larger spatial scales. Lastly, at the continental scale I show the relationship between preceding vegetation and locust outbreaks vary considerably between regions and seasons. However, regardless of this variation, the spatiotemporal structure of geographic zone > bioregion > season holds constant in two locust species. Understanding the biologically relevant spatial and temporal scales from individual gregarization (e.g. micro-habitat) to massive swarms (e.g. landscape to continental) is important to accurately predicting where and when outbreaks will happen. Over-

all, my research highlights that understanding animal population dynamics requires a multi-scale and trans-disciplinary approach. Into the future, integrating locust research from organismal to landscape levels can aid in forecasting where and when locust outbreaks occur.

DEDICATION

To Caitlin, beers, and inquiries

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PREFACE

At the turn of the 20th century, a swarm of Rocky Mountain locusts (*Melanoplus spretus*, Walsh, 1866) moved across the western United States, resulting in the largest locust swarm ever recorded in history (Lockwood, 2001). Many western settlers recounted five days of darkness as the locust plague blocked the sun; devastating multitudes of crops in its path. Back of the envelope calculations estimate 12-25 trillion individual locusts migrated in the swarm. The devastation of this swarm was not limited to crops; nothing could be protected from the plague. An 1874 report found that only one out of ten families had enough food to survive the following winter (Lockwood, 2004). Despite the severity of this event, the last Rocky Mountain locust was collected in 1902. While locusts no longer inflict damage within the United States, many locust species continue to affect livelihoods globally, further indicating their profoundly interesting dynamics and the need to develop sustainable approaches for their management.

Figure 1: 19th Century Cartoon Depiction of a Locust Swarm in Midwest America. Worrall, Henry. Henry Worrall Collection, 1853-1902, Kansas State Historical Society, Library Collection No. 23

Chapter 1

INTRODUCTION

There has been long withstanding interest in understanding what Evelyn Hutchinson called the Ecological Theater (Hutchinson, 1965) back in the mid-20th century. Hutchinson, along with other early ecologists, paved the way into investigating the complex processes that operate throughout the biosphere, which is the large-scale focus of modern ecology. One of these processes is understanding what regulates animal populations. Early population ecologists identified the importance of bottom-up variables like food availability (Davidson and Andrewartha, 1948; Keith, 1983) and top-down variables like predator/pathogen presence (McLaren and Peterson, 1994). Whether animal populations were solely regulated through top-down or bottom-up factors is an important historical debate. However, what came from these discussions was an understanding that it is likely multiple factors interactively influencing animal populations simultaneously (Hunter and Price, 1992). Regardless of whatever the regulatory factors may be, they likely change in space and time, which complicates the story further (Gripenberg and Roslin, 2007). Therefore, to develop a comprehensive understanding of what drives animal populations, a multi-scale approach must be taken. For my dissertation, I pull from multiple research fields to understand what influences the boom-and-bust cycles of locust swarms on multiple scales: from individual aggregations to landscape level processes.

As Wiens (1989) put it, "acts in what Hutchinson (1965) has called the ecological theatre are played out on various scales of space and time. To understand the drama, we must view it on the appropriate scale." Landscape ecology was formed to address the spatial and temporal variation of life seen throughout the biosphere (Forman,

1983; Turner, 1989; Wu, 2017). Scaling ecological phenomenon, which is the process of theoretically and/or statistically acknowledging multi-spatial and temporal scales, is a prevalent way to account for the complexities of life (Wiens, 1989; Levin, 1992; Wu and Li, 2006). For example, through the use of the hierarchical patch dynamics paradigm (Kotliar and Wiens, 1990; Wu and Loucks, 1995), we are able to understand the spatial organization of many animals from krill to caribou (Johnson, 1980; Murphy *et al.*, 1988; Fauchald *et al.*, 2000; Decesare *et al.*, 2012). However, even though the ecological community at large acknowledges the multi-scale nature of life (Senft *et al.*, 1987; Wiens, 1989; Levin, 1992; Wu and Loucks, 1995), few authors theoretically or statistically account for it. For example, in a multi-scale habitat selection review, McGarigal *et al.* (2016) showed that only 20% (173 out of 859 studies) were quantitative and met the most basic definition of being multi-scale, which is modeling multiple levels independently. One excellent model organism for understanding the multi-scale nature of life are locusts.

Locusts are a subset of grasshoppers that undergo immense plagues and threaten global food security. For example, the 2003-2005 desert locust (*Schistocerca gregaria*) plague inflicted $2.5 billion in damage even after $500 million in mitigation (Belayneh, 2005). Once a plague begins it is challenging to control and is usually only stopped due to changes in large-scale weather patterns. Biologically, locusts demonstrate an extreme form of phenotypic plasticity called phase polyphenism, which means they have two phenotypic phases: solitarious and gregarious (Uvarov, 1921; Pener and Simpson, 2009). These phases represent two ends of a continuum and phase transition is mediated by environmental cues. Solitarious individuals are less active and avoid one another. But when solitarious individuals receive visual, tactile, and/or olfactory cues from conspecifics, it induces a physiological and behavioral transformation to the gregarious phase where they become more active, aggregate, and swarm (Anstey *et al.*,

2009; Pener and Simpson, 2009; Cullen *et al.*, 2010, 2017). The denser the local locust population is, the greater chance of having gregarious individuals through increasing the likelihood of conspecific interaction. To understand what causes a locust swarm, there needs to be a multi-scale and interdisciplinary approach. This is because the genesis of a swarm begins with an individual level physiological transformation that eventually has landscape level effects. Whereas this phase transformation has been well documented in lab settings, it is harder to capture in more natural settings (Despland *et al.*, 2000) but nonetheless important. Landscape structure (e.g. food availability both spatially and temporally, soil characteristics, habitat vs non-habitat patches) drive this individual transformation (Despland *et al.*, 2000; Veran *et al.*, 2015; Mangeon *et al.*, 2020). However, few studies have investigated or accounted for the multi-scale nature of locust swarms (but see Collett et al. 1998). Using the Hierarchical Patch Dynamics paradigm, we can start to tease out the drivers of locust gregarization at relevant scales.

My dissertation takes form in four chapters of increasing spatio-temporal scale and encompasses multiple fields from behavioral ecology to remote sensing to investigate the causes of locust swarms on three continents: Australia, Africa, and Asia. A conceptual scaling diagram for this dissertation can be found in figure 1. In the first chapter, I show that clumpy distributions of nutritionally optimal food can influence locust distributions and gregarization. In the second chapter, I show that locust populations avoid woody vegetation likely due to the interactive effect of plant nutrients, temperature, and predators. In the third chapter, I show that locusts are usually within nutritionally suboptimal environments and are likely able to meet nutritional needs by migrating to optimal habitats. Lastly, in the final chapter I show that the relationship between preceding vegetation and nymphal outbreaks vary by species, however the response is spatiotemporally structured.

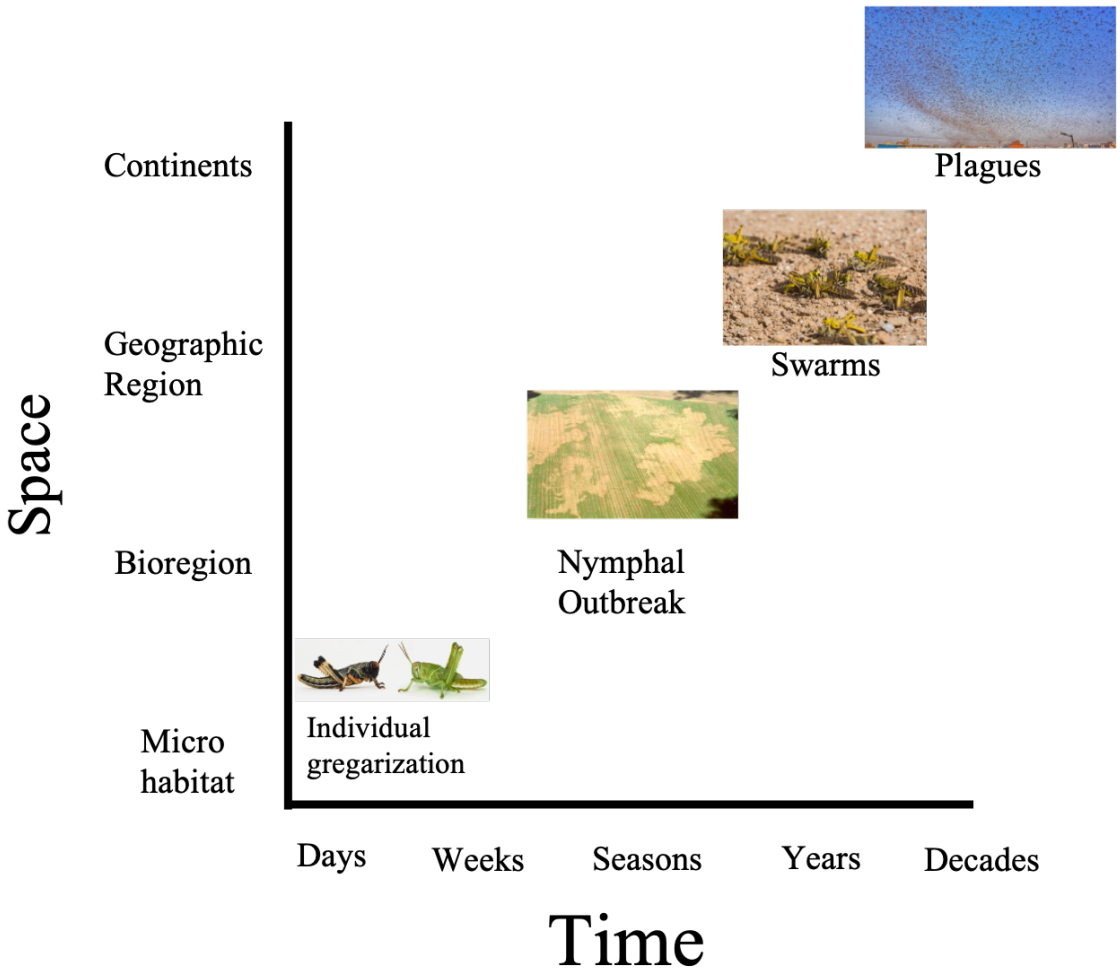

Figure 1.1: Theoretical Scaling Diagram for Locust Swarms. Each Level Poses a Bottleneck as if One Level Is Not Favorable, the Swarm Will Not Form. At the Smallest Scale Is Individual Locust Gregarization. At This Scale, the Spatial Distribution and Availability of Food Are Important. If Locust Gregarization Happens, Then Nymphal Outbreaks Can Happen Which Depend on Previous Rainfall Conditions and Vegetation Amount and Quality. If the Nymphal Outbreaks Are Successful and the Individuals Reach Adulthood, Localized Swarms Can Happen. Having Enough Successful Locust Swarms Is Critical for Plagues Which Happen at the Continental and Decadal Scales.

Chapter 2

THE EFFECTS OF FOOD QUALITY CLUSTERING IN LANDSCAPES ON LOCUST FEEDING AND GREGARIOUS BEHAVIOR

2.1 Introduction

Understanding how landscape patterns drive ecological processes such as animal movement and behavior is a key aspect of landscape ecology (Turner, 1989). Locusts (Orthoptera: Acrididae) are excellent model organisms to understand how patterns influence processes due to their extreme form of phenotypic plasticity called phase polyphenism, regulated primarily through changes in population density. Under high density, locusts shift from a solitarious phase, actively avoiding other individuals, to a gregarious phase where they aggregate and form massive swarms (Pener and Simpson, 2009; Cullen *et al.*, 2017). Resource limitation is one factor that can modulate this behavioral switch via crowding, and these resulting changes in behavior presumably allow locusts to locate more food (Uvarov, 1977). For example, when food patches are limited and clustered, desert locusts, *Schistocerca gregaria* (Forsskål, 1775), will aggregate on them, increasing conspecific interactions and thus promoting gregarization and subsequent mass migration (Collett *et al.*, 1998). In contrast, gregarious groups of other locust species can originate in grasslands or landscapes with presumably more homogenous distributions of suitable host plants like the Australian plague locust (*Chortoicetes terminifera*, Walker, 1870) (Veran *et al.*, 2015) and the South American locust (*Schistocerca cancellata*, Serville, 1838) (Medina *et al.*, 2017), indicating food patch clustering likely plays a weaker role in promoting gregarization in this species. This pattern suggests that there are other important characteristics of

how food is distributed within an environment for gregarization. However, the landscape structure's role in driving the shift between solitarious and gregarious phases is not well understood. The nutrient availability and spatial distribution throughout a landscape likely influences population movement and organization like swarms, though it remains to be generally tested (Lihoreau *et al.*, 2018). In this study, we investigated the impact of nutritional landscape structure on Australian plague locust gregarious behavior.

Meeting nutritional demands is important for animal performance from reproduction and growth (Joern and Behmer, 1997; Raubenheimer and Simpson, 2003) to immune function (Srygley *et al.*, 2009; Ponton *et al.*, 2011; Graham *et al.*, 2014) and migration (Rankin and Burchsted, 1992). Thus, the spatial distribution of nutrients and their acquisition within a landscape are important factors that affect animal distributions from insects (Behmer, 2009; Joern *et al.*, 2012) to mammals (Felton *et al.*, 2009; Rothman *et al.*, 2011; Nie *et al.*, 2015). For example, *Oedaleus spp.* locusts have increased migratory performance on carbohydrate biased as compared to protein biased diets (Cullen *et al.*, 2017; Le Gall *et al.*, 2019b). Accordingly, they are more abundant in degraded fields that harbor low nitrogen and subsequently carbohydrate biased foods, as compared to fields with high nitrogen and protein biased plants (Cease *et al.*, 2015; Le Gall *et al.*, 2019b; Word *et al.*, 2019). Since this is shown in multiple locust and grasshoppers species (Le Gall *et al.*, 2019a), understanding the nutritional preferences and underlying physiological demands is important for predicting grasshopper distribution in general.

Most research on the ecological factors promoting locust gregarization has focused on the spatial distribution of resources (e.g. plant vs. bare ground). Because the switch from solitarious to gregarious behavior is mediated by visual, olfactory, and tactile stimuli from other locusts (Roessingh *et al.*, 1998; Simpson *et al.*, 2001; Rogers

et al., 2003), any landscapes that bring locusts in close proximity to each other should promote gregarization. On a small scale (< 1 m^2), clustered resources induced desert locust gregarization (Despland and Simpson, 2000a; Despland *et al.*, 2000), but no trend was found at large-scale distributions (ca. 2.4 million km^2; 76,000 km^2 patch size) (Despland *et al.*, 2004). In addition to resource distribution, the nutritional quality of the resources affects desert locust gregarization. A small-scale landscape (i.e., ca. 1 m^2) with two complementary but nutritionally opposite resource choices increased the contact and movement of solitarious desert locusts, which promoted gregarization (Despland and Simpson, 2000b). In nature, the spatial heterogeneity of resource nutritional quality may arise from differences of: species (Arzani *et al.*, 2004), phenology (Jackson *et al.*, 1988), rainfall (Feral *et al.*, 2003), and soil parameters (Clarkson, 1985). This variability likely affects the spatial distribution of locusts throughout a landscape but remains understudied.

The Australian plague locust is a major agricultural pest species in Australia (Hunter 2004). For example, it is estimated that there would have been USD $963 million in damage during the 2010–2011 Australian plague locust plague without control (Millist and Abdalla, 2011). Generally, this locust can be found in tussock grasslands and open woodlands throughout Australia's arid interior and there is some evidence that widespread introduction of livestock led to increased swarms by expanding suitable grassland habitat (Deveson, 2012, 2017; Adriaansen *et al.*, 2015; Lawton *et al.*, 2020). Further, this species also expresses density-dependent behavioral phase polyphenism (Gray *et al.*, 2009a) predominately promoted by antennae mechanostimulation (Cullen *et al.*, 2010). Since gregarization is triggered through contact with conspecifics, similar to the desert locust (Rogers *et al.*, 2003), it is conceivable that clustered resources also promotes gregarization in this species.

In this study, we tested how the spatial distribution of food differing in nutri-

tional quality affects Australian plague locust gregarization. We predicted that homogeneously distributed nutritionally optimal diet would allow solitarious locusts to maintain activate avoidance behavior, decreasing propensity to become gregarious. In contrast, we expected that as nutritionally optimal resources became clustered, locusts would overcome their solitarious aversion of conspecifics to eat from the nutritionally optimal resource. This response would, in turn, increase antennal contact between locusts, promoting gregarious behaviors (time spent near stimulus group, distance walked, time spent walking, mean distance to stimulus group of locusts). We predicted that there would be a nutritional quality threshold in the behavior of locusts. For example, if the homogeneously distributed food was only slightly suboptimal, we predicted solitarious locusts would eat from the dispersed landscape to actively avoid each other. Whereas, if the homogeneously distributed food was highly suboptimal, they would group together on the optimal clustered food patch, promoting gregarization.

This study was constructed and carried out with 15 undergraduates through a course-based undergraduate research experience "CURE" class (Bangera and Brownell, 2014) in the Fall 2017 and 2018 semesters. A CURE class is designed to increase the participation of undergraduates, specifically those who are underrepresented, in novel research (Auchincloss *et al.*, 2014). This is done by teaching basic biological concepts through conducting a novel experiment. The impacts of a CURE class are two-fold benefiting both students and faculty. For undergraduate students, CURE classes have been shown to increase: research skills, retention rates in science, technology, engineering and mathematics (STEM) fields, the likelihood of graduating with a STEM degree in six years, and knowledge of experimental design and research practices when compared to students in traditional STEM classes (Nagda *et al.*, 1998; Kardash, 2000; Lopatto, 2004; Junge *et al.*, 2010; Kloser *et al.*, 2013; Brownell *et al.*, 2015; Roden-

busch *et al.*, 2016). While CURE courses can be impractical to implement without supportive academic infrastructure (Shortlidge *et al.*, 2016), there can be marked benefits for faculty. For example, implementing CURE courses has been attributed to promotion, tenure, and research productivity through reducing time conflicts between educational and research components of professorial positions (Shortlidge *et al.*, 2016; National Academies of Sciences and Medicine, 2017).

2.2 Methods

This class was a collaborative effort between the School of Sustainability and the School of Life Sciences at Arizona State University (ASU) who supported two cross-listed CURE courses in the fall semesters of 2017 and 2018. We collected additional data after the class in January and March 2019, with the assistance of students from the original courses.

2.2.1 Locusts

The locusts used in this experiment were from a lab reared colony at ASU. This colony has been in captivity for five years at ASU and originated from a seed colony housed at The University of Sydney in New South Wales, Australia. The Sydney colony was initiated around 2006 from several migrating populations collected in eastern and western Australia. The ASU colony was kept in an environmental chamber (Conviron®) at 34 C, on a 14 Light (L) : 10 Dark (D) cycle, and fed wheat grass (*Triticum*) and wheat germ daily. Since individuals are kept in large colonies, they are by default gregarious. Solitarization was induced through a protocol originally designed for the desert locust (Roessingh *et al.*, 1993) and adapted later for Australian plague locusts (Gray *et al.*, 2009b; Cullen *et al.*, 2010). Locusts were kept in individual cages for seven days to ensure full solitarization. Cages had plastic cards

in between and individual air supply to prevent visual and olfactory stimulation.

2.2.2 Diets

Locusts were fed their standard colony diet (see section 2.1) until they were added into the experiment. To control the nutrient availability within the experiments, we used isocaloric artificial diets made up of 42% macronutrients (differing ratios of protein and carbohydrates), 32% cellulose, and 4% of salt, sterols and vitamins. This artificial diet mixture has been used with this species before (Clissold *et al.*, 2014) and was developed by Simpson and Abisgold (1985) from Dadd (1961). We used the following macronutrient ratios: 5 Protein (P) : 1 Carbohydrate (C), 2P : 1C, 1P : 1C, and 1P : 1.5C. These ratios were selected based on previous nutritional ecology research on locusts (Raubenheimer and Simpson, 2003; Cease *et al.*, 2017) and the ASU Lab colony final juvenile instar preference of 1P : 1.5C (Brosemann et al., unpub. data). We only used suboptimal protein biased diets because this prevented the locusts from balancing their nutritional intake through preferentially selecting between high carbohydrate and high protein diets.

2.2.3 Experimental Design

Locust Rearing

For each trial, we collected approximately 80 juvenile locusts from the crowd-reared lab colony and put them in individual isolated cages for one week to promote solitarization (see 2.1). Instar stage varied based on what was available during the class schedule (Table A.1). Previous studies used 10 solitarious desert locusts for similar arena experiments (Despland and Simpson, 2000b,a), however the desert locust is approximately three times bigger than the Australian plague locust. As such in all trial periods, we randomly added 25 solitarized Australian plague locusts with roughly an

equal sex ratio to each treatment arena. All remaining solitarious locust individuals were kept in isolated rearing cages and were used as the solitarious behavior control. Gregarious controls were collected from the original high-density colony during the behavioral testing period. Total number of locusts and instar stages can be seen in Table A.1.

Arenas

Each arena was constructed in a Nalgene tub (51 cm width x 69 cm length x 58 cm height). We coated the walls with Fluon (Insect-A-Slip) to prevent locusts from walking on the walls. All treatments had the same structure of 21 small and one large petri dish (Fig. 2.1). We will refer to the homogeneously distributed small dishes as "small patches" and the large petri dish as the "large patch." Water was provided ad lib with cricket water pillows (Zilla®). We kept the arenas in an environmental chamber with a 14 L: 10 D hour cycle. To ensure there was enough time for locusts to become gregarious, we left them in the treatment arenas for 48 hours which is the time required for a complete phase change in this species (Rogers et al. unpub. data). To determine the amount of artificial diet consumed, we weighed the dry diets before placing them in each arena. After the trial was completed, we collected the diets, dried them for 48 hours at 60^{o} C in a drying oven and weighed the final mass. This allowed us to calculate diet consumed for each dish with little error due to water absorption.

Arenas: contrasting nutritional landscapes experiment

To determine whether nutritional landscape heterogeneity effects locust phase change, we first used two treatments. Both treatments had the same diet pairing of extreme ratios: a nutritionally optimal ratio (1P : 1.5C) and one nutritionally suboptimal

ratio (5P : 1C) while the spatial distribution varied. Optimal patch treatment had a nutritionally optimal large patch and suboptimal small patches. Conversely, the suboptimal patch treatment had a nutritionally suboptimal large patch and optimal small patches (Fig. 2.1 Top). We used fifth instar locusts for this part of the experiment and collected these data in September 2017 (Table A.1).

Arenas: approaching nutritional optimality experiment

To determine the threshold when attraction to a nutritionally optimal food patch outweighs the solitarious aversion behavior, we used four arenas with varying small patch composition. In these trials, we kept the large patch constant with a nutritionally optimal ratio (1P : 1.5C) and adjusted small patch macronutrients with the following ratios: treatment 1 – 5P:1C, treatment 2 – 2P:1C, treatment 3 – 1P:1C, and treatment 4 – 1P:1.5C (Fig. 2.1 Bottom). This part of the experiment was conducted three times with the available instar stage in September 2018, January 2019, and March 2019 (Table A.1). Due to logistical challenges, these trials were held at different temperatures (30 C or 34 C). We statistically accounted for this unintended variation by holding trial period as a random effect (Bolker *et al.*, 2009).

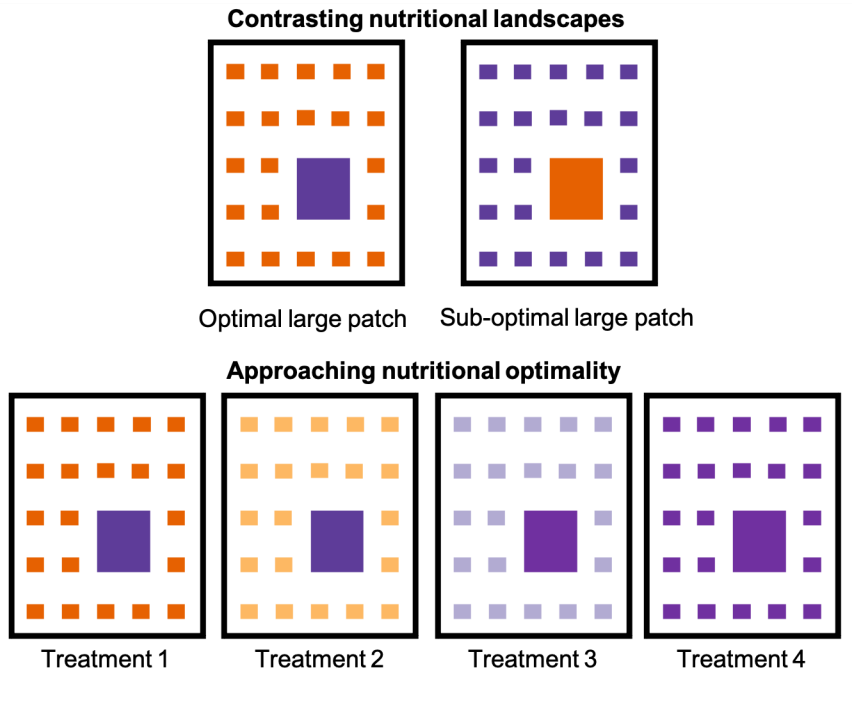

Figure 2.1: Experimental Design for the Contrasting Nutritional Landscapes (Top) and Approaching Nutritional Optimality Experiments (Bottom). Orange Represents Nutritionally Suboptimal (5 Protein : 1 Carbohydrate) and Purple Represents Nutritionally Optimal (1 Protein : 1.5 Carbohydrate Ratios). Small Boxes Represent Small Diet Patches and Large Boxes Represent Large Diet Patches.

2.2.4 Behavior phase state

At the end of each trial, we measured gregarious behavior for all locusts following an assay developed by Roessingh *et al.* (1993) and modified for Australian plague locusts by Cullen *et al.* (2010) and Gray *et al.* (2009a). Briefly, we used an arena (36 cm x 15 cm x 10 cm) with a gregarious stimulus group on one side and empty on the other. We used a modified plastic syringe to insert the test individual into the middle and we tracked behavior for 480 seconds in real time using a color CCTV camera. All behavior tracking was conducted between 09:00 and 17:00 and each trial assay was completed in one day. We used Ethovision® XT 10 (Noldus®) to calculate the raw behavior variable values for each locust. We measured total distance moved, rest time

fraction, time spent near gregarious stimulus, and mean distance towards stimulus which are commonly used variables in determining locust phase state (Anstey *et al.*, 2009; Gray *et al.*, 2009a; Cullen *et al.*, 2010). After each individual was assayed, we marked and returned them to their respective treatment. This process maintained the proper density in the arenas during the assay. To reduce the amount of unintended variation, each trial conducted had a control group of known solitarious and gregarious locusts. Control locusts were analyzed randomly throughout each assay period, in between measuring treatment locust behavior.

2.2.5 Statistics

All data were assessed for normality and heteroskedasticity where appropriate. We ran the same statistics for experiments when appropriate.

Diet consumption: total consumption

For the contrasting nutritional landscapes experiment (Fig. 2.1 Top) we did not have a large enough sample size to run statistics on total diet consumption. To look at the consumption from small and large patches in approaching nutritional optimality experiment (Fig. 2.1 Bottom), we constructed additive models with either large or small patch consumption as the dependent variables, treatment as the independent variable, and trial period as a random effect. This allowed us to account for unintended variation between trial periods and pseudoreplication (Bolker *et al.*, 2009; Davies and Gray, 2015). If there were significant differences in the model, we then used Tukey multiple comparisons to compare each treatment together.

Diet consumption: Spatial distribution of consumption

To determine how diet consumption changed spatially, we used Moran's I, a classic test to investigate spatial autocorrelation (Moran, 1950). Moran's I values above the expected value, which is dependent on the sample size (-1/(N-1)), signify positive spatial autocorrelation (i.e. similar values occur near each other) and values below the expected value signify negative spatial autocorrelation (i.e. dissimilar values occur near each other). Values close to the expected value signify there is no discernable pattern, and the distribution is random.

Locust phase state

To determine locust phase state, we followed roughly the protocol of previous studies (Gray *et al.*, 2009a; Cullen *et al.*, 2010). We first built a control model of known gregarious (N: 63) and solitarious (N: 63) locusts then we used this model to predict the probability of being gregarious (pGreg) for each locust in all treatments. To do this, we used a random forest model following the protocol in Wang *et al.* (2018). Random forest is a decision tree ensemble technique introduced by Breiman (2001) which improves regression accuracy. This allowed us to make the overall model less sensitive to overfitting as compared to a single decision tree. This modeling technique is non-parametric and can handle non-linear and additive relationships. Further, it ranks the importance of each predictor variable in influencing the response variable. We trained the model using 70% of the control dataset by bootstrap sampling with replacement to 'grow' the random forest of 2001 decision trees. Then this model was validated with the remaining 30% of the control data set which produces an 'area under the ROC curve' (AUC). This AUC value reports how well the model fits (0.00-0.50 = bad classifier, >0.50 = somewhat predictive, 1 = perfect predictor). To ensure

model AUC fit, we resampled the training and validation sets and constructed 1000 independent random forests. All random forest models were then combined into a final model following the protocol of Wang et al. (2019). We then used the validated final model to predict the probability of being gregarious (pGreg) for all locusts in each treatment.

Statistical software

All statistics were conducted in the *Tidyverse* framework (Wickham, 2018) within the R statistical environment (R Core Team, 2018). The generalized additive models was constructed using the *mgcv* package (Wood, 2017) and validated with *mgcViz* (Fasiolo *et al.*, 2018). Tukey's multiple comparisons were computed with multcomp (Hothorn *et al.*, 2009). Moran's I was calculate with *ape* (Paradis and Schliep, 2018). Random forest models were conducted using the *randomForest* package (Liaw and Wiener, 2002) and AUC curves were constructed using the *pROC* package (Turck *et al.*, 2011).

2.3 Results

2.3.1 Diet Consumption

Contrasting nutritional landscapes

Consumption of the small patch diet was higher in the sub-optimal patch treatment than in the optimal patch treatment (Fig. 2.2a and d). Spatially, locust food consumption was more clumped when the large patch was nutritionally optimal (Optimal patch treatment) as compared to when nutritionally optimal food was the small patches (Sub-optimal patch treatment), although both treatments had positive autocorrelation (Fig. 2.2b and c; Table 2.1)

Approaching nutritional optimality

Overall consumption of small diet patches increased from Treatment 1 to 4 (Fig. 2.2 Treatment 1e-Treatment 4h, Table 2.2), except for consumption between 2 and 3 (Table 2.3). Large patch consumption remained consistent through all treatments (Table 2.4). Spatially, diet consumption in Treatment 2 and 4 were clumped around the large patch and there was no autocorrelation in Treatments 1 or 3 (Fig. 2.2 Treatment 1-4; Table 2.1).

2.3.2 Locust phase state

The final phase state model had a decent fit (AUC 0.717) to control data (Table A.1). Total distance moved and mean distance to gregarious stimulus were the most important variables whereas total time spent at stimulus and rest time fraction were less important (Fig. 2.3).

Contrasting nutritional landscapes experiment

The final random forest model indicated that pGreg increased in both the optimal patch and the sub-optimal patch treatment (Kruskal-Wallis: X^2: 14.207, df: 3, P-value: 0.002) (Fig. 2.4A, Fig. A.2, and Table A.2). The two treatments were different from the solitarious control but not from the gregarious control or each other.

Approaching nutritional optimality experiment

We took the validated model and calculated pGreg for Treatments 1–4 (Fig. 2.4B, Fig. A.3 and Table A.3). There were significant differences between the control and treatment groups (Kruskal-Wallis: X^2: 110.8, df: 5, P-value: $<<0.001$) (Fig. 2.4B). Both solitarious and gregarious controls were different from each other and the treatment groups. However, treatment groups did not differ between each other.

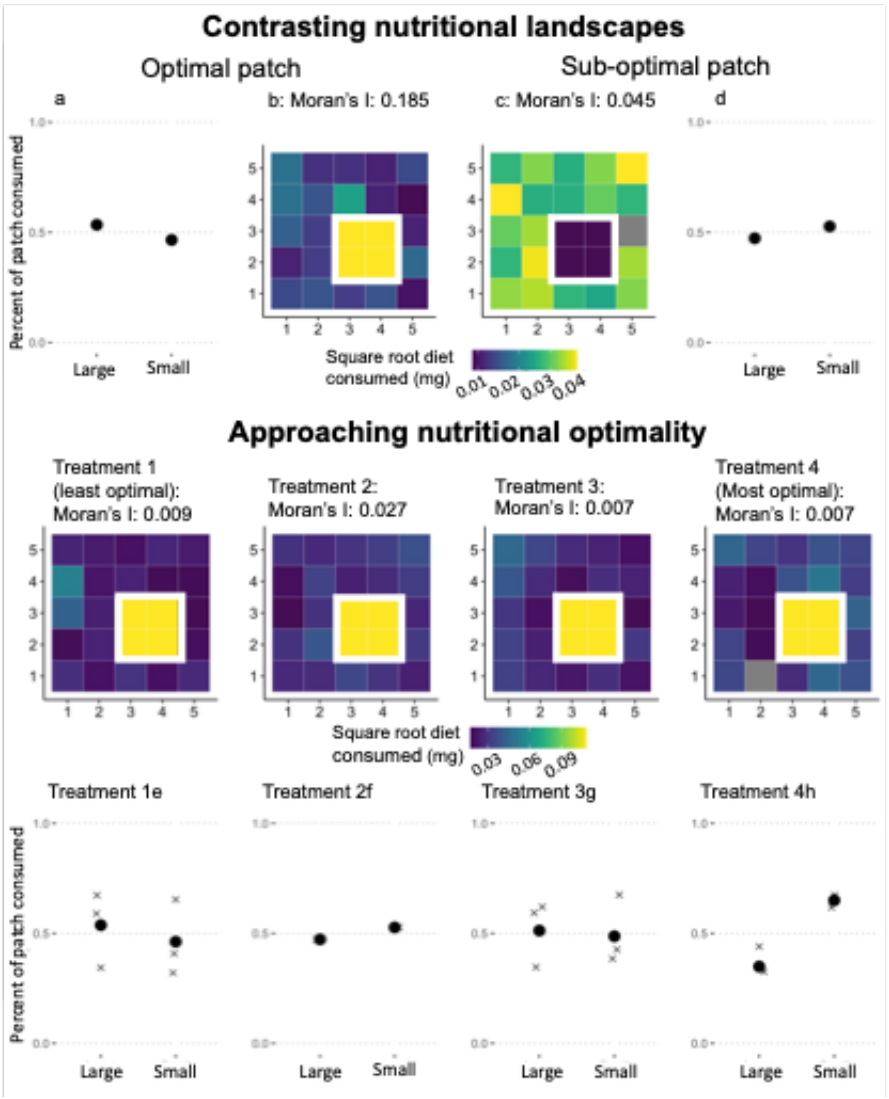

Figure 2.2: The Spatial Distribution (B and C; Treatment 1–4) and Total Consumption (a and D; 1e–4h) of Small and Large Diet Patches for Contrasting Nutritional Landscapes (Top) and Approaching Nutritional Optimality (Bottom) Experiments. For the Spatial Distribution Plots, White Outline Represents Large, While Small Boxes Represent Small Diet Patches. Moran's I Expected Uniform Distribution Was 0.0417. Values Above the Expected Distribution Signify Positive Autocorrelation (e.g. Like Things Are Near Each Other). Gray Boxes Represent an Error in Data Collection. For the Total Consumption Plots, Circles Represent the Mean Consumption and X's Represent Replicates. Experiment a Only Had One Replicate.

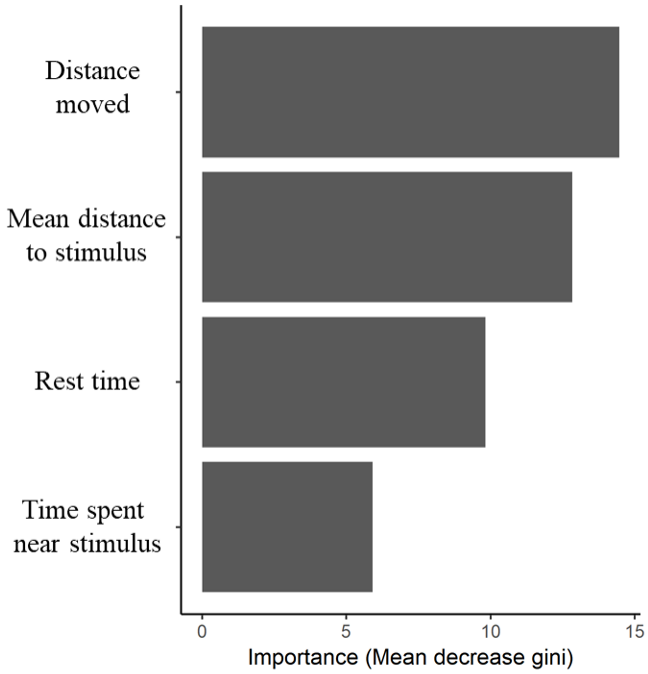

Figure 2.3: The Relative Importance (Mean Decrease Gini) for Each Predictor Variable.

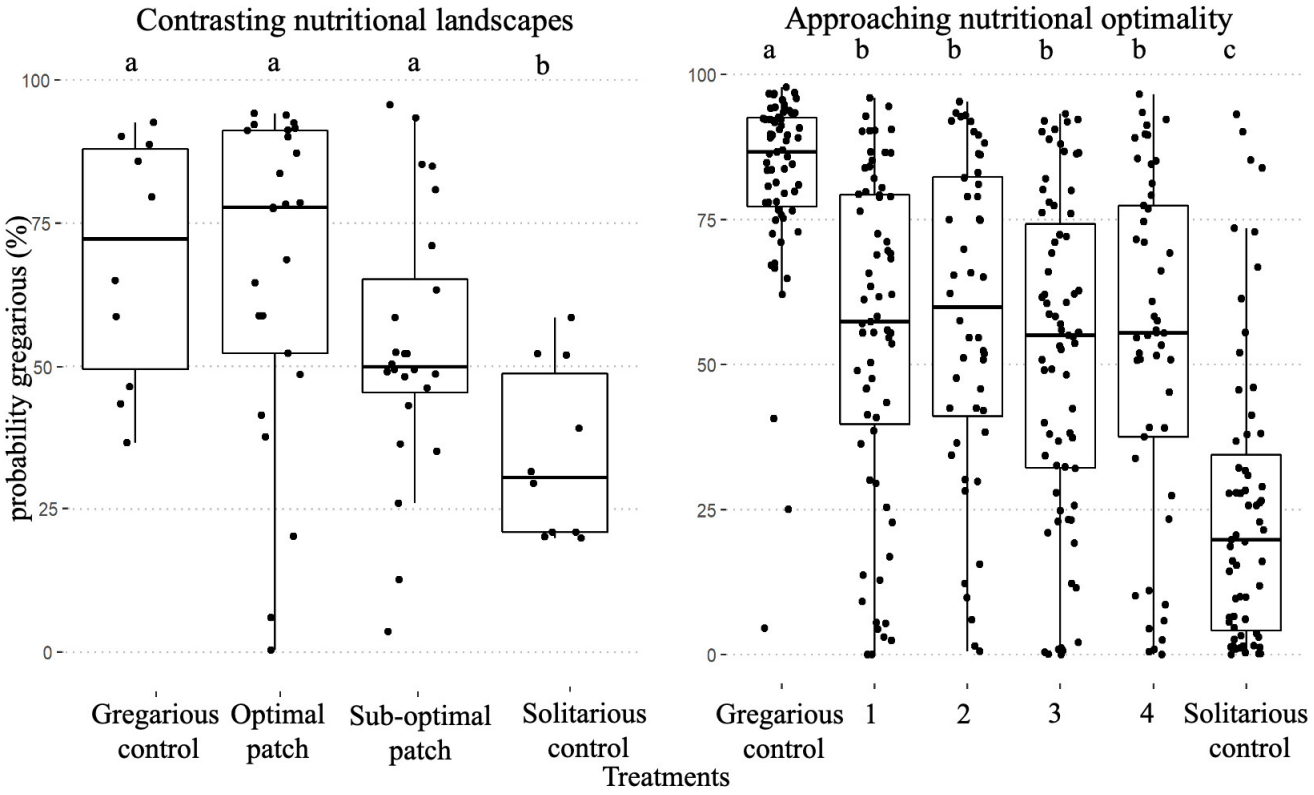

Figure 2.4: Model Predictions for Gregarious Behavior for Controls and Treatments in Both Contrasting Nutritional Landscapes (A) and Approaching Nutritional Optimality (B) Experiment. 100% Denotes Fully Gregarious and 0% Denotes Fully Solitarious. Letters Represent Significance Based on Nemenyi Posthoc Analyses. Left: A = Optimal Cluster and B = Optimal Homogeneous. Right: 1 = Most Suboptimal Homogeneous Distribution, 4 = Most Optimal Homogeneous Distribution.

Table 2.1: Spatial Autocorrelation Results on the Diet Consumed for Each Experiment. Values Are Compared to an Expected Uniform Distribution. Since All Treatments Were the Same Size (e.g. 5x5 Grid) the Expected Moran's I Is Uniform Across Treatments. Values Above the Expected Value Are Considered Clustered Whereas Values Below Are Considered More Randomly Distributed. Significant Adjusted P-Values Are in Bold.

Experiment	Treatment	Observed I	Expected I	Standard Deviation	P-value
Contrasting nutritional	Optimal large patch	0.185	-0.042	0.029	<<0.001
landscapes	Sub-optimal large patch	0.045	-0.042	0.018	<<0.001
	1	0.009	-0.042	0.028	0.071
Approaching Nutritional	2	0.027	-0.042	0.028	0.014
optimality	3	0.007	-0.042	0.028	0.084
	4	0.031	-0.042	0.029	0.012

Table 2.2: Additive Model Results for Homogeneous Nutrient Consumption Regressed on Treatment With Trial Period as a Random Effect for the Approaching Nutritional Optimality Experiment. Significant P-Values Are in Bold. Treatment 1 = Most Suboptimal Small Patch Diets, Treatment 4 = Most Optimal Small Patch Diets.

Parametric terms

	Estimate	standard error	t-value	p-value
Intercept	0.017	0.003	5.785	<<0.001
Treatment 2	0.003	0.001	2.225	0.026
Treatment 3	0.004	0.001	3.432	<<0.001
Treatment 4	0.016	0.001	12.375	<<0.001

Smoothing terms

	estimated degrees freedom	X^2	P-value
Trial period (random effect)	1.942	100.800	<<0.001

Table 2.3: Tukey Multiple Comparison Results for Small Patch Consumption for the Approaching Nutritional Optimality Experiment. Significant P-Values Are in Bold. Treatment 1 = Most Suboptimal Small Patch Diets, Treatment 4 = Most Optimal Small Patch Diets.

Comparison	Estimate	Error	Z-value	P-value
Treatment 1 - Treatment 2	0.209	0.061	3.430	**0.003**
Treatment 1 - Treatment 3	0.244	0.052	4.678	**<0.001**
Treatment 1 - Treatment 4	0.751	0.061	12.328	**<0.001**
Treatment 2 - Treatment 3	0.035	0.061	0.579	0.930
Treatment 2 – Treatment 4	0.542	0.064	8.508	**<0.001**
Treatment 3 - Treatment 4	0.507	0.061	8.281	**<0.001**

Table 2.4: Additive Model Results for Large Patch Consumption Regressed on Treatment With Trial Period as a Random Effect for Approaching Nutritional Optimality Experiment. Significant P-Values Are in Bold. Treatment 1 = Most Suboptimal Small Diets, Treatment 4 = Most Optimal Small Diets.

Parametric Coefficients

Variable	Estimate	Error	Z-value	P-value
Intercept	-2.181	0.141	-15.446	<<0.001
Treatment 2	-0.056	0.081	-0.688	0.492
Treatment 3	0.042	0.070	0.607	0.544
Treatment 4	0.158	0.081	1.936	0.053

Smoothing Terms

Variable	Estimated degrees freedom	DF	X^2	P-value
Month	1.902	2	30.270	<<0.001

2.4 Discussion

In this study, we show that landscape structure influences locust gregarization even when food was homogeneously distributed throughout a landscape. The clustering of nutritionally optimal food led locusts to eat more from those dishes (Fig. 2.2), resulting in a general trend of gregarization in one experiment but not the other (Fig. 2.4). The high density of locusts used in our trials may have masked the influence of the nutritional landscape structure on gregarization. Studies on locust populations at lower densities and/or over larger scales may reveal stronger effects.

2.4.1 Diet consumption and aggregation

In line with our predictions, in the contrasting nutritional landscapes experiment, locusts ate more from the small patches as those patches became more nutritionally optimal (Fig. 2.2), supporting the hypothesis that the spatial distribution of nutritionally optimal vs suboptimal diets affects the fine-scale spatial distribution of locusts. However, the consumption pattern was not significant in the approaching nutritional optimality experiment under finer scale nutritional landscape shifts, potentially due to a low sample size. The logistical setup constrained the number of replicate trials we could run over the course of the CURE classes. However, a power analysis on the data collected suggests that including 10 replicates could reveal a significant difference between landscapes in the approaching nutritional optimality experiment design (power analysis: power: 0.80, effect: 0.49, alpha: 0.05).

2.4.2 Locust gregarization

Whereas diet consumption became more aggregated when nutritionally optimal food was more clustered (Fig. 2.2b and c, Treatment 1-4), we only saw a general trend

of gregarization in the contrasting nutritional landscapes experiment (Fig. 2.4A). In the approaching nutritional optimality experiment, all landscape treatments induced phase change to the extent that treatment locusts which started out as fully solitarious individuals began to express at least some gregarious behaviors post treatment (Fig. 2.4B). Combined, the results from these two experiments suggest that locusts can still become gregarious when resources are homogeneously distributed and that the probability of gregarization in such a landscape is heightened when high quality foods are clumped. This outcome may contradict the common conception that solitarious-phase locusts, regardless of species, actively avoid each other when food is homogeneously distributed throughout landscapes (Roffey and Magor, 2003; Pener and Simpson, 2009). Since gregarization happens to individuals, understanding behavioral foraging strategies, and potential variation among individuals, will be important to understanding the overall collective movement of locust populations.

Gregarization in our study could have been impacted by sample size, arena size, or by biological variation in gregarization between locust species. Our model fit to the control data (AUC: 0.717) is not as good as other locust behavior models (AUC: >0.90) (Anstey *et al.*, 2009; Gray *et al.*, 2009a; Cullen *et al.*, 2010; Verdonck, 2017). This could be because of a smaller control sample size of 63 individuals compared to other reported sample sizes of 123 (Cullen *et al.*, 2010). Arena size is important because effective density alone could spur gregarization. Despland and Simpson (2000b) used an arena size of 70 cm width x 70 cm length and 10 2nd instar desert locusts. In this experiment, our arenas were 51 cm width x 58 cm height and 25 Australian plague locusts since this species is approximately 3 times smaller than the desert locust. To our knowledge this is the first study to conduct an arena experiment for Australian plague locusts and further research is needed to know an adequate effective density to maximize treatment effectiveness. Another important contributing factor could

have been differences in biology. Locust research has been heavily biased towards two species: the desert locust and the migratory locust (*Locusta migratoria*) (Cullen *et al.*, 2017). Desert locust gregarization over time follows a logistic curve with a very short transition period (Rogers *et al.*, 2014). In contrast, Australian plague locust gregarization is more linear and gradual (Rogers et al. unpub. data). However, literature describing Australian plague locust gregarization is limited and future studies are needed to elucidate the effective density required for phase change, in addition to the physiological mechanisms regulating this polyphenism for non-model species. Locust phase polyphenism has evolved independently multiple times within the family Acrididae, with about 20 species showing some locust-like characteristics (Pener and Simpson, 2009; Song, 2011). Therefore, the landscape structure characteristics that cause a locust population to collectively move and migrate likely changes between species and geographic locations and happens over different time scales.

2.4.3 From arena to natural landscapes

To understand life history traits like gregarization, any experiment should be placed in context of the environment in which an organism is found (Ricklefs and Wikelski, 2002). In the field, locusts aggregate and gregarize (Despland *et al.*, 2000; Despland and Simpson, 2000b; Babah and Sword, 2004; Cisse *et al.*, 2013) and move more (Ellis and Ashall, 1957) in landscapes with clustered vegetation as compared to homogeneously distributed vegetation. Interestingly, vegetation clustering is more important for gregarization at small versus large spatial scales (Collett *et al.*, 1998; Babah and Sword, 2004; Despland *et al.*, 2004). Our study shows that even when food resources are homogeneously distributed, the spatial change of nutritional quality can influence aggregation. Despite the implications of these studies, apart from identifying where or what landscape characteristics correlate with gregarious and soli-

tarious locust populations (Werf *et al.*, 2005; Babah and Sword, 2004; Cisse *et al.*, 2013, 2015; Piou *et al.*, 2017), few have looked at gregarization of a field population over time or connected lab- and field-based gregarization experiments, largely due to the complexity of the system (Despland and Simpson, 2000b).

2.4.4 A call for more entomological and Orthopteran research-based CURE classes

A CURE class is an excellent opportunity to engage undergraduates in biological research and it's benefits are two-fold for both faculty and students (Bangera and Brownell, 2014; Shortlidge *et al.*, 2016). Whereas this study focused on behavioral ecology, this format can be used within all research areas. One excellent source for already implemented CUREs is CUREnet (https://serc.carleton.edu/curenet). This is a network of faculty that facilitates the course construction, teaching, and development of new tools and strategies. There is great potential for the inclusion of CUREs in the entomological community. Orthopterans are excellent model organisms for undergraduate research projects because they are low maintenance, easy to catch and handle, are widely recognizable by the general public, and can be a charismatic introduction to entomology. However, as we encountered, experimental timing can be challenging if specific insect developmental stages required for the research do not align with the course schedule as planned. Thus, careful planning of studies that can be flexible to meet the more rigid course schedule work best.

The CURE format was well received by the students in our class and we hope that it stands as an example of how entomological and Orthopteran research can be used within the CURE framework. While we did not explicitly collect data on student perceptions and outcomes, this study anecdotally demonstrates the benefits of implementing CUREs within curricula. For example, here are a few anonymous quotes from the former students:

- The CURE class was an amazing opportunity for me to expand my knowledge and skills in research. The structure of pairing lecture sessions with hands-on work in the lab was beneficial in that it allowed me to directly see and apply the information provided in lecture, further solidifying my understanding of the material. Overall, the class was a defining experience that heightened my interest in scientific research.

- I believe that classes like this [CURE course] give everyday students who may or may not have had an opportunity or a network connection into research a gradual start and a safe environment to learn. I am fortunate enough to be introduced to a seamless transition into this environment, and now I love it. If it hadn't been for this class, I would have been too intimidated to get into research and would not have learned major skills that I carry with me through my journey through [graduate] school today.

- The class allowed more hands-on opportunities than a standard lecture-based course as students helped collect data for a current experiment. Using different aspects of the scientific method while working on an actual experiment provides an understanding that cannot be gained from a regular lecture class. Active learning was employed with students reading primary research articles prior to class. Discussions with instructors were great and many different aspects of science were discussed from getting articles published to applying for graduate [school]. Another benefit was that the instructor to student ratio was much higher than a standard university course.

Chapter 3

WOODY VEGETATION REMNANTS WITHIN PASTURES INFLUENCE LOCUST DISTRIBUTION: TESTING BOTTOM-UP AND TOP-DOWN CONTROL

This chapter has been published in *agriculture ecosystems and environment*; See Appendix B

Chapter 4

MISMATCHED DIETS: DEFINING THE NUTRITIONAL LANDSCAPE OF GRASSHOPPER COMMUNITIES IN A VARIABLE ENVIRONMENT.

4.1 Introduction

Environmental variability has an important influence on animal population dynamics (Bjornstad and Grenfell, 2001) especially in drylands (Noy-Meir, 1973, 1974; Whitford, 2002). For example, female kangaroos (*Macropus spp.*) can delay egg development for months until food is available (Clark and Poole, 1967; Dawson, 1995). This creates boom and bust population dynamics that correspond with the variable rainfall of inland Australia (Caughley *et al.*, 1985; Morton *et al.*, 2011). Nutrient availability is generally recognized as an important driver for animal populations (Andrewartha and Birch, 1954; White, 1993; Denno, 2012; Hunter *et al.*, 2012). However, few studies have looked at the relationship between free-ranging herbivore nutritional demands and available plant nutrient dynamics within variable environments (Nie *et al.*, 2015). In this study, we examined how the nutritional preferences of three grasshopper species, two migratory and one non-migratory, vary with grassland nutrient content.

Plant nutrient contents (e.g, macronutrients like protein and carbohydrate or elements like carbon, nitrogen, and phosphorus) are more variable than the body composition of herbivores (Elser J. J. *et al.*, 2000). To address this imbalance, generalist herbivores graze multiple plants to acquire an optimal nutrient blend, termed the intake target (Simpson and Raubenheimer, 1993, 2012; Behmer, 2009). The balance of protein and carbohydrates is particularly important for insect herbivores (Behmer,

2009). For example, Mongolian locusts (*Oedaleus asiaticus*) restricted to suboptimal diets that were either too high in protein or carbohydrates had reduced survival, growth rate, and migratory capacity compared to individuals given an optimal diet (Cease *et al.*, 2012, 2017). When confronted with suboptimal nutritional landscapes, herbivores can behaviorally select for optimal food sources (pre-ingestively regulate), ingest suboptimal foods and extract optimal nutrients in the gut (post-ingestively regulate), or a combination of both (Behmer, 2009). One option to pre-ingestively regulate nutrients may be migration. Migration is an important aspect for many animals ranging from vertebrates to invertebrates (Dingle, 2014) and with global change, migrations are being altered or disappearing completely (Wilcove and Wikelski, 2008). Understanding the nutritional foraging strategies of migratory animals can illuminate mechanisms of their persistence in variable environments.

Grasshoppers (Orthoptera: Acrididae) are the dominant herbivores in grasslands (Branson *et al.*, 2006) and are important for nutrient cycling (Belovsky and Slade, 2000), food chains (Gandar, 1982; Schmitz, 1994), and can threaten food security as pests (Cease *et al.*, 2015; Cullen *et al.*, 2017). Therefore, understanding how grasshoppers meet their nutritional demands in the face of environmental variability has important multifaceted implications from conservation to agriculture. Migration is a common trait in grasshoppers, especially in locusts. For example, the Australian plague locust (*Chortoicetes terminifera*, Walker 1875) is able to fly over 500 km in a single night (Symmons and McCulloch, 1980). However, there is a spectrum of migratory capacity within grasshoppers with some species entirely lacking flight capacity (e.g. the Plains lubber grasshopper, *Brachystola magna*) to extreme migratory capacity (e.g. locusts). This difference likely impacts how individuals meet nutritional demands with some species being able to access more plants (e.g. migratory species) than others (e.g. non-migratory species).

In this study, we investigated the spatiotemporal variation in grass nutrient contents and intake targets of three grasshopper species: *C. terminifera*, *Oedaleus australis* (Saussure, 1888), and *Aiolopus thalassinus dubios* (Willemse, 1923) at three locations in New South Wales, Australia. *C. terminife* and *O. australis* are highly migratory (Rentz 2003) while *A. thalassinus* is likely non-migratory (Hafez and Ibrahim, 1962; Heifetz and Applebaum, 1995). Since grass nutritional content changes with phenological stages, we predicted that the nutritional landscape for grasshoppers would temporally change, with early season grasses (e.g. sprouting/growing) being higher in protein (Skarpe and Bergström, 1986). Spatially, since the marginal croplands of eastern Australia have a higher soil fertility than the arid interior (Morton *et al.*, 2011), we predicted that grasses closer to the coast would have more protein relative to those further inland (Fig. 4.1). Since migratory species can migrate to locate nutritionally optimal plant sources, we expect them to keep their intake targets constant. Whereas, non-migratory species have access to fewer plants, we expect them to change their intake targets to reflect a given environment, as we predict they will rely more heavily on post-ingestive regulation.

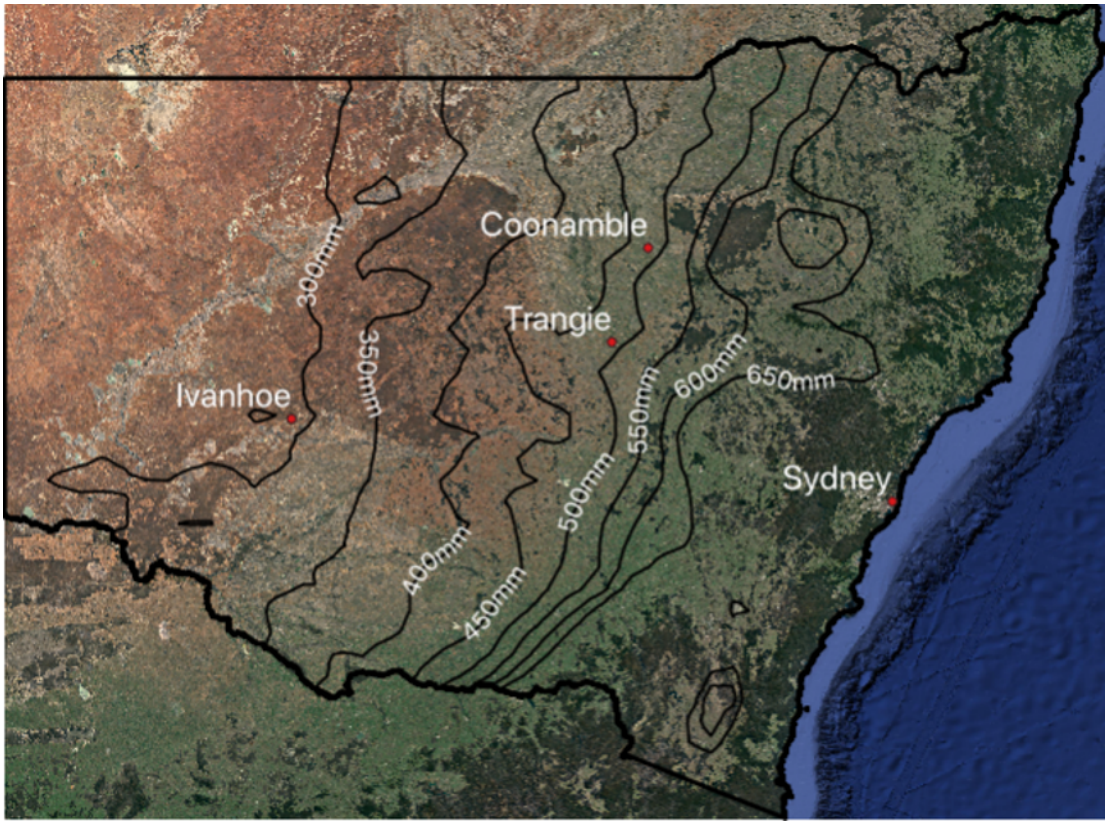

Figure 4.1: Site Locations in New South Wales, Australia. Average Rainfall Shown as Isohyets.

4.2 Methods

4.2.1 Natural history of species

C. terminifera is a widely distributed grasshopper throughout Australia's arid interior (Hunter *et al.*, 2001; Chapuis *et al.*, 2011) and can migrate long distances given optimal weather patterns (Symmons and McCulloch, 1980). This species is also a major economic pest of rangeland crops (Adriaansen *et al.*, 2015). Whereas other species in the genus are pests (Le Gall *et al.*, 2019a), *O. australis* is not a pest species but is widely distributed and highly migratory (Rentz, 2003). *A. thalassinus* is not an pest species however little has been reported on this Australian subspecies

(Rentz, 2003). All species are likely grass generalists, although more is known about *C. terminifera* than either *O. australis* or *A. thalassinus* (Key, 1945, 1959; Bernays and Chapman, 1973; Rentz, 2003).

4.2.2 Field surveys

Field selection

We selected three locations where we were likely to find significant grasshopper populations throughout New South Wales, Australia: Trangie, Coonamble, and Ivanhoe (Fig. 4.1). At each location, two fields (ca. 5-10 km_2) were selected to account for localized variation. Due to a low regional population of grasshoppers, we were only able to collect data from one field in Ivanhoe. All fields except for Ivanhoe were used for livestock grazing and dominated by native grasses. The Ivanhoe field was a grassy roadside area. On the landscape level, the areas surrounding Trangie and Coonamble included a mixture of crop fields (predominately wheat) and grazing areas, whereas Ivanhoe was predominantly made of grazing fields (Jackson *et al.*, 2018).

Vegetation survey

To define the nutritional landscape, we conducted vegetation surveys using the relevé method (Poore, 1955; Resources, 2013) and collected plant samples for nutrient analyses. In general, assessing plant communities is difficult, however the relevé is a common technique that balances efficiency and time and is widely used (Mueller-Dombois and Ellenberg, 1974; Barbour *et al.*, 1980; Moore and Chapman, 1986; Committee, 2000). We randomly selected 5 points within each field. Each point was at least 10 m from the field edge and 20 m from each other. The sampling quadrat was 5 m by 5 m. Within the quadrat, we recorded total aboveground vegetation cover, percent manure, litter, rock, and the top three plant species cover (Table C.1 & C.2, Figure

C.1). All cover variables were given a ordinal categorical level as follows: 0 = 0% cover, 1 = 1% - 5% cover, 2 = 6% - 10% cover, 3 = 11% - 25% cover, 4 = 26% - 50% cover, 5 = 51% - 75% cover, 6 = 76% - 100% cover as done previously (Resources 2013, Word et al. 2019).

For nutrient analysis, we only collected leaves and not stems since they are preferentially eaten by grasshoppers and avoided dead or dry plant material. Leaves of each species were collected randomly from individual plants throughout the quadrat and gathered in one species-specific sample. Plants were put into a drying oven at 60^{o}C for 48h soon after sampling. Dried samples were carried back to Arizona State University and ground using a Retsch MM 400 ball mill for 30 seconds at 200 rpm. To measure leaf carbohydrate and protein content, we used the Bradford protein (Bradford 1976) and phenol-sulfuric carbohydrate (Dubois *et al.*, 1956) colorimetric assays following the Deans *et al.* (2018) procedure.

Grasshopper abundance. — To determine how grasshopper populations changed, we sampled grasshoppers at each field site and time point. The collection dates were as follows:

- Trangie early: October 19th, 2017
- Trangie late: November 23rd and 24th, 2017
- Coonamble: November 29th, 2017
- Ivanhoe: December 3rd, 2017

We also recorded temperature, geographical coordinates, and wind speed (Ambient weather WM-4) (Table C.3). Grasshopper abundance was assessed with sweep netting along 5, 100 m transects evenly distributed throughout the field. At the end of each transect, sweep net content was stored in a gallon plastic bag and placed in

a cooler on ice. To avoid sampling bias, the same observer (D. Lawton) recorded all grasshopper abundance data. Bags were then frozen and stored at -20°C for two days after which grasshoppers were identified to species level if possible and counted as either adult or nymph (Table C.4). For a given time point (early or late in the season) and location, we collected all data on the same day within 6 hours.

4.2.3 Grasshopper intake target experiment

Grasshopper collection

We attempted to collect 24 adult individuals (12 males and 12 females) for each species at each location and time point where they were present. However, due to the population sizes we were unable to collect 24 of each species and there were significant die offs in some populations (Table C.5). We performed intake targets on adult grasshoppers only because they were usually the most dominant life stage and more accessible overall (Table C.5). Grasshoppers were collected in the same field, kept in mesh cages for a maximum of 24 hours, and fed a mix of grass species from the area they were collected until they were added to the intake target experiment.

Diet preparation

To control for nutrient availability within the experiments, we used isocaloric artificial diets made up of 42% macronutrients (differing ratios of protein and carbohydrates), 32% cellulose, and 4% of salt, sterols and vitamins. All diets were made in the laboratory at ASU and kept in a freezer whenever possible following protocol similar to other studies (Clissold *et al.*, 2014; Cease *et al.*, 2017; Le Gall *et al.*, 2019b) which was developed by Simpson and Abisgold (1985) from Dadd (1961).

Intake target collection

To confirm that populations were regulating protein and carbohydrates, individuals from each species received two synthetic diet pairings differing in their protein (P) and carbohydrates (C) ratios (P35:C7 and P7:C35 or P28:C14 and P7:C35) (Chambers *et al.*, 1995). Grasshoppers were kept in plastic containers (26 x 20 x 5 cm) with holes for aeration for three days. Each cage contained one pair of diet dishes, a water tube, and a perch. For each cage, we collected grasshopper initial and final mass and consumption.

We ran the experiments at the Trangie Agricultural Research Centre, Trangie, NSW where grasshoppers were exposed to the natural photoperiod (12:12 h L:D). In addition, we hung 6, 60 W light bulbs above the cages and set an automatic timer to turn on between 10:00 and 16:00. We recorded temperature (^{o}C) and relative humidity (RH) using Hobos (Thermochron, Maxim Integrated) placed on the shelves in between cages (Table C.6). All diets were kept in a freezer until needed. Afterwards, we dried all diet dishes for 48 hours at 60 ^{o}C which allowed us to control for biases from water absorption.

Spatial change in intake target

At each location, we ran intake target experiments on the two or three dominant grasshopper species:

- Trangie: *C. terminifera* and *A. thalassinus* (started on November 11th, 2017)
- Coonamble: *C. terminifera* and *O. australis* (started on November 29th, 2017)
- Ivanhoe: *C. terminifera*, *A. thalassinus*, and *O. australis* (started on December 4th, 2017)

4.2.4 Temporal change in intake target

We repeated the experiment twice for *C. terminifera* grasshoppers caught at the Trangie field station. The early intake target was collected on October 13th, 2017 and late intake targets on November 11th, 2017.

4.2.5 Statistical approach

All data were assessed for normality and heteroskedasticity before statistical analyses. Transformations or nonparametric analyses were conducted where appropriate. For grass nutrients, we performed ANOVAs, Tukey HSDs for spatial variation and Welch's t-tests for temporal variation tests (e.g. Fig. 4.2). Traditionally, intake targets are analyzed through multivariate analysis of covariance (MANCOVAs) with initial starting mass as a covariate (Le Gall *et al.*, 2019b). However, we used generalized additive models because they could be constructed with the same statistical family (multivariate gaussian distribution) (Wood, 2017) and have the added benefit of selecting for non-linear relationships. This allowed us to statistically test whether there was a trend (linear or nonlinear) between macronutrient content consumption and initial body mass. We constructed a model for each species with the dependent variables being total protein and carbohydrates consumed and independent variables being location, sex, treatment pair (to determine non-random feeding), and initial body mass. To determine the best fit models, we first used null space parametrization (Marra and Wood, 2011) then Akaike information criterion (AIC). Since we were interested in sex and treatment differences, we left these in the models and selected only for the inclusion of initial body mass being either a non-linear effect, linear effect, or removed entirely for each macronutrient (Table C.7-C.9). To determine how well each intake target overlapped with the available grass nutrients, we calculated

Euclidean distances of each grass sample to the intake target slope (the ratio of P:C) using the following equation, similar to Le Gall *et al.* (2019b):

$$\frac{m(X_o) - Y_o}{\sqrt{1 + m^2}} \tag{4.1}$$

where m is the slope of the intake target, X_o and Y_o are each unique grass specimen's coordinates. Positive Euclidean distances represent plants that are protein-biased and negative distances are carbohydrate-biased, relative to the grasshopper population intake target. To test for differences between intake targets and plant nutrient contents, we used one sample t-tests with $\mu = 0$. To test the differences between species dominance within communities, we conducted MANOVAs for spatial variation and t-tests for temporal variation tests. Since there are issues with depicting changes in nutrients as ratios (Raubenheimer, 1995), we have included separate plots with intake targets represented as slopes for each species by location for comparison (e.g. Fig. 4.5). This allows for visualization of changes in both nutrients that may be masked by taking a simple ratio. All statistics were conducted in the *tidyverse* framework (Wickham, 2018) within the R statistical environment (R Core Team, 2018). Generalized additive models were constructed with *mgcv* (Wood, 2017) and validated with *mgcViz* (Fasiolo *et al.*, 2018). Multicomponent analyses were conducted in *multcomp* (Hothorn *et al.*, 2009).

4.3 Results

4.3.1 Spatial variation

Grass nutrient content

Grass protein content varied while carbohydrate content did not significantly differ among sites (Fig. 4.2A). Grass protein content at Trangie was significantly higher than at either Coonamble or Ivanhoe (Fig. 4.2A). This shift in the protein content led to a change in the overall P:C ratio from being more carbohydrate biased in Coonamble and Ivanhoe to protein biased in Trangie.

Grasshopper abundance

Grasshopper species dominance varied spatially (MANOVA: $F_{4,19}$= 21.341, Pillai's= 1.620, P-value: $<< 0.001$). *C. terminifera* was the dominant species in Ivanhoe, *A. thalassinus* was the dominant species in Trangie, and *O. australis* was the dominant species in Coonamble (Fig. 4.3A; Table C.10).

Intake target variation

Both *C. terminifera* and *A. thalassinus* intake targets changed between locations, whereas *O. australis* did not (Fig. 4.4 & 4.5; Table 4.1 & 4.2). However, *A. thalassinus* intake targets changed considerably more than *C. terminifera* populations. *C. terminifera* intake targets at Trangie and Ivanhoe were roughly 0.55 P : 1 C and changed to 0.73 P : 1 C in Coonamble while *A. thalassinus* was 1 P : 1 C in Trangie and 0.58 P : 1 C in Coonamble (Table 4.3, Figs. C.2 and C.3).

A. thalassinus carbohydrate consumption was significantly higher in Trangie than Ivanhoe populations (Fig. 4.4A; Table 4.1). All *C. terminifera* populations had roughly the same intake targets with the Ivanhoe population slightly changing protein

consumption. The Coonamble population ate more macronutrients combined than either Trangie or Ivanhoe even when body mass was accounted for (Figs. 4B & 5A, D, G).

Intake target and nutritional landscape

For both *C. terminifera* (t-test: t = 3.583, df = 15, P = 0.003) and *A. thalassinus* (t-test: t = 3.155, df = 15, P = 0.007), the grass at Trangie was more protein biased than their intake targets (Figs. 5D & E, 6A). There was a general trend of grasses at Ivanhoe being too carbohydrate biased compared to their intake targets for both *A. thalassinus* and *C. terminifera* (Figs. 4.5A & B, 4.6A). *O. australis* had landscapes that matched their intake targets (Figs. 4.5C & H & 4.6A).

Between locations, there were mismatches of plant nutrients and intake targets for *C. terminifera* and *A. thalassinus*, but not *O. australis*. For the different *C. terminifera* populations, grass nutrients differed from their intake targets (ANOVA: $F_{2,36} = 8.671$, P = 0.001), with Trangie being more protein biased than Coonamble and Ivanhoe (Tukey HSD: Trangie-Coonamble: P = 0.041; Trangie-Ivanhoe: P = 0.004) (Figs. 4.6A, 4.7A). For *A. thalassinus* populations, grass nutrients differed from their intake targets (t-test: t = 3.555, df = 10.304, P = 0.005), with Trangie being protein biased and Coonamble being more carbohydrate biased (Figs. 4.6A, 4.7B). For *O. australis*, grass nutrients did not differ from their intake targets between locations (Figs. 4.6A, 4.7D).

4.3.2 Temporal variation

Vegetation

We found a similar trend for temporal variation as spatial variation in that protein differed (Welch two sample t-test: t = 6.270, df = 41.60, p < 0.001) and carbohydrates

remained constant (Welch two sample t-test: t = -1.650, df = 48.6, P=0.105) between early and late season. Protein content was higher early in the season as compared to late (Fig. 4.2B). This led to a change in the overall P:C ratio from protein biased in the early season to carbohydrate biased four weeks later.

Grasshopper abundance

C. terminifera had low abundances in Trangie early and late in the season (Fig. 4.3B). There was no significant difference between early and late season *C. terminifera* or other grasshopper species dominance (MANOVA: Pillai's: 0.116, F2,17: 1.113, P-value: 0.351).

Intake target variation

Temporally, *C. terminifera* intake targets did not significantly differ (Table 4.4).

Intake targets and nutritional landscape

The available nutritional landscape was more protein biased than the intake targets in both early (t-test: t = 12.790, df = 14, P = $<<$ 0.001) and late (t-test: t = 10.670, df = 14, P = $<<$ 0.001) season for *C. terminifera* (Fig. 4.6B). Between the two time points, early season was more protein biased than late season as compared to *C. terminifera's* intake target (Figs. 4.5F, 4.5I, 4.6B).

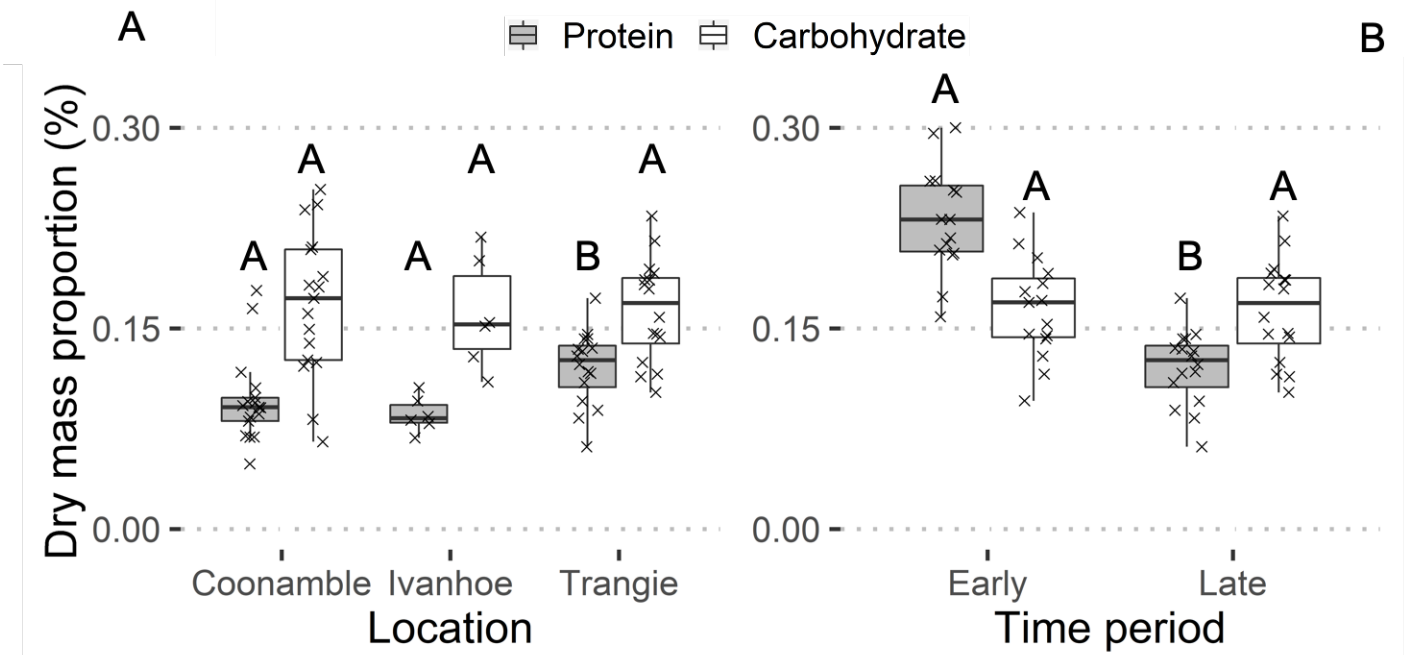

Figure 4.2: Spatiotemporal Variation in Grass Protein: Carbohydrate Ratios. A: Spatial Variation Between Coonamble, Ivanhoe, and Trangie, New South Wales. B: Temporal Variation Between Early and Late Season With ca. Four Weeks in Between. Letters Represent Significance Between Location/Time Point and Nutrient. A: Protein (ANOVA): $F_{2,36} = 4.560$, P-Value = 0.017. Carbohydrate (ANOVA): $F_{2,36} = 0.059$, P-Value = 0.943. B: Protein (Welch Two Sample T-Test): T = 6.270, Df = 41.60, P-Value = < 0.001, Carbohydrate (Welch Two Sample T-Test): T = -1.650, Df = 48.60, P-Value = 0.105.

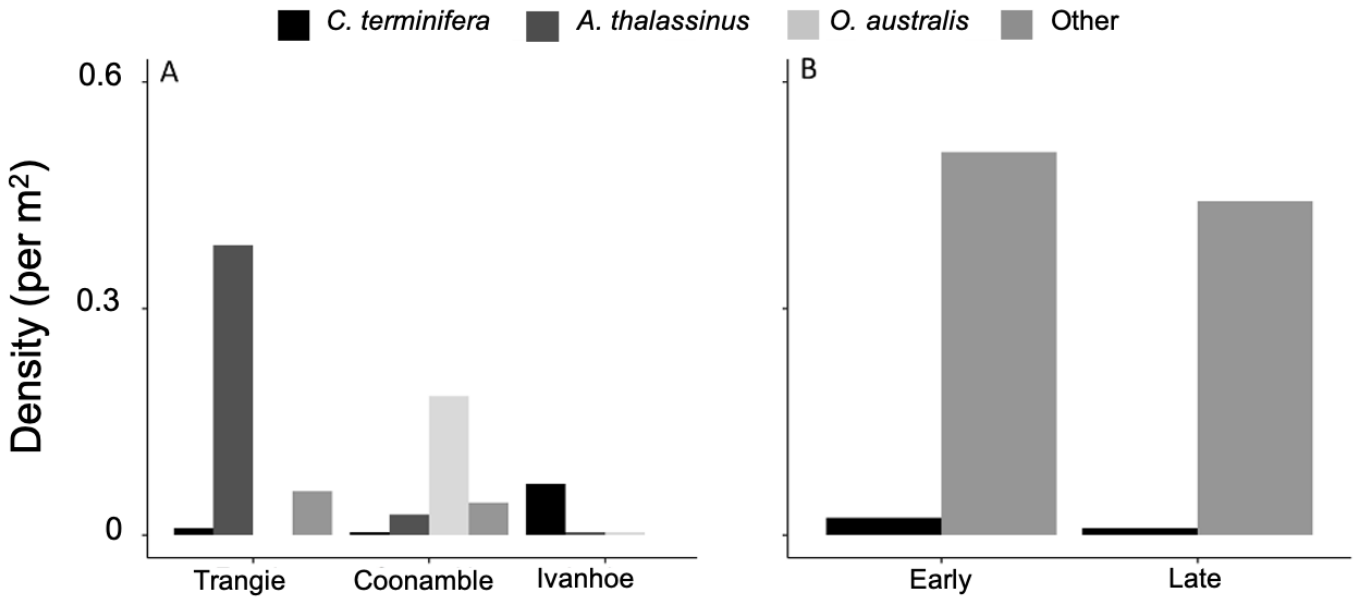

Figure 4.3: Grasshopper Community Composition for Spatial (A) and Temporal (B) Studies. Note That the Temporal Study Was Only Conducted in Trangie.

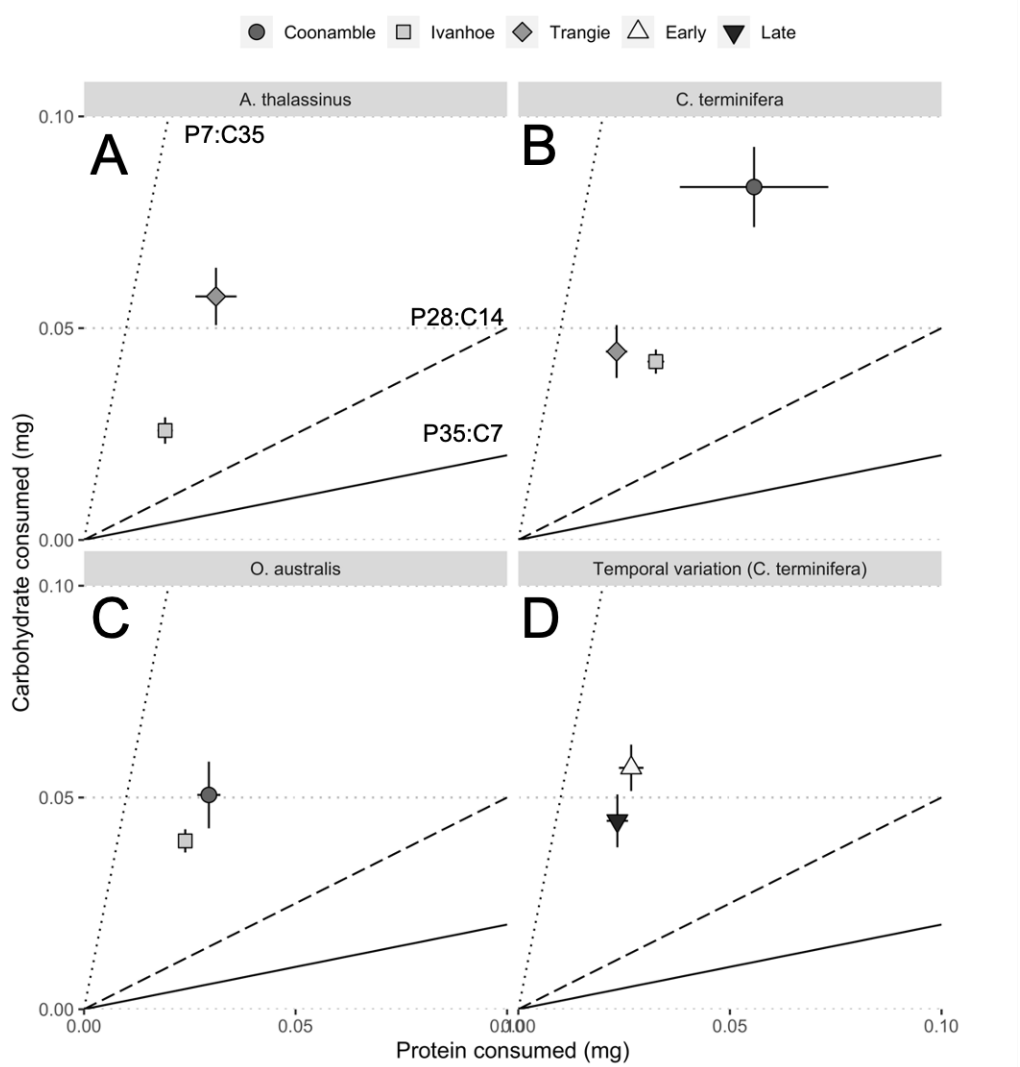

Figure 4.4: Intake Targets for Each Species by Location (Panels A, B, and C) and for C. Terminifera Through Time (Panel D). The Dotted Lines Represent the P7:C35, Dash Lines Represent P28:C14, and Solid Lines Represent P35:C7.

Table 4.1: Generalized Additive Model Parametric Coefficient Results for the Spatial Change of Macronutrient Consumption (Carbohydrate and Protein) by Species. Bold Values Indicate Significance. Models Were Selected via AIC and Can Be Seen in C.7-C.9.

Species	Macronutrient	Variable	Estimate	Std. Error	Z value	P-value
C. terminifera	Carbohydrates	Intercept	0.12	0.011	10.901	**<<0.001**
		Ivanhoe	-0.047	0.009	-5.328	**<<0.001**
		Trangie	-0.047	0.009	-5.078	**<<0.001**
		Sex	-0.06	0.017	-3.6	**<<0.001**
		Treatment	0.005	0.006	0.733	0.464
	Protein	Intercept	0.069	0.015	4.657	**<<0.001**
		Ivanhoe	-0.028	0.014	-1.994	**0.046**
		Trangie	-0.039	0.014	-2.734	**0.006**
		Sex	-0.01	0.012	-0.863	0.388
		Treatment	-0.009	0.01	-0.889	0.374
A. thalassinus	Carbohydrates	Intercept	0.023	0.009	2.672	**0.008**
		Ivanhoe				
		Trangie	0.033	0.008	4.222	**<<0.001**
		Sex	-0.006	0.013	-0.447	0.655
		Treatment	0.006	0.008	0.831	0.406
	Protein	Intercept	0.018	0.006	2.899	**0.004**
		Ivanhoe				
		Trangie	0.012	0.006	1.85	0.064
		Sex	-0.005	0.007	-0.834	0.404
		Treatment	0.006	0.006	0.951	0.341
O. australis	Carbohydrates	Intercept	0.051	0.01	4.905	**<<0.001**
		Ivanhoe	-0.01	0.015	-0.651	0.515
		Trangie				
		Sex	-0.003	0.013	-0.257	0.797
		Treatment	0.001	0.012	0.107	0.915
	Protein	Intercept	0.034	0.003	10.102	**<<0.001**
		Ivanhoe	-0.005	0.005	-1.069	0.285
		Trangie				
		Sex	-0.002	0.004	-0.512	0.609
		Treatment	-0.007	0.004	-1.675	0.094

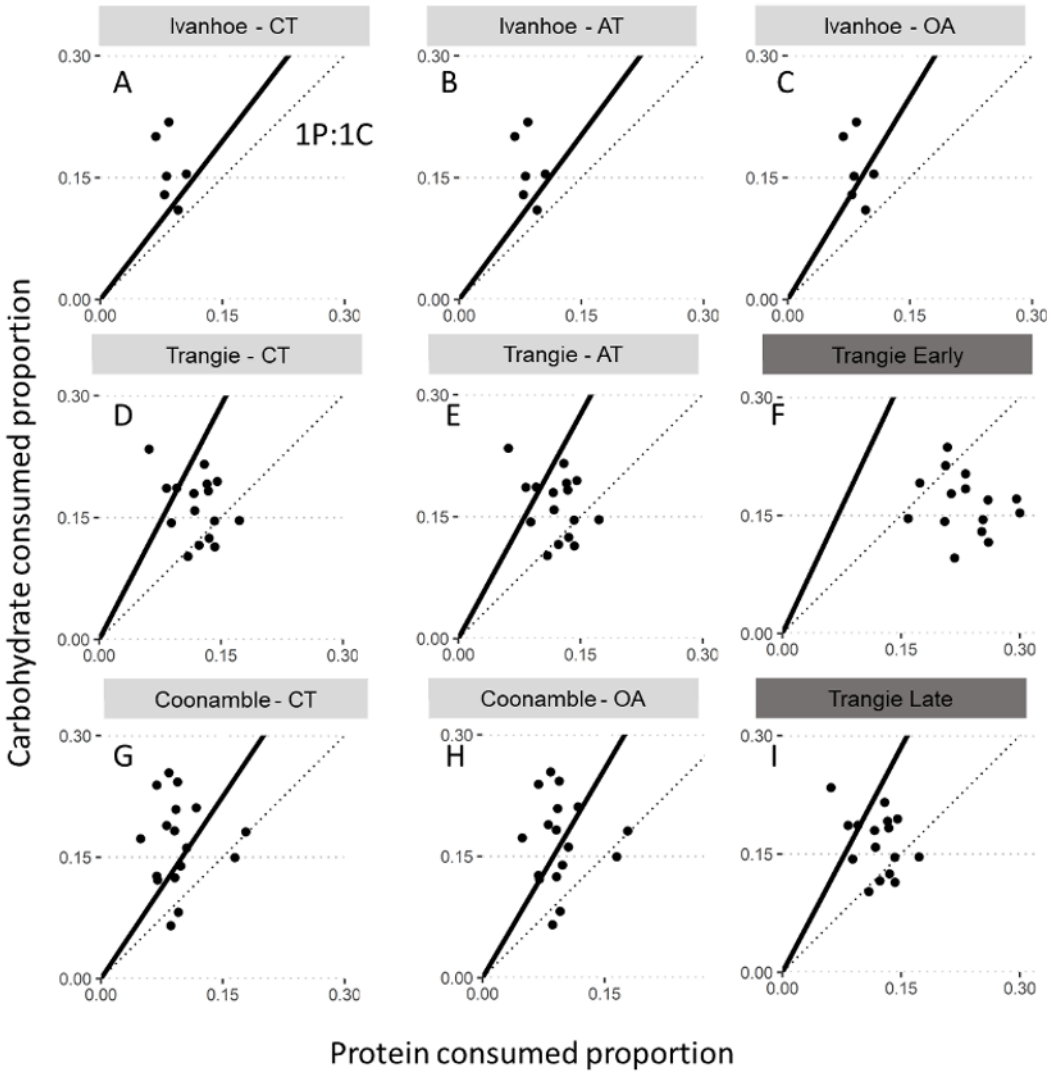

Figure 4.5: Intake Target C:P Ratio (Solid Line) Overlapping With Grass Nutrient Availability (Points) by Species in Each Location and Time Point. Dotted Line Is a Reference Line With Slope of 1P:1C. Early and Late Graphs Are With C. Terminifera Only. CT: C. Terminifera, At: A. Thalassinus, OA: O. Australis.

Table 4.2: Generalized Additive Model Non-Parametric Coefficient Results for the Spatial Change of Macronutrient Consumption (Carbohydrate and Protein) by Species. O. Australis' Model Did Not Have Non-Parametric Coefficients. Models Were Selected via AIC and Can Be Seen in C.7-C.9. Significance Shown in Bold. EDF = Estimated Degrees Freedom.

Species	Macronutrient	Variable	edf	Ref.df	X_2	p-value
C. terminifera	Carbohydrate	Grasshopper Weight	1.565	9	11.461	**<<0.001**
A. thalassinus	Carbohydrate	Grasshopper Weight	2.231	9	19.85	**<<0.001**

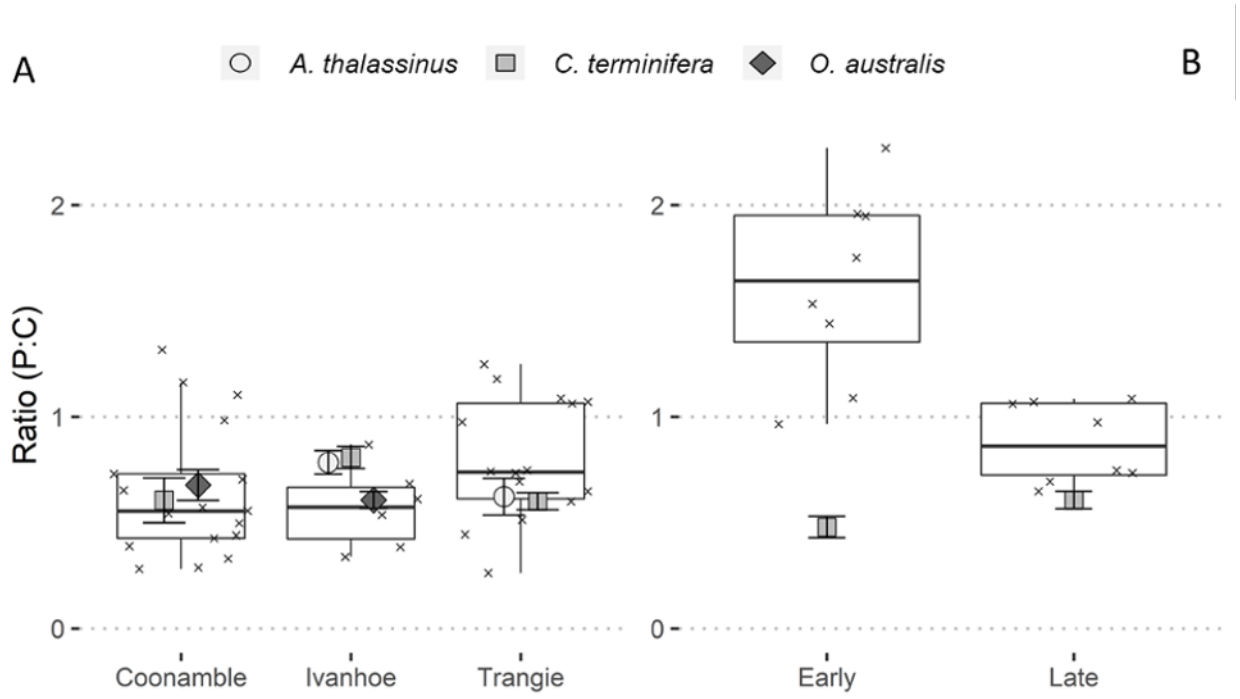

Figure 4.6: Grasshopper Population Intake Targets (Solid Symbols), Overlaying Their Available Nutritional Landscape (Boxplots and X Symbols). Panel A: Spatial Change in Intake Targets and Grass Protein (P) : Carbohydrates (C). Panel B: Temporal Change in C. Terminifera Intake Targets and Grass P : C.

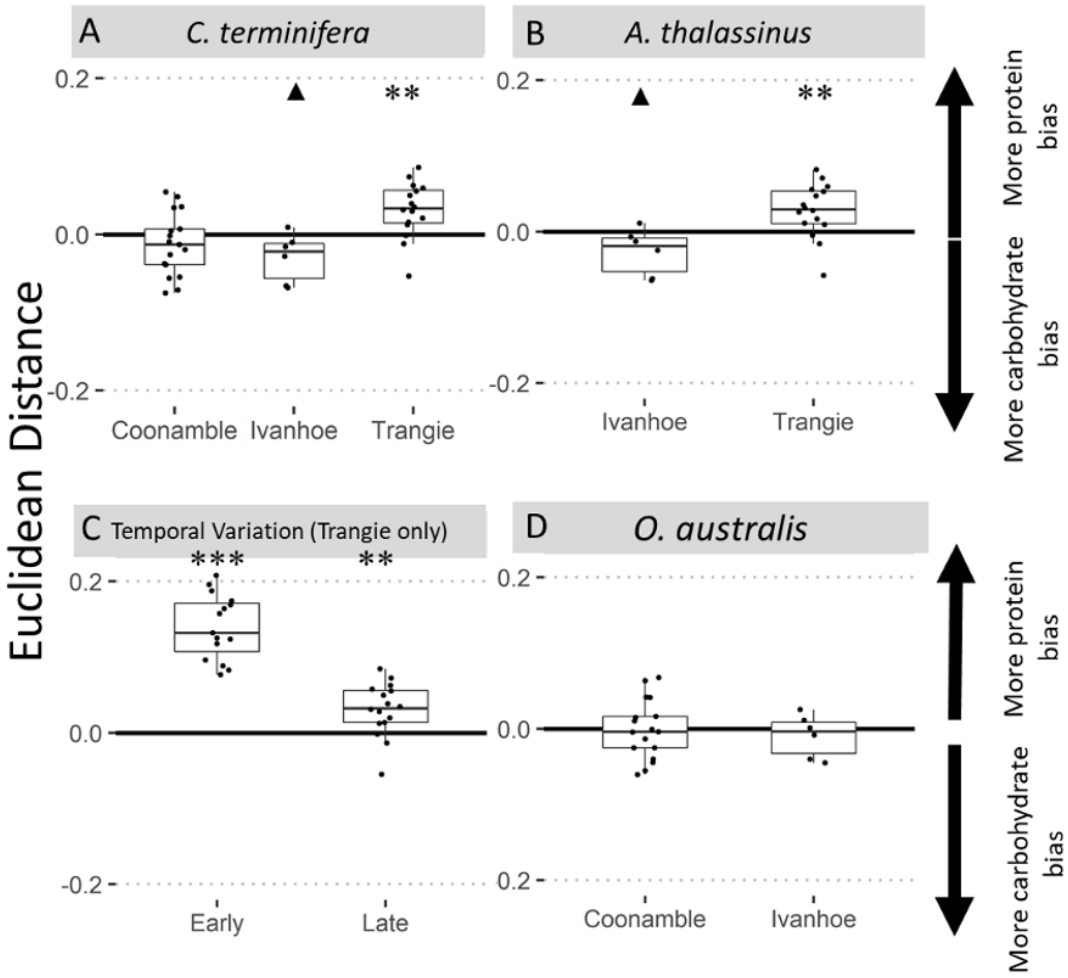

Figure 4.7: The Euclidean Distance Between the Grasshopper Intake Targets and the Grass Nutrients Available in the Landscape at the Given Place (A,B,D) and Time (C). Negative Values Represent Vegetation That Was Carbohydrate-Biased Relative to Each Grasshopper Species' Intake Target; Positive Values Represent Vegetation That Was Protein-Biased Relative to the Intake Target. Distances of 0 Represent a Perfect Match of Grass Relative Protein and Carbohydrate Contents With an Intake Target. Asterisks Represent a Significant Deviation From a Euclidean Distance of 0 for a Given Grass Community and Grasshopper Intake Target (From One Sample T-Tests (= 0), Denoted by ▲ $P < 0.10$, $*$ $P < 0.05$, $**$ $P < 0$ .01, and $***$ $P < 0.001$). Significant Deviations Suggest That a Given Grasshopper Population Will Have Difficulty Reaching Their Intake Target.

Table 4.3: Tukey Multiple Comparison Results for C. Terminifera Macronutrient Consumption. Significance Shown in Bold.

Macronutrient	Comparison		Estimate	Error	Z value	P value
Carbohydrate	Ivanhoe	Coonamble	-0.047	0.009	-5.328	**<<0.001**
	Trangie	Coonamble	-0.047	0.009	-5.078	**<<0.001**
	Trangie	Ivanhoe	<<0.001	0.008	-0.003	1.000
Protein	Ivanhoe	Coonamble	-0.031	0.014	-2.156	0.078
	Trangie	Coonamble	-0.043	0.015	-2.917	**0.010**
	Trangie	Ivanhoe	-0.012	0.013	-0.975	0.592

Table 4.4: Generalized Additive Model Results for the Temporal Change of Macronutrient Consumption (Carbohydrate and Protein) for C. Terminifera. Models Were Selected via AIC and Can Be Seen in C.3-C.5. Significance Shown in Bold.

Macronutrient	Variable	Estimate	Standard error	z value	P-value
Carbohydrates	Intercept	0.126	0.028	4.454	**<<0.001**
	Time	-0.017	0.010	-1.759	0.079
	Sex	-0.062	0.016	-3.922	**<<0.001**
	Treatment	0.008	0.008	1.061	0.289
	Weight	-0.133	0.054	-2.473	**0.013**
Protein	Intercept	0.047	0.012	3.825	**<<0.001**
	Time	-0.004	0.004	-1.057	0.291
	Sex	-0.021	0.007	-3.101	**0.002**
	Treatment	0.002	0.003	0.675	0.499
	Weight	-0.037	0.024	-1.579	0.114

4.4 Discussion

In this study, we found that at both spatial and temporal scales, host plant protein content significantly differed whereas carbohydrate content remained constant (Fig. 4.2). This was expected as early season plants had higher protein content than later season plants, and the site furthest east in the marginal croplands (Trangie) had higher protein in pastures than sites closer to the arid interior (Fig. 4.1 & 4.2). Despite the spatiotemporal shift in plant nutrient contents, both migratory grasshopper species collected from across these environments largely maintained the same preferred ratio of protein to carbohydrates when given a choice. One species (*C. terminifera*) kept the ratio constant even in suboptimal locations. In contrast, the non-migratory species changed its intake target greatly across environments, potentially to redress a nutrient imbalance driven by the locally available plants.

To persist in variable environments like the Australian arid interior, animals need to be flexible foragers, obtaining the nutrients required to meet environmentally driven and phenological demands. For example, animals will select diets that help mediate trade-offs between migration (Rankin and Burchsted, 1992), reproduction (Joern and Behmer, 1997), and growth (Joern and Behmer, 1997; Raubenheimer and Simpson, 2003). Some grasshoppers may be able to better post-ingestively regulate to meet these demands while others might employ migration to find adequate nutrients. Our results suggest that different herbivore foraging responses may reflect the unique life histories of migratory vs. non-migratory species in variable environments. However, our study was restricted to three species. We hope our initial findings spur more comprehensive studies in the future.

4.4.1 Plant nutrient content

Plant nutrients varied spatially and temporally in protein but not in carbohydrate content. A change in protein content is likely influenced by species composition, plant phenology, and climatic factors. Soil nutrient uptake varies considerably between species and it is thought uptake differences are accentuated with nitrogen (Bradshaw *et al.*, 1964; Lunt, 1972). Since most plant protein is in the form of nitrogen (White, 1993), a spatiotemporal variation in protein content is not unexpected. Ivanhoe is not within the cropping zone and was a road side, unlike Trangie and Coonamble which likely have a history of fertilizer application and/or greater naturalized legume populations (Jackson *et al.*, 2018). Therefore, grasses in Ivanhoe may have less soil nitrogen available to uptake. However, Coonamble had similar protein levels as Ivanhoe which may be an indication of the differing plant species life histories, soil types, fertilization or livestock rates than Trangie.

4.4.2 Grasshopper intake target regulation

Spatiotemporally, all grasshopper populations, except for the *C. terminifera* Coonamble population, consumed a consistent amount of protein. The demand for protein may remain relatively constant because it is important for maintaining and repairing body tissues as compared to carbohydrate consumption (Harrison *et al.*, 2012). On the other hand, carbohydrates and lipids are important for providing animal energy requirements (Chapman, 1998). Since energy demand will vary in response to changing activity levels (Arrese and Soulages, 2010), carbohydrate consumption will likely be based on environmental cues and life history traits. For example, *Locusta migratoria* (Linnaeus, 1758) individuals that conducted a long distance flight of 120 minutes significantly impacted the carbohydrate but not the protein consumption compared

to inactive individuals (Raubenheimer and Simpson, 1999).

We found that grasshopper intake targets varied between populations but were consistently carbohydrate biased and never had an intake target ratio more protein biased than P1:C1. This suggests that their demands for carbohydrates never exceeded their demands for protein. This is congruent with previous studies that found many locust or swarming grasshopper species are carbohydrate biased overall (Cease *et al.*, 2012; Le Gall *et al.*, 2019b,a), in contrast to the nitrogen limitation (e.g. protein biased) paradigm that fits for many herbivores (Mattson, 1980; Scriber, 1984; White, 1993). However, the intake targets in this study were short (three days long) and could indicate a redressing of a nutrient imbalance. Due to this, further research is needed to understand the tradeoffs between animal nutrient intake plasticity in relation to a given environment and physiological demands (e.g. development vs. migration).

4.4.3 Adaptations to nutritionally variable environments

Environmental variability influences responses at the individual organism to the population levels (Lande, 1993). There are many approaches for accommodating changes in nutritional landscapes which are likely life history specific. Migrations are hypothesized to play an important role in the overall persistence of many animals in variable environments (Southwood, 1962), like the arid interior of Australia (Morton *et al.*, 2011)). In two of the three populations, *C. terminifera* intake targets remained constant and when compared to the shift seen in *A. thalassinus*, it was largely negligible (Figs. C.2 & C.3). The Coonamble *C. terminifera* population had an equal nutrient ratio but consumed more protein and carbohydrate altogether (e.g. total nutrient consumption increased) as compared to Trangie and Ivanhoe. Since the Coonamble nutritional landscape matched this species' self-selected nutri-

ent ratio, it suggests that when times are good, this species will eat more. A similar trend of holding the intake target constant was seen in *O. australis*, however we did not find a population of this species in a nutritionally suboptimal location nor was a temporal change tested. Not all grasshoppers are capable of long migrations and therefore they may have different coping strategies. *A. thalassinus* is thought to be less migratory and when confronted with suboptimal landscapes they shifted their intake-target. This suggests that they do not have the capacity to migrate across landscapes to balance their diet and are redressing a nutritional imbalance. Whereas *C. terminifera* even in the same landscape (Trangie) at two different time points held their intake target constant. This indicates that they may rely more on migration to acquire nutrients as compared to redressing a nutrient imbalance locally. However, we only investigated the intake targets of three species and the results could have been due to other life history traits. We hope that this work will spur more comprehensive studies in the future. Further, investigating the post-ingestive regulation abilities of *C. terminifera* will likely illuminate how this migratory species deals with nutritionally suboptimal landscapes.

Nevertheless, there may be foraging trade-offs between migration and post-ingestive regulation to achieve an optimal balance of nutrients. There has been much research regarding habitat stability and the evolution of migratory species and phenotypes (Roff, 1994; Dingle, 2014). While there has been some consideration in optimal forging theory and nutritional ecology (Raubenheimer and Simpson, 2018), few have looked at the migratory tradeoffs in terms of balancing nutrients. Migration is energetically intensive and in variable environments there is no guarantee that the animal or population will end up in a nutritionally optimal landscape. In environments with a high degree of rainfall variability, opportunities for follow-up rainfall at the same location and subsequent pasture growth may be rare, making it a challenge for an

animal to meet nutritional needs. Comparative nutritional studies between migratory and non-migratory animals may reveal different coping strategies for living in variable nutritional environments.

4.4.4 Nutritional landscapes within metapopulations networks

At larger scales, the landscape structure may ensure the persistence of a species within variable environments. At this scale there are many sink (e.g. suboptimal nutritional landscape) and source (optimal nutritional landscape) habitats, coined the metapopulation (Hanski *et al.*, 1997). A strong network of these habitats can lead to the overall persistence of a species. For example, even with extinction-prone local populations of two predator/prey protists species, they are able to persist in a metapopulation structure (Holyoak and Lawler, 1996a,b). The total number of patches and interconnectivity of the metapopulation structure is important for the overall persistence of organisms (Wu *et al.*, 1993; Hill *et al.*, 1996; Hanski, 1998). Thus, an insect herbivore species may be able to obtain the required nutrients in variable environments at larger scales.

Chapter 5

SEEING THE LOCUST IN THE SWARM: ACCOUNTING FOR SPATIOTEMPORAL HIERARCHY IMPROVES ECOLOGICAL MODELS OF INSECT POPULATIONS

5.1 Introduction

The spatiotemporal dynamics of populations has been a central theme in ecology for over a century (Grinnell, 1917; Davidson and Andrewartha, 1948; Andrewartha and Birch, 1954; Macarthur, 1958; Hanski, 1998). However, there remains wide scope for investigating and understanding the abiotic (e.g. climate, geological variances) and biotic (e.g. food availability) factors affecting each species (Council, 2001; Sutherland *et al.*, 2013; Padilla *et al.*, 2014; Stacey, 2017). Numerous researchers have acknowledged that ecological phenomena operate on multiple spatiotemporal scales (Senft *et al.*, 1987; Wiens, 1989; Levin, 1992; Wu and Loucks, 1995). For example, caribou and elk populations are distributed by multi-scale resource selections: from individual and herd home ranges, to the entire species range (Johnson, 1980; Johnson and Barton, 2004; Coe *et al.*, 2011; Decesare *et al.*, 2012). Schooling fish and krill organize into three levels: individuals congregate in schools or swarms which are congregated into patches linked to mesoscale environmental features, and finally these patches are aggregated in areas that reflect habitat constraints at range boundaries (Murphy *et al.*, 1988; Fauchald *et al.*, 2000; Fauchald and Erikstad, 2002; Fauchald and Tveraa, 2006). Since vegetation and consequently animals are heterogeneously distributed because of spatiotemporal variation in climatic and other abiotic factors (Watt, 1947; Greig-Smith, 1979; Condit *et al.*, 2000; Ives *et al.*, 2008), a spatiotemporal hierarchy

of animal population dynamics must be acknowledged.

The hierarchical patch dynamics paradigm (HPD) allows for linkages between spatial and temporal scales through a nested model of patches within patches (Kotliar and Wiens, 1990; Wu and Loucks, 1995). This paradigm can capture the inherent complexity of landscape level analyses which have emergent properties that arise across different scales (Newman *et al.*, 2019). HPD can integrate multiple scales whereas most current approaches that attempt to address scale, model the levels independent of each other. In a review of multi-scale habitat selection studies, McGarigal *et al.* (2016) found only 20% (173 out of 859) were quantitative and met the definition of being multi-scale (modeling multiple levels independently). This can be problematic because many animal populations do not act on single spatiotemporal levels. Here we model the hierarchical nature of outbreaks of two locust species (Fig. 5.1): the desert locust (*Schistocerca gregaria*, Forskål 1775) and the Australian plague locust (*Chortoicetes terminifera*, Walker 1870).

Locusts are grasshoppers that go through periodical population irruptions (outbreaks) which influence ecosystem functioning (Barbosa *et al.*, 2012) and also pose significant issues to food security globally (Cullen *et al.*, 2017). Therefore, it is important to understand locust population regulation. The majority of locust species live within variable dryland ecosystems which are characterized by the resource-pulse paradigm (Noy-Meir, 1973, 1974; Whitford, 2002; Schwinning and Sala, 2004; Morton *et al.*, 2011). Specifically, precipitation leading to vegetation growth supports increases in locust populations (Chapman and Joern, 1990). Most forecasting and predictive models have therefore been driven by some combination of preceding climate including precipitation, soil moisture and vegetation growth, such as the normalized difference vegetation index (NDVI) derived from earth observation satellites (Cressman, 2013; Deveson, 2013; Piou *et al.*, 2013, 2019; Mangeon *et al.*, 2020).

Several locust species are suitable models for examining scaling issues in animal population dynamics. This is because locust outbreaks develop in response to ecological conditions across very large geographical ranges. For example, Veran *et al.* (2015) showed using an occupancy modeling approach that Australian plague locust outbreak probability changes spatially and a hierarchical modeling approach can improve predictive and forecasting models. Similarly, desert locust outbreak probability likely varies spatially as well since desert locusts can outbreak anywhere from West Africa to India (Uvarov, 1977), an area encompassing enormous variations in abiotic and biotic variables. Vegetation, which is important for locust populations to build, changes in structure, nutrient availability, and community composition between geographical areas and seasons (Watt, 1947; Greig-Smith, 1979; White, 1983). Therefore, accounting for multiple spatiotemporal levels via the HPD in a single modeling framework could support hypotheses about locust plague ecology that are untested at local to global scales.

For this study, the spatiotemporal hierarchy of locust outbreaks are broken into four biologically relevant levels (Fig. 5.1; larger pictures can be found in Figs. D.1-D.3). The 'species range' level is the entire range where outbreaks of each locust species have been observed. At this level, the important factors are migration (and large-scale climatic factors (e.g. El Niño Southern Oscillation, Indian Ocean Dipole, Southern Annular Mode, and climate change). The second level involves large geographic areas that experience similar climatic conditions (e.g. seasonal rainfall zones). The third level includes bioregions or ecoregions with similar abiotic and biotic conditions (e.g. soil characteristics, rainfall, vegetation condition, etc.). The final level is a temporal division by season, as all higher levels vary based on the time of the year due to changing temperature and rainfall. Each level poses a bottleneck which could constrain locust breeding and population increase. Therefore plagues (large-

scale outbreaks) can develop when favorable habitat conditions occur over multiple regions throughout multiple seasons.

In this study, we investigate how changes in preceding vegetation growth predicts nymphal outbreaks of two locust species that occur on different continents using four, nested spatiotemporal levels: species range > geographic region > ecoregion > season (Fig. 5.1). Since preceding herbaceous vegetation productivity is assumed essential for nymph growth and survival to adulthood, we expect it will be an important factor determining outbreaks. Due to the spatiotemporal variation of biotic and abiotic variables we expect the specific relationships between preceding vegetation growth and outbreaks to be different for each species. However, we expect that the nested spatiotemporal hierarchy will emerge as a crucial characteristic for any outbreak.

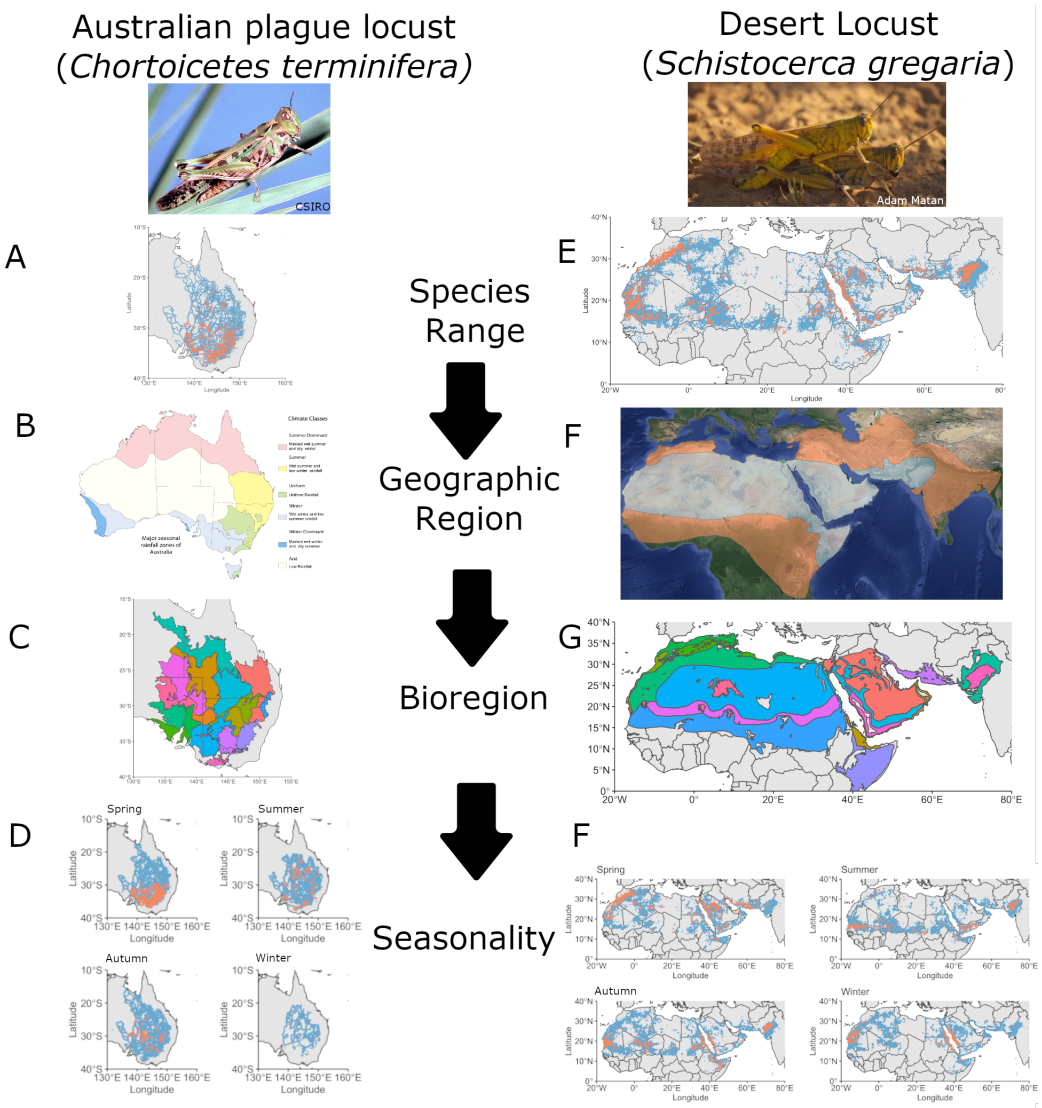

Figure 5.1: Figure 1. The hierarchical structure of Australian plague locust (A-D) and desert locust (E-H) ecology. The hierarchy is as follows: species range (A & E), geographic regions which vary based on large scale climatic patterning (B & F), bioregions which vary based on abiotic and biotic conditions (C & G), and seasonality (D & H). For clarity, we have included individual pictures within the appendix D. Pictures are both under Creative Commons 3.0 license with credit given within.

5.2 Methods

5.2.1 Locust outbreak data sources

Data for both species were obtained from survey and controls databases. We chose to analyze only nymph data as their presence more closely reflects prior proximal habitat conditions, while adults are highly mobile and can migrate over long distances. As a result of discrepancies in density categorization and identification between observers, and the low detection probability of nymphs at low densities, we decided to identify probable non-outbreaks (e.g. "0") and outbreaks (e.g. "1"). This binary threshold differed between species because data collection differed as discussed below.

Australian plague locust

Australian plague locust data between the years 2000-2017 (about 185,000 survey or report records) was provided by the Australian Plague Locust Commission and the state agricultural agencies of Queensland, New South Wales, South Australia, and Victoria. Records from each agency were adjusted to the same nymph density class schema (Deveson and Hunter, 2002). The data structure is georeferenced points with ordinal categorical response values for both adult and nymph densities. The value ranges for nymphs were: 0 = nil, 1 = <5 m^2, 2 = 5-30 m^2, 3 = 30-80 m^2, 4 = >80 m^2. Point distributions can be seen in Fig. 5.1A and a larger picture can be found in Fig. D.1A. We used a binary data schema by selecting density categories 0-2 as non-outbreaks (e.g. '0') and categories 3-4 as successful nymph outbreaks (e.g. '1').

Desert locust

Desert locust outbreak data was provided by the Food and Agriculture Organization (FAO) of the United Nations (FAO, 2020). FAO stores and cleans the data coming from the affected countries that conduct ground surveys with trained officers and generalized common standards of information reporting. This dataset spanned 19 years from 2000 to 2019, with a total of about 340,000 records. The data structure is georeferenced points that identify whether solitarious, transient, or gregarious locusts were present based on morphological characteristics of the individuals observed in each location (Cressman, 2001). Distribution of points can be seen in Fig. 5.1E with a larger picture found in Fig. D.1B. If transient or gregarious nymphs were present the record was classified as a successful outbreak. Non-outbreak records were classified if there were solitarious or no nymphs identified. This approach is similar to other studies analyzing desert locust reproduction successes (Piou *et al.*, 2017; Kayalto *et al.*, 2020).

5.2.2 From points to gridded data

We centered all data points within either a 1 km^2 grid for Australian plague locusts or 25 km^2 grid for desert locusts and collected data from that entire area to reflect nymph mobility of each species. The desert locust is considerably larger than the Australian plague locust (Fig. 5.1) and nymphs may walk up to 5 km (Ellis and Ashall, 1957), whereas Australian plague locusts generally only walk 2 km from the hatching site before becoming adults (Hunter *et al.*, 2008).

5.2.3 Biological relevant spatial level sourcing

All levels were selected to best reflect the spatiotemporal variation within each species range (Table 5.1). For the Australian plague locust, we used the major rainfall

classification zones as the geographic region level which are six large climatic zones based on seasonal rainfall distribution (https://www.bom.gov.au) (Fig. 5.1B; Figure D.2). For bioregions, we used the Interim Biogeographic Regionalisation for Australia (IBRA) version 7 dataset (https://www.environment.gov.au/land/nrs/science/ibra) (Fig. 5.1C; Fig. D.2). For seasonality, there are few records from winter months because the bulk of the population are in dormant eggs stages, as such we left winter out of the models. Seasons were separated by the following dates:

- Spring: September 2nd – December 1st
- Summer: December 2nd – February 29th
- Autumn: March 1st – June 1st
- Winter: June 2nd – September 1st

For the desert locust, we used the outbreak area model as suggested by Uvarov (1928) (Fig. 5.1F; Fig. D.4) for the geographic region level. There are two categories at this level which are recession and invasion zones. These zones represent desert locust ecology where they persist throughout generations in the recession zone and periodically swarm and outbreak in the invasion zones. For the bioregion level, we used the World Wildlife Fund's Terrestrial Ecoregions of the World (Fig. 5.1G; Fig. D.5) (Olson *et al.*, 2001). Lastly, since the species range encompasses a large geographic area, traditional seasons are not applicable in this situation. Instead, we used a temporal grouping that reflected large scale migration trends of this species (Symmons and Cressman, 2001) (Fig. 5.1F, Fig. D.1D). This led to the following seasonal division:

- Spring: April 1st – June 30th

- Summer: July 1st – September 30th
- Autumn: October 1st – December 31st
- Winter: January 1st – March 31st

5.2.4 Remotely sensed data preparation

The normalized difference vegetation index (NDVI) (Pettorelli, 2013) is an established method for estimating vegetation amount and condition from multispectral scanners. The index is calculated as a ratio of surface reflectance in near infra- and visible- red wavelength bands, which indicates the amount of actively photosynthetic material covering the pixel. We used 8-day averaged MODIS (Terra Surface Reflectance 8-Day Global 250 m) imagery captured between 2000 and 2019, collected from Google Earth Engine (Gorelick *et al.*, 2017). We used the fixed 1 km^2 and 25 km^2 grids established for the locust data to resample the 250 m^2 pixels from sequential MODIS composite images. For all observation grids, we sampled 10 prior 8-day interval images and calculated the mean and standard deviation for all pixels within or touching each grid cell. The total number of pixels in each cell varied slightly over time as a result of image navigation and registration. Image overpass observation dates were used to calculate the number of days prior to the locust observation. Since image overpass and locust observation dates did not frequently align, the 10^{th} prior image was not always exactly 80 days before. Therefore, the two main variables used in the following models are the NDVI value and days before locust observation.

5.2.5 Model construction

Hierarchical generalized additive models (Wood, 2017; Pedersen *et al.*, 2019) (Family: Binomial, Link: Logit) were fitted to the nymph density data with the variables

listed in Table 5.1. We created two dimensional smoothers (Wood *et al.*, 2016) for both NDVI values and the number of days prior to locust observation dates and latitude and longitude. This allowed us to create probability heat maps from the modeled results (e.g. Fig. 5.3B). The inclusion of latitude and longitude allowed us to account for spatial autocorrelation (Clayton *et al.*, 1993) in the locust survey datasets that, if left unaccounted, would bias the results for both Australian plague locust (Moran's I: observed: 0.18, expected: 0, P-value: < 0.001) and desert locust (Moran's I: observed: 0.06, expected: 0, P-value: < 0.001). We ensured spatial autocorrelation was low by mapping residuals for each species (Fig. D.6).

Model validation and selection

Overall, models were first validated using diagnostic plots (Fig. D.7 & D.8). Basis dimensions were insured large enough to capture nonlinear trends while accounting for computational time (Wood, 2017) (Table D.1-D.8) before models were selected. We used null space penalization to test whether there were nonlinear or linear trends in the model (Marra and Wood, 2011; Wood *et al.*, 2016). Since there can be discrepancies between different model selection criteria (Pedersen *et al.*, 2019), we reported four metrics: Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC), the deviance from an out-of-sample (OOS) dataset (e.g. cross-validation) termed OOS deviance as discussed by Pedersen *et al.* (2019), and Area under the Receiver operating characteristic curve (AUC). For OOS deviance, we built models using 70% of the dataset, termed the training set. We then quantified predicted deviance from known outbreak and non-outbreak data using the remaining 30% of the dataset, termed the validation set. This deviance can be interpreted similarly as residual sum of squares for a linear regression with lower values meaning a better fit model (Wood, 2017; Pedersen *et al.*, 2019). Receiver operating characteristic curves (ROC) for the

final models are shown in Fig. D.9.

Hierarchical structure

To confirm the levels selected (geographic zone, ecoregion, and season) were biologically relevant, we constructed models with all combinations of the three levels and selected as discussed above (section 2.4.1). We constructed all models under the same framework (Model G; Fig. 5.2), since we were not concerned about spatiotemporal hierarchy yet and used only 70% of the data to increase computational speed (Fig. 5.2). Therefore, it not advisable to compare selection criteria values between these models and the final hierarchical model testing (Tables 5.2 and 5.3). We tested the validity of our hypothesized structure (species range > geographic zone > ecoregion > and season) after confirming that including all biologically relevant levels performed better than any subset. To do this, we constructed six different models with varying structures including all biological levels following the protocol of Pedersen *et al.* (2019). Briefly, we constructed a model with no hierarchy (model N), a model with only a global level (model G), a model with global and similarly smoothed group level trends (model GS), a model with similarly smoothed group level trends only (model S), a model with global level and differently smoothed group level trends (model GI), and a model with only differently smooth group level trends (model I) this is explained further in figure 2.

Statistical and GIS software used

GIS imagery and data preparation were done using QGIS (Team, 2020) and in the python environment with *GeoPandas* (Jordahl, 2014). Statistics were conducted in R (R Core Team, 2018) within the *tidyverse* framework (Wickham, 2018). All models were constructed and selected using the *mgcv package* (Wood, 2017) and validated

with *gratia* (Simpson, 2019).

5.3 Results

5.3.1 Species range view

Overall, nymph outbreaks at the level of the entire geographic range for each species were distinct from non-outbreaks in terms of preceding NDVI values resulting from vegetation growth (Fig. 5.3). However, the two species show clearly differing responses. Australian plague locust outbreaks were preceded by vegetation growth between 78 and 32 days before the observation (Fig. 5.3A & B). On the other hand, desert locust outbreaks were characterized by vegetation pulses within 32 to 20 days before the observation (Fig. 5.3C & D).

5.3.2 Geographic region view

Outbreak response to preceding vegetation growth varied between geographic regions (Fig. 5.4 & 5.5). For the Australian plague locust, vegetation pulses up to 32 days prior were associated with summer outbreaks in summer-dominant rainfall geographic zones (Fig. 5.4A-C), whereas outbreaks in all other zones required longer preceding vegetation growth (Fig. 5.4D & E). For the desert locust, outbreaks in both invasion and recession zones were characterized by short prior vegetation pulses (Fig. 5.5). However, NDVI values before outbreaks were higher in the invasion zone than in the recession zone. Further, vegetation in the invasion zone was drier in outbreak episodes compared to non-outbreaks.

5.3.3 Bioregion, ecoregion, and season levels

Due to the large number of bioregions separated into three or four seasons each, we are unable to explicitly report on all findings. However, each bioregion/ecoregion is given a summary document within the appendix with both trend lines (e.g. Fig. 5.3A) and modeled results for model GS and S (e.g. Fig. 5.3B) reported (appendix E-J). There are notable differences in outbreak response to vegetation both between and seasonally within bioregions.

5.3.4 Statistical modeling

Biologically relevant level selection

For both species, all statistical criteria selected for the inclusion of all scale levels (geographic zone, bioregion, and season), although there were ties with models that left out some levels (Table 5.2). For the desert locust, AIC, BIC, OOS deviance selected to include all levels: geographic zone, bioregion, and season while AUC selected for two models: all levels and geographic zone and bioregion only models (Table 5.2). For the Australian plague locust, AIC, BIC, and AUC selected to include all levels. OOS deviance was equal between three models: all levels, bioregion and season, and geographic zone and bioregion models.

Overall hierarchy selection

All criteria selected either for model GS (global and group level) or model S (group level trends with no global trend) for both species (Table 5.3). This indicates that regardless of the relationship between preceding vegetation growth and outbreaks, the responses of both species were spatially structured. However, model selection results differed between model GS and model S for both species (Table 5.3). For the

Australian plague locust, all model selection criteria selected for model GS (Table 5.3). For the desert locust, AIC and BIC both selected model S, whereas OOS deviance was lowest with model GS (Table 5.3). OOS deviance values for each level are given in Tables D.9 and D.10. Model GS and model S summaries can be seen in Tables 5.4 and 5.5. The other model summaries can be seen in the appendix (Tables D.11 – D.16).

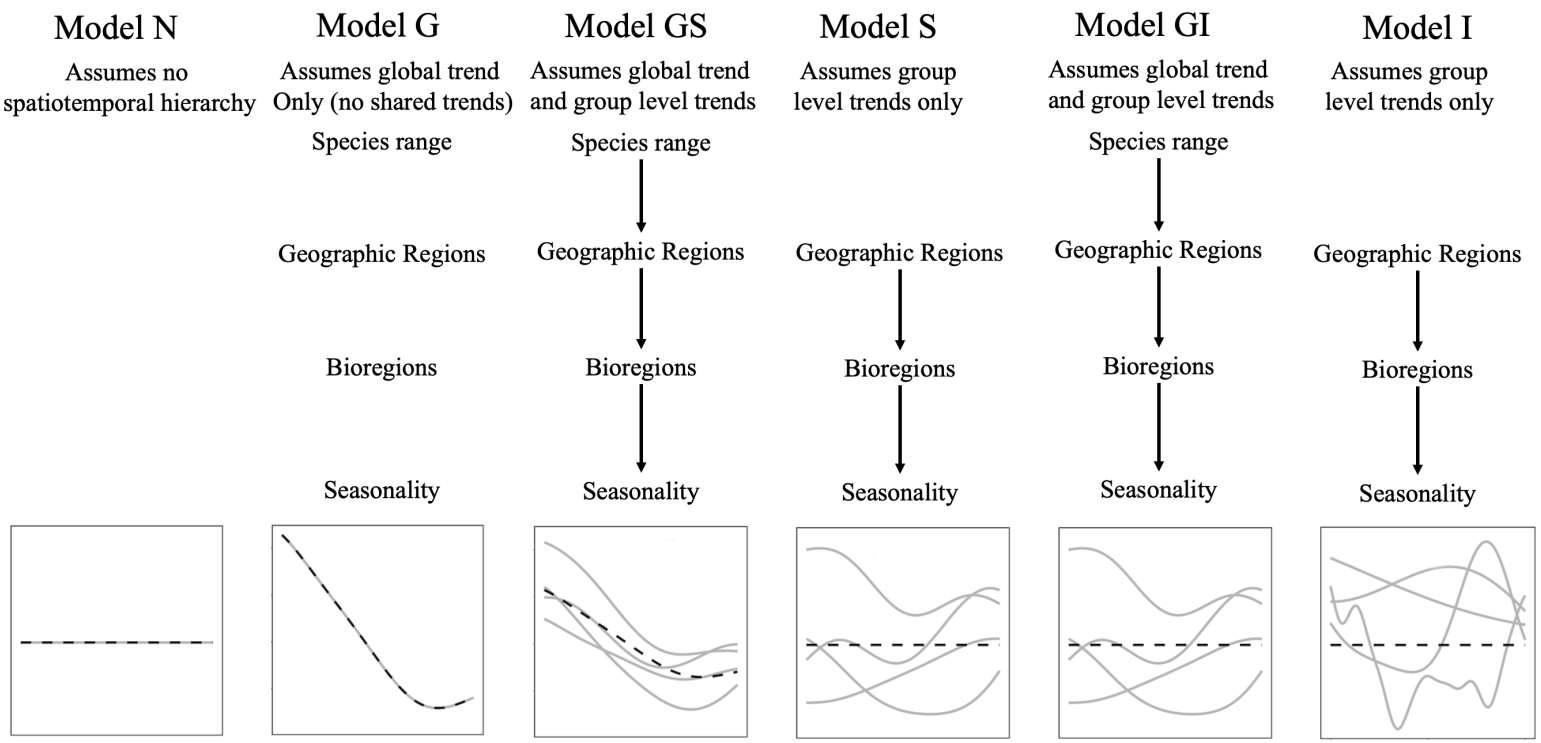

Figure 5.2: Hierarchical model structure used to test the spatiotemporal nature of locust outbreaks. Top: shows the varying hierarchical leveling between model design. Bottom figures graphically show the differing model design. Black dashed lines represent average global trend and grey solid line represents group level trends. The model GS and S have similar smoothed group level trends whereas model GI and I have different group level trends. Bottom figures are from Pedersen *et al.* (2019)

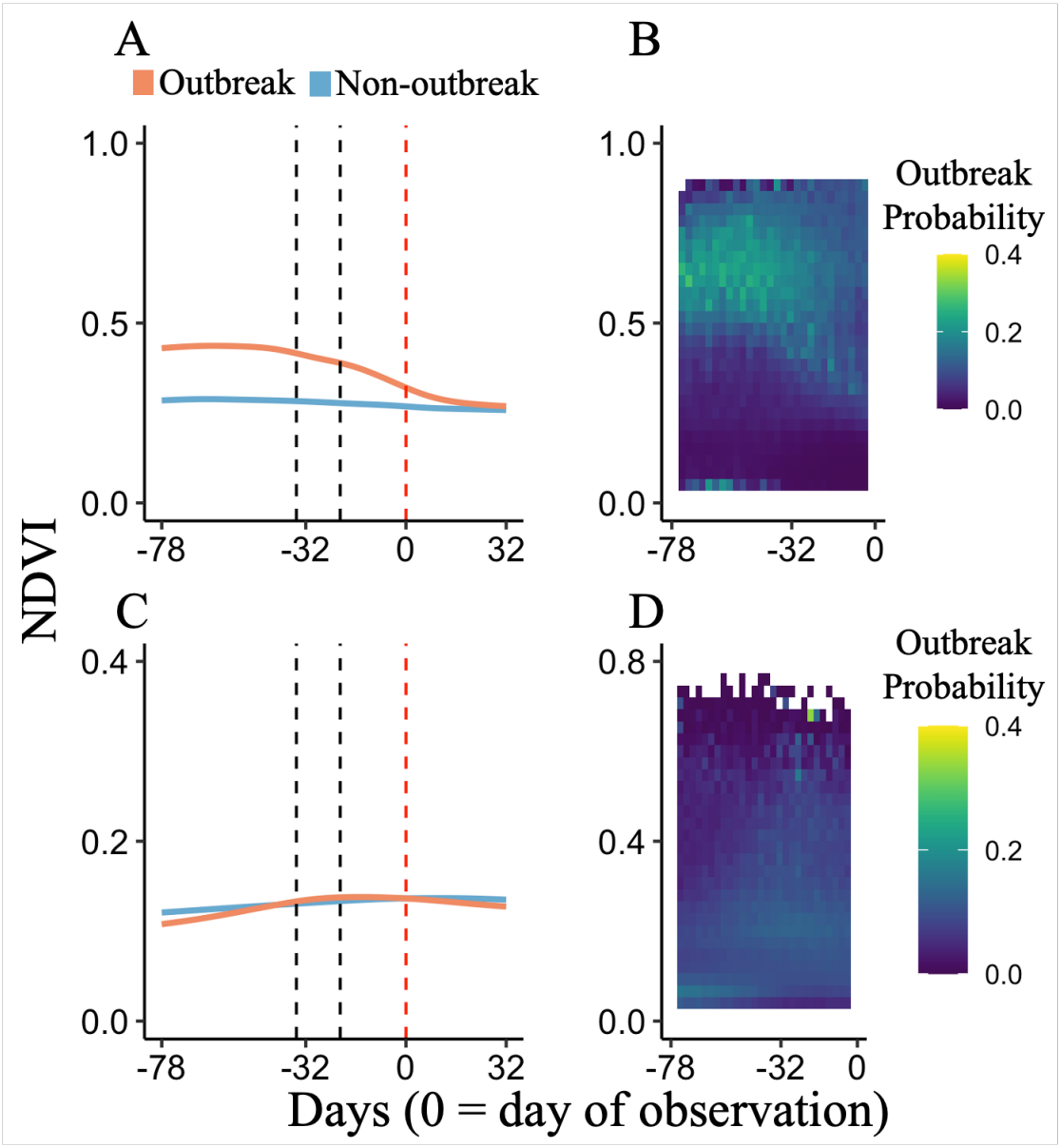

Figure 5.3: Global pattern for the Australian plague locusts (A & B) which are characterized by long preceding vegetation growth between 78 and 32 days before outbreaks and desert locust (C & D) which are characterized with vegetation pulses 32 to 20 days before outbreaks. Left: NDVI trends for outbreak and non-outbreak observations over time. Vertical red line is the observation date, black lines represent hypothesized nymph hatching date. Right: Modeled outbreak probability for preceding NDVI. We did not include succeeding NDVI values into models.

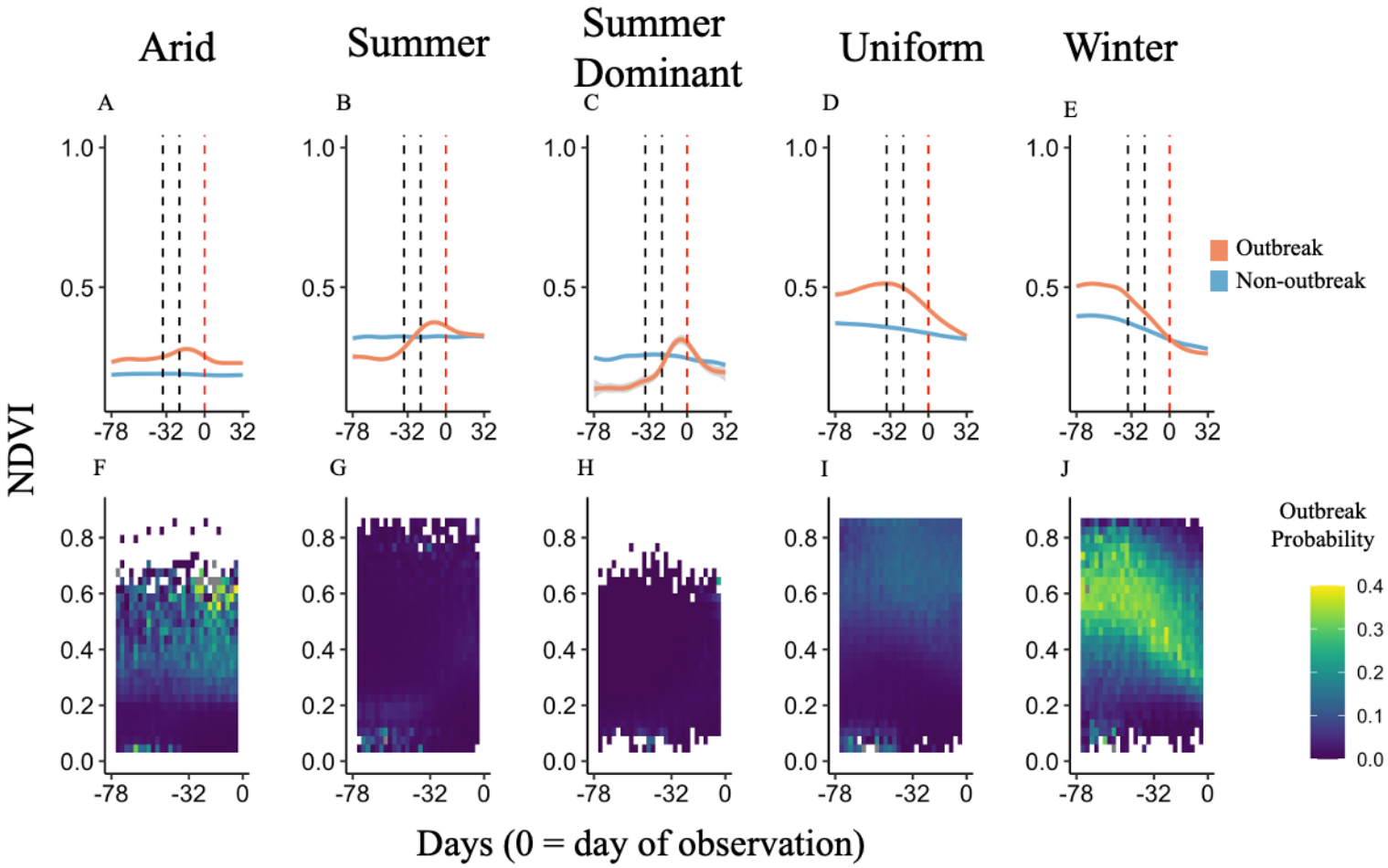

Figure 5.4: Australian plague locust geographic region pattern for raw (A-E) and modeled probability (F-J) for the relationship between preceding vegetation growth and outbreaks. Two patterns emerged: long preceding vegetation growth in uniform and winter geographic regions (D & E; I & J) and vegetation pulses in Arid Summer and Summer Dominant regions (A-C; F-H) Top: raw NDVI trends for outbreak and non-outbreak observations over time. Vertical red line is the observation date, black lines represent hypothesized nymph hatching date. Bottom: Modeled outbreak probability for preceding NDVI. We did not include succeeding NDVI values into models.

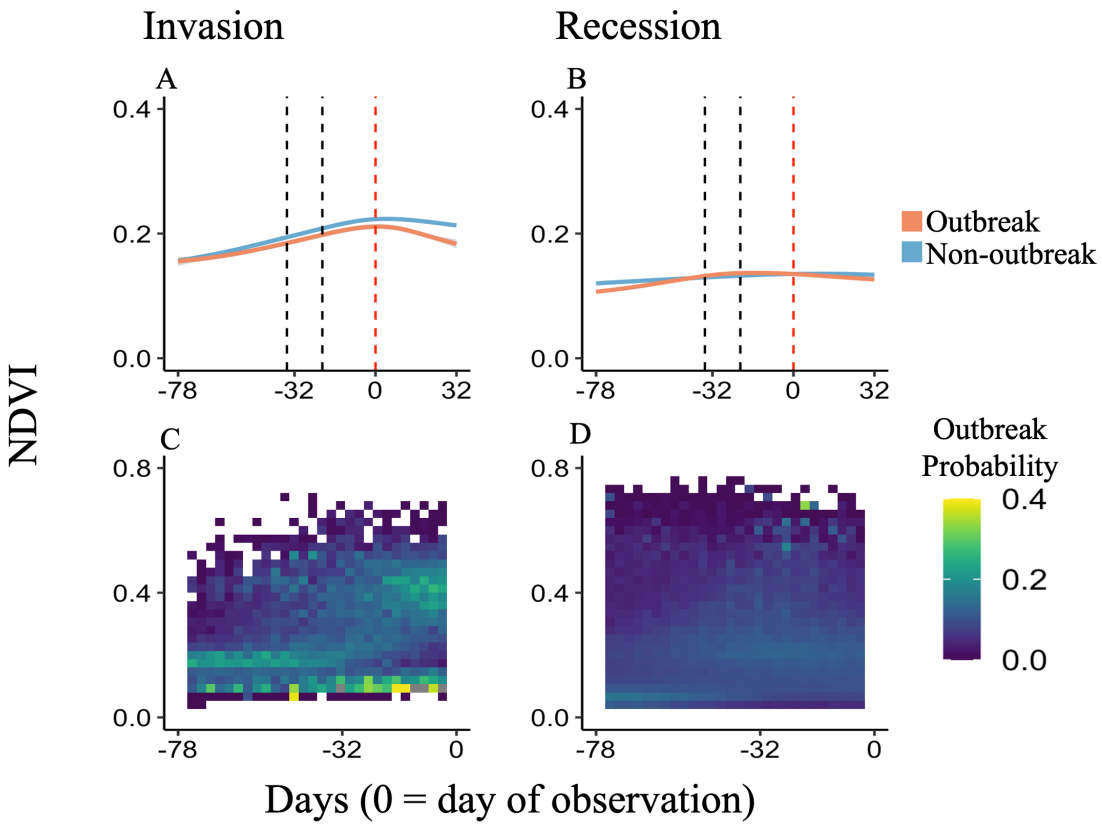

Figure 5.5: Desert Locust Geographic Region Level Pattern for Raw (A & B) and Modeled Probability (C & D) for the Relationship Between Preceding Vegetation Growth and Outbreaks. Both Regions Are Characterized by Vegetation Pulses. Top: Raw NDVI Trends for Outbreak and Non-Outbreak Observations Over Time. Red Line Is the Observation Date, Black Lines Represent Hypothesized Nymph Hatching Date. Bottom: Modeled Outbreak Probability for Preceding NDVI. We Did Not Include Succeeding NDVI Values Into Models.

Table 5.1: Variables Used in This Study With Structure and Source.

Species	Variable	Structure	Source
Australian plague locust	Outbreak occurrence (response)	binary	APLC database
	NDVI (predictor)	proportion	MODIS
	Days before (predictor)	Integer, -78 to 0	MODIS
	Seasonal rainfall zone (random effect)	factor	Australian Government BOM
	Bioregion (random effect)	factor	Australian Government DAWE
	Season (random effect)	factor	n/a
Desert locust	Outbreak occurrence (response)	binary	FAO database
	NDVI (predictor)	proportion	MODIS
	Days before (predictor)	Integer, -78 to 0	MODIS
	Geographic zone (random effect)	factor	CIRAD
	Bioregion (random effect)	factor	World Wildlife Federation
	Season (random effect)	factor	n/a

Table 5.2: AIC, BIC, out-of-Sample (OOS) Deviance, and AUC Model Selection for Differing Structured Models for Both the Desert Locust and Australian Plague Locust. The Lower the Value for AIC, BIC, and OOS the Better Fit Model. The Higher the AUC the Better the Model. Bolded Numbers Represent Best Fit Model. Z = Zone, S = Season, B = Bioregion

	Desert locust							Australian plague locust						
Structure	AIC	ΔAIC	BIC	ΔBIC	OOS deviance	Δ OOS deviance	AUC	AIC	ΔAIC	BIC	ΔBIC	OOS deviance	Δ OOS deviance	AUC
Z	1107383	69717	1108474	63651	335561	4527	0.748	382441	11720	383345	11554	163269	4923	0.866
S	1104692	67026	1106351	61527	335561	4527	0.744	375175	4454	376053	4262	160134	1788	0.872
ZS	1098738	61072	1100644	55820	333590	2556	0.749	372648	1928	373576	1785	159069	723	0.873
B	1090936	53270	1093937	49113	333964	2930	0.750	382719	11999	383718	11926	163493	5147	0.868
ZB	1089731	52065	1093495	48672	332180	1146	**0.754**	380165	9445	381212	9421	162401	4055	0.870
BS	1041707	4041	1048474	3650	332857	1823	0.750	373082	2361	374103	2312	159350	1004	0.874
ZBS	**1037666**	**0**	**1044824**	**0**	**331034**	**0**	**0.754**	**370721**	**0**	**371791**	**0**	**158346**	**0**	**0.876**

Table 5.3: AIC, BIC, out-of-Sample (OOS) Deviance, and AUC for Six Models With Differing Hierarchical Structures for Both the Desert Locust and Australian Plague Locust. The Lower the Value for AIC, BIC, and OOS the Better Fit Model. The Higher the AUC the Better the Model. Bolded Numbers Represent Best Fit Model. Model Descriptions Can Be Found in Figure 2.

	Desert locust							Australian plague locusts						
Model	AIC	ΔAIC	BIC	ΔBIC	OOS deviance	ΔOOS deviance	AUC	AIC	ΔAIC	BIC	ΔBIC	OOS deviance	ΔOOS deviance	AUC
N	1126823	93656	1127690	87262	337746	25592	0.742	385123	56487	385977	47973	164412	23915	0.865
G	1104353	71186	1105454	65026	331665	19511	0.755	370721	42085	371791	33787	158346	17849	0.876
I	1083813	50645	1087567	47139	325396	13242	0.770	352850	24214	357260	19256	150986	10489	0.897
GI	1083518	50351	1087061	46633	325277	13123	0.770	352049	23413	356565	18561	150699	10202	0.897
GS	1033892	724	1041033	605	312154	0	0.803	328636	0	338004	0	140497	0	0.920
S	1033168	0	1040428	0	312290	136	0.803	332082	3446	341862	3858	141874	1377	0.917

Table 5.4: Model GS and Model S Results for Australian Plague Locust (APL) Outbreaks. Model GS Has a Global Smooth With Similarly Smoothed Group Levels (Zone > Bioregion > Season). Model S Only Has Similarly Smoothed Ground Levels. Model Descriptions Can Be Seen in Table 5.2. EDF = Estimated Degrees Freedom.

	APL - Model GS				APL - Model S			
Variable	EDF	df	X^2	P-value	EDF	df	X^2	P-value
(days before, NDVI)	19.49	24	357.97	**<<0.001**				
(days before, NDVI, Zone, Bioregion, Season)	709.8	1251	28940.41	**<<0.001**	765.1	2266	34292.45	**<<0.001**
(Latitude, Longitude)	47.77	49	14036.23	**<<0.001**	46.6	49	12211.40	**<<0.001**

Table 5.5: Model GS and Model S Results for Desert Locust (DL) Outbreaks. Model GS Has a Global Smooth With Similarly Smoothed Group Levels (Zone ¿ Bioregion ¿ Season). Model S Only Has Similarly Smoothed Ground Levels. Model Descriptions Can Be Seen in Table 5.2. EDF = Estimated Degrees Freedom.

	DL - Model GS				DL - Model S			
Variable	EDF	df	X^2	P-value	EDF	df	X^2	P-value
(Days before, NDVI)	5.95	24	188.75	**<<0.001**				
(Days before, NDVI, Zone, Bioregion, Season)	511.15	760	58699.36	**<<0.001**	527.97	947	65191.36	**<<0.001**
(Latitude, Longitude)	48.96	49	61761.55	**<<0.001**	48.96	49	61702.37	**<<0.001**

5.4 Discussion

We modelled the incidence of locust outbreaks for two species (*Chortoicetes terminifera* and *Schistocerca gregaria*) using hierarchical generalized additive models driven by NDVI as an indicator of herbaceous vegetation productivity. Our study uses the Hierarchical Patch Dynamics (HPD) framework to account for the spatiotemporal variation of locust swarms and demonstrates that model performance is improved by the integration of biologically relevant scales. This is shown in two taxonomically distinct locust species where the relationship between preceding vegetation growth and outbreaks varies spatiotemporally (Figs. 3 - 5). However, regardless of their inherent ecological differences, adding biologically relevant spatiotemporal hierarchy greatly improved model fit in both species (Table 5.3). This suggests that when making large scale conclusions about the ecological causes of locust swarms, and likely other mobile animals, spatial hierarchy should be considered. The relationship between preceding vegetation growth and locust outbreaks likely varies between these species due to the large climatological differences between Africa and Australia and their distinct ecologies. Further modeling could consider other important variables such as temperature and nutrition which have impacts on the organismal to landscape levels for locusts.

For locust management, our study reinforces the importance of prior rainfall-induced vegetation growth on the likelihood of outbreaks. The results support the current strategies of using plant productivity measures such as NDVI in increasing the probability of detecting nymph outbreaks to allow for possible proactive intervention (Pedgley, 1973; Cressman, 2008, 2013; Deveson, 2013). Further, it highlights the spatiotemporal structuring of outbreaks which is important for forecasting efforts globally. Our use of HPD and hierarchical generalized additive models allows for spatiotemporal variation to be directly modeled and identified. Therefore, the methods

and findings provide a useful tool in understanding and predicting the spatiotemporal variation of population dynamics broadly.

5.4.1 Preceding vegetation growth and locust outbreaks

It is well documented that preceding vegetation growth is an important predictor of acridid population dynamics (Chapman and Joern, 1990). The environments of both species are arid lands characterized by the resource pulse paradigm, meaning that primary productivity and herbivore response is driven largely by variable rainfall events (Noy-Meir, 1973, 1974). In their arid habitats, if there is not enough vegetation, the local nymph population will be unable to develop into adults, which is the breeding and migratory stage. However, few researchers have statistically investigated the daily temporal dynamics of this relationship. Our study generalizes the findings of previous studies that used NDVI binned or averaged into discrete time ranges in both species (Piou *et al.*, 2013; Deveson, 2013). Additionally, we show there are important differences between preceding vegetation growth and outbreak responses at different spatiotemporal levels which were not accounted for statistically in previous studies.

Spatiotemporal variation between preceding vegetation and outbreaks

Regardless of species and spatiotemporal level, two major patterns between vegetation growth and outbreaks emerged: long preceding vegetation growth (>32 days) and vegetation pulses (32 days). The vegetation pulses occurred around the time of the hypothesized hatching date for the nymph outbreak which is two to three weeks before outbreak observation (e.g. Fig. 5.3). This is supported by model criteria selecting model GS and S (similar smoothed relationships between levels) over model GI and I (differently smoothed relationships between levels) (Fig. 5.2, Table 5.3). Most of the desert locust models at all levels had vegetation pulses whereas the Australian plague

locust levels had both patterns. These patterns are a product of climatic differences between the habitat and each species' ecology. The majority of the desert locust habitat is hyper-arid and hot and given the wide geographic distribution, winter does not halt population growth (Uvarov, 1977; Ceccato *et al.*, 2007). As such, responses to brief vegetation pulses are therefore prominent. The Australian plague locust's environment has on average a higher mean annual precipitation and experiences a cold winter which does halt population growth for part of the year (Wardhaugh, 1986; Hunter *et al.*, ????). Long preceding vegetation growth is associated with bioregions within the winter and uniform dominant rainfall zones which is in the southern half of the species range (Fig. D.2). This indicates that late winter and early spring temperature and rainfall-induced vegetation growth is important for nymph survival. Within the summer and arid rainfall zones in the northern half of the species range, the shorter preceding vegetation pulse is prominent (Fig. 5.4). Outbreaks in these areas happen later in the season and vegetation growth following rainfall is needed for successful breeding.

While we did not explicitly model adult migration and behavioral ecology, it is important to discuss because the presence of nymphs acknowledges prior adult oviposition choices. Without egg laying in the localized area, there would be no nymphs to consume the available vegetation. Both species conduct wind-assisted migrations which increases the chances of breeding in habitat areas with recent rain (Dingle, 2014). Egg-laying and the resulting nymph hatching have a greater chance to correspond with vegetation growth in these areas. There are migratory differences between species based on large-scale climatic patterning. It is important to note that these migratory trends for both species are generalized. It is common for locusts to migrate on particular wind movements and not just with the prevailing wind patterns. Further, not all wind patterns lead to areas which experienced previous rainfall-induced-

vegetation growth (Farrow, 1990). Our modeling demonstrates episodes where rainfall, adult migration, and vegetation growth all occur at the appropriate timing to have a successful outbreak.

For the Australian plague locust, any migration southward in autumn (into winter dominated rainfall regions) and northward in late spring (into summer dominated rain regions) have increased probability of successful breeding (Clark, 1970, 1971; Deveson and Walker, 2005a; Deveson *et al.*, 2005). Most laid eggs go into diapause (a period of suspended development) due to the onset of winter and colder temperatures, which delays hatching until spring. Grasses remain green throughout winter and into spring due to lower temperature and decreased evaporation which explains the long preceding vegetation growth prior to outbreaks in these areas (Fig. 5.4D & E). Northward migrations relocate locusts into the summer dominant rainfall zones in early summer which corresponds with the commencement of the wet season. Therefore, any nymphal outbreaks are preceded by vegetation pulse (Fig. 5.4A-C).

For the desert locust there are two large-scale migration trends in West Africa and the Red Sea area. In West Africa, migrations usually follow the Inter-Tropical Convergence Zone (ITCZ) with southward in winter/spring and northward displacements in summer (Rainey 1963, Pedgley 1980). In the Red Sea area, winter migrations from the Middle East occur to the Indo-Pakistan and the Red Sea's western shores areas. Summer migrations then head back towards the Middle East. Overcoming cooler temperatures for desert locusts is not as important as compared to the Australian plague locust due to being in a hotter climate. The important factor is predominately locating recent rainfall and vegetation pulses for outbreaks to occur. Therefore, most of the desert locust hierarchical levels demonstrated the vegetation pulse pattern. While both the invasion and recession zone demonstrate this pulse, outbreaks in the invasion zone on average was greener than those in the recession zone (Fig. 5.5). This

is partly because the invasion zone has a higher mean annual precipitation than the recession zone.

The smaller deviations seen between all spatiotemporal levels are likely the result of other environmental variables in particular vegetation. Vegetation communities differ considerably in their composition among the Australian bioregions (Thackway and Cresswell, 1995) and among the African ecoregions (Olson *et al.*, 2001) considered in this study. Thus, the extent and intensity of outbreaks in each bioregion/ecoregion, including the incidence of no outbreaks will be influenced by the unique composition of plant communities within ecoregions and bioregions, and how these communities respond to the changes in available soil composition, nutrients, temperature, and precipitation (Werf *et al.*, 2005; van Huis, 2007; Hassler *et al.*, 2010; Mao *et al.*, 2014). These deviations could lead to interesting hypotheses about the spatiotemporal population dynamics of higher trophic levels. Importantly, populations in our study responded differently to the same precipitation regime in different regions due to vegetation productivity being spatially variable.

Additional environmental factors and hierarchical levels for outbreaks

There are also other factors that influence population dynamics such as: migration (Farrow, 1979, 1982; Deveson and Walker, 2005b), nutrition (Cease *et al.*, 2012, 2017), temperature (Bozinovic *et al.*, 2011), and soil texture (Clark, 1965). We did not include these factors because this would introduce concurvity (the non-linear version of collinearity) and overcomplicate the models. Going into the future, including scale-relevant measures of these variables would increase model fit and provide insight into other factors that induce locust swarms. Due to the nature of these datasets, we were unable to recognize smaller hierarchical levels such as within-bioregion abiotic/biotic variation, microhabitats, and smaller temporal scales (e.g. days and weeks). Within

bioregions there could be differences between populations (Mangeon *et al.*, 2020) and microhabitats. For microhabitats, temperature and soil moisture likely play an important role in regulating individual locust performance and work is currently underway at this scale (Kearney and Porter, 2009; Kearney *et al.*, 2014).

5.4.2 Hierarchical Patch Dynamics: integrating ecology on multiple scales

The Hierarchical Patch Dynamics theory is a way to account for emergent properties that arise as a result of interactions at and between different scales (Newman *et al.*, 2019). In this study, we show that breaking down species range trends into discrete biologically relevant levels reveals patterns and processes that are not apparent at other scales. If this spatiotemporal variation is not accounted for, species population will be limited. Spatiotemporal variation is clearly an important aspect for locust swarms, and this is also likely the case for a broad range of animals. There is a need for explicitly integrating ecological phenomena across multiple scales (Carpenter and Turner, 2017). Hierarchical generalized additive models allow for information to be shared between levels (Pedersen *et al.*, 2019) and could increase both the theoretical and practical applications of the HPD theory. This approach provides a useful tool for integrating ecology at multiple scales. We hope this study spurs further research in explicitly accounting for spatiotemporal variation within population dynamics.

The ecological theatre has many intricate parts all working simultaneously to produce the patterns and processes we see around us. Where and when things happen throughout the biosphere is a crucial step in understanding animal population dynamics broadly. In my dissertation, I began to account for spatiotemporal variation using locust swarms as a model study system. However, there is still much work to be done, such as seeing how this hierarchical scaling diagram can be generalized to other locust species and further to other insects and animals. Traditionally, ecologists have been focused on developing large generalizable statements about the biosphere that hold true everywhere. This is a valid effort, however, often it is marred by not considering spatiotemporal variation. While many ecologists acknowledge that scaling and spatiotemporal variation are important factors to consider, multi-scale approaches to assess variation are still rare, perhaps as a result of statistical complexity. I hope that my dissertation acts as an example how scale relevant approaches can be applied to other ecological systems.

The causes of animal population booms and busts are a multitude of biotic and abiotic variables interactively working together. As such, developing generalizable statements about exact cause and consequences of animal population dynamics is not feasible as this varies between animal species, populations, and in space and time. Instead, developing biologically relevant levels can help quantify the spatiotemporal components of this broad question and allows for further investigation into what drives animal populations on their own.

Landscape ecology is a dynamic field with the ambitious goal of quantifying the spatiotemporal variation seen throughout the biosphere. Much has been discussed and identified through the years in this field. However, few have taken landscape ecology principles and applied them to insect outbreaks. There is great opportunity to merge the fields of landscape ecology and entomology together which can help predict when

and where insect outbreaks happen. For example, through the use of the Hierarchical Patch Dynamics paradigm, I was able to identify the relevant scales for locust swarm formation: from individual gregarization to landscape wide migrations.

My dissertation introduces a scaling diagram with four hierarchical scales that act as a bottle necks for locust plague formation (Fig. 1.1). Since all scale are dependent on one another, all predictor variables are important to some extent at each scale. However, the relative importance and relationship with locust outbreaks change between scales. I highlight the most important variables for each scale in Fig. 5.6. Smaller scales (phase change and nymphal outbreaks) are associated with smaller scale environmental features such as spatial distribution of food, overall food availability, and the nutritional landscape (Fig. 5.6A and 5.6B). If these bottlenecks are satisfied, then an adult swarm can form (Fig. 5.6C). Localized adult swarms are common and most of the time they do not lead to a plague, as can be shown in the middle arrow in the figure below. Given the right climatic conditions, they can still lead to localized phase change events. However, these events are spatiotemporally sporadic and unless rainfall events become more frequent, they do not lead to plague formation but instead aid in the persistence of locust populations. When large scale climatic patterns are favorable, such as during the La Niña phase of the El Niño-Southern Oscillation for the Australian plague locust and there are enough broad scale rainfall events to promote vegetation growth for increased adult swarms, the cycle can be pushed into plague formation (Fig. 5.6D). The plague cycle continues until climatic patterns become more normal and the populations are reduced to smaller, localized outbreak events. For either adult swarms or a plague to occur, climatic conditions for adult migrations and subsequent ovipositing of egg beds are crucial at the phase change scale (Fig. 5.6A). There must be eggs in the localized area for nymphs to hatch and potentially become gregarious. As such, the largest scale circles

back to the smallest scale allowing for locusts to persist in highly variable global drylands.

Locusts are a product of the environment they evolved in and provide a dynamic system to understand how animals persist through climatic extremes which are characteristic of dryland environments. Food availability and nutrition are two important variables to consider not just for locusts, but many dryland animals. These factors are driven by large scale climate (food availability) and land use (nutrition) variables. As such, it is imperative to explore the interplay between climate and human land-use and land-change. Understanding the interactive effect of land use and climate can then help predict how locust swarms are being impacted by global change. The future of locust research is bright due to the increasing availability of remotely sensed data, large dataset availability, and the inclusion of diverse researchers from multiple research fields: from physiology to social sciences.

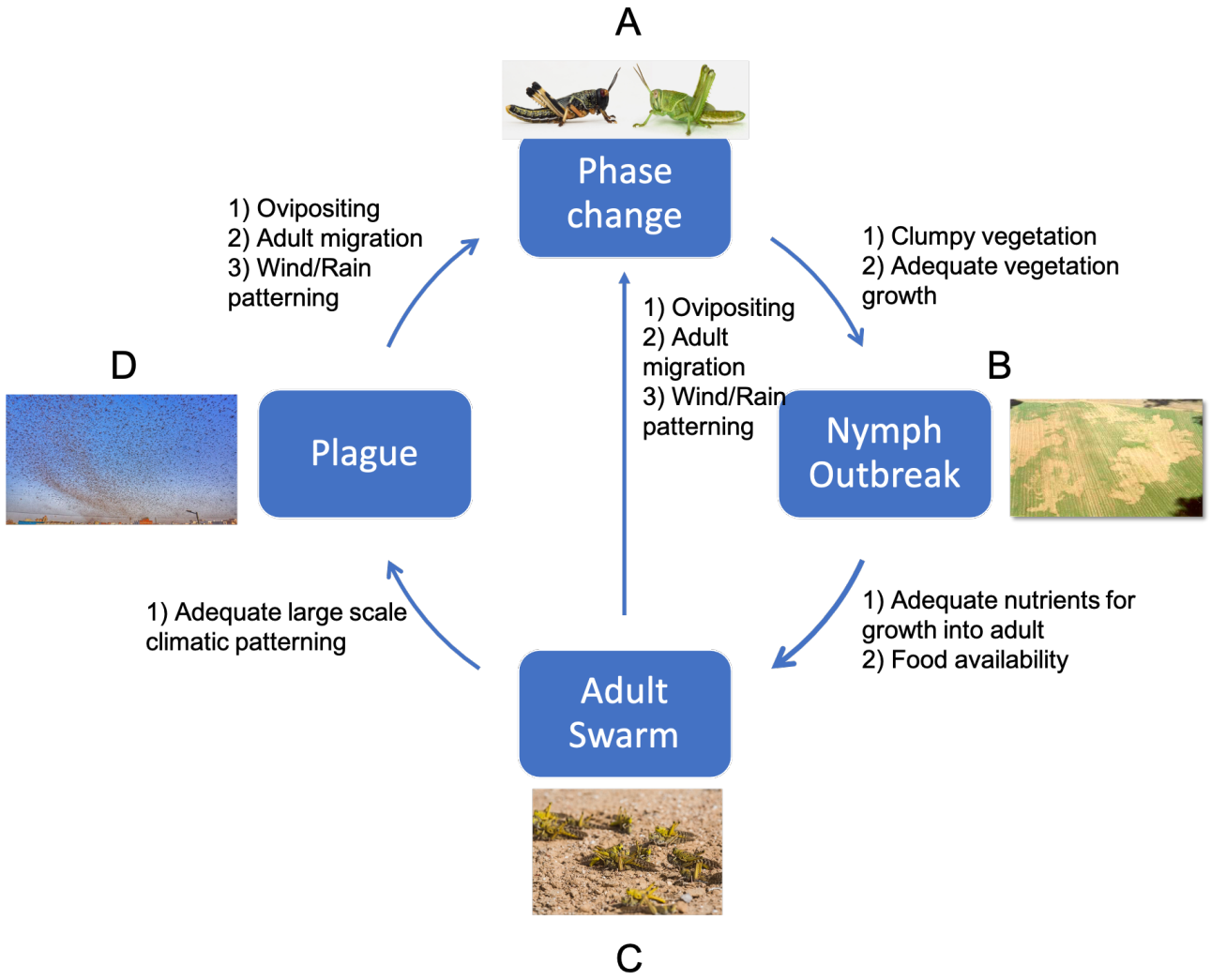

Figure 5.6: The Multi-Scale Cycle (A-D) of Locust Plague Formation. Each Scale Represents a Bottleneck Which Can Prevent Subsequent Population Upsurges. Most Important Variables for Each Bottle Neck Are Shown.

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APPENDIX A

SUPPLEMENTARY DATA FOR CHAPTER 2

Table A.1: Number Replicates (N) per Treatment and Number of Locusts by Instar Used for Each Treatment.

Experiment	Treatment (N)	Nymph stage			
		1-3rd	4th	5th	Total
Contrasting nutritional landscapes experiment	Gregarious control (1)			10	10
	Sub-optimal large patch (1)			25	25
	Solitarious control (1)			10	10
	Optimal-large patch (1)			24	24
Approaching nutritional optimatliy	1 (3)	21	8	38	67
	2 (2)	8	16	24	48
	3 (3)	27	10	34	71
	4 (2)	7	16	26	49
	Gregarious control (5)	11	11	41	63
	Solitarious control (5)	12	10	41	63

Table A.2: Nemenyi Posthoc Results (P-Values) for the Contrasting Nutritional Landscapes Experiment. Significance Values Are in Bold.

	gregarious Control	optimal patch	sub-optimal patch
optimal patch	1.00		
sub-optimal patch	0.47	0.20	
Solitarious control	**0.02**	**0.00**	0.20

Table A.3: Nemenyi Posthoc Results (P-Values) for the Approaching Nutritional Optimality Experiment. Significance Values Are in Bold.

	gregarious control	1	2	3	4
1	**0.00**				
2	**0.00**	1.00			
3	**0.00**	0.96	0.80		
4	**0.00**	1.00	0.97	1.00	
solitarious control	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**

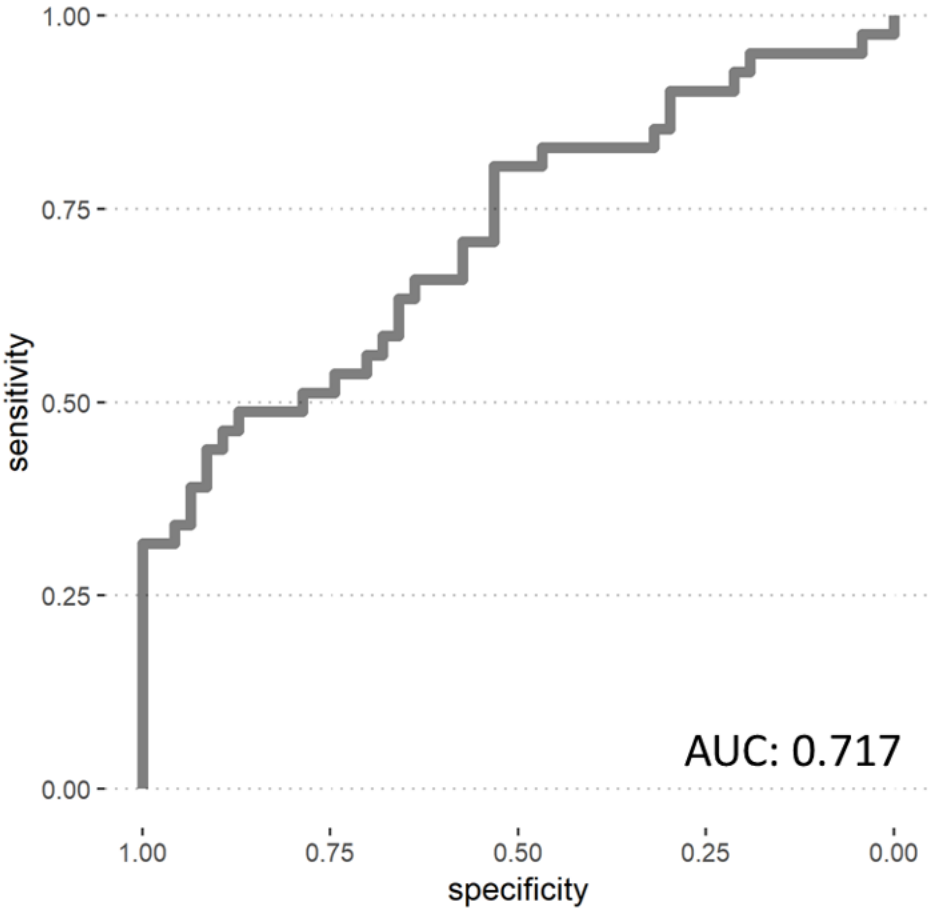

Figure A.1: ROC Curve of the Gregarious Random Forest Model. AUC Values Between 0 and 0.50 Are Considered Bad Classifiers, Whereas Those Above 0.50 Have Some Predictability, With 1.00 Being a Perfect Classifier.

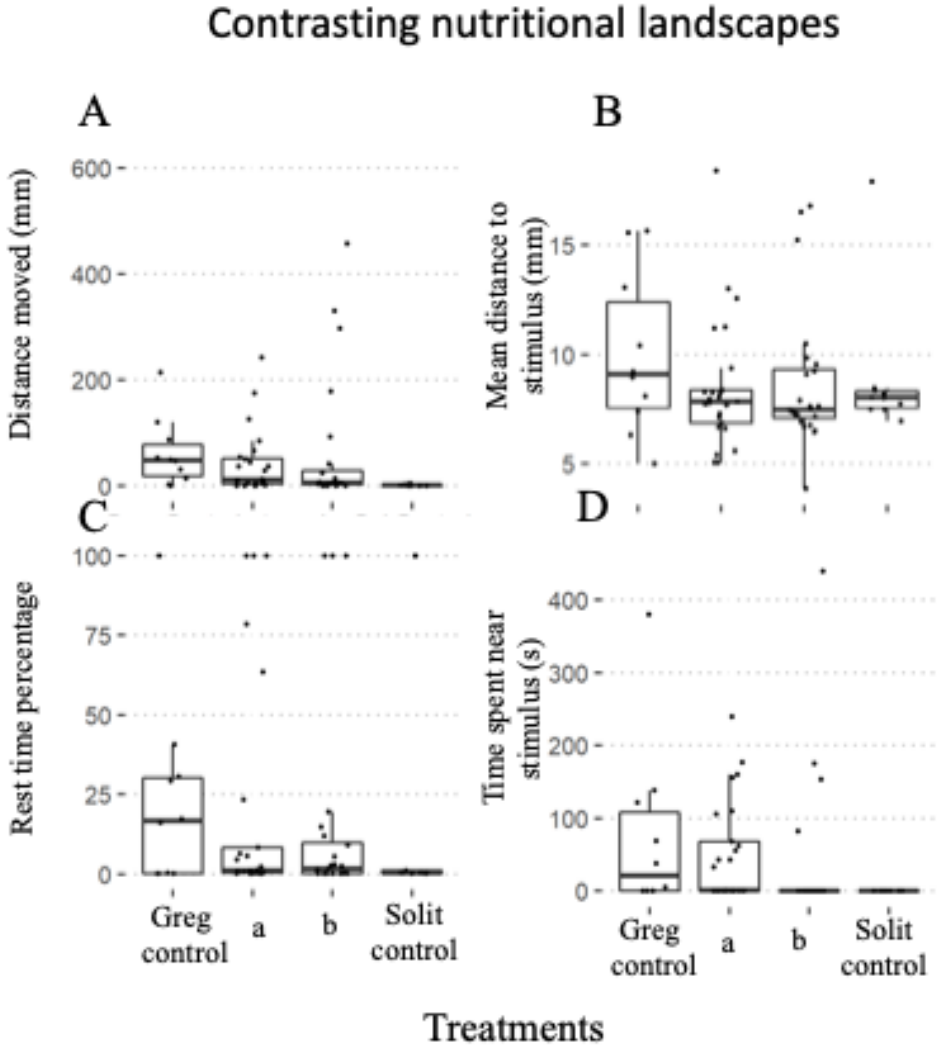

Figure A.2: The Four Behavior Variables Tracked for Optimal Patch and Suboptimal Patch Treatments in the Contrasting Nutritional Landscapes Environment. Greg: Gregarious, Solit: Solitarious. a: Optimal Patch, and b: Suboptimal Patch.

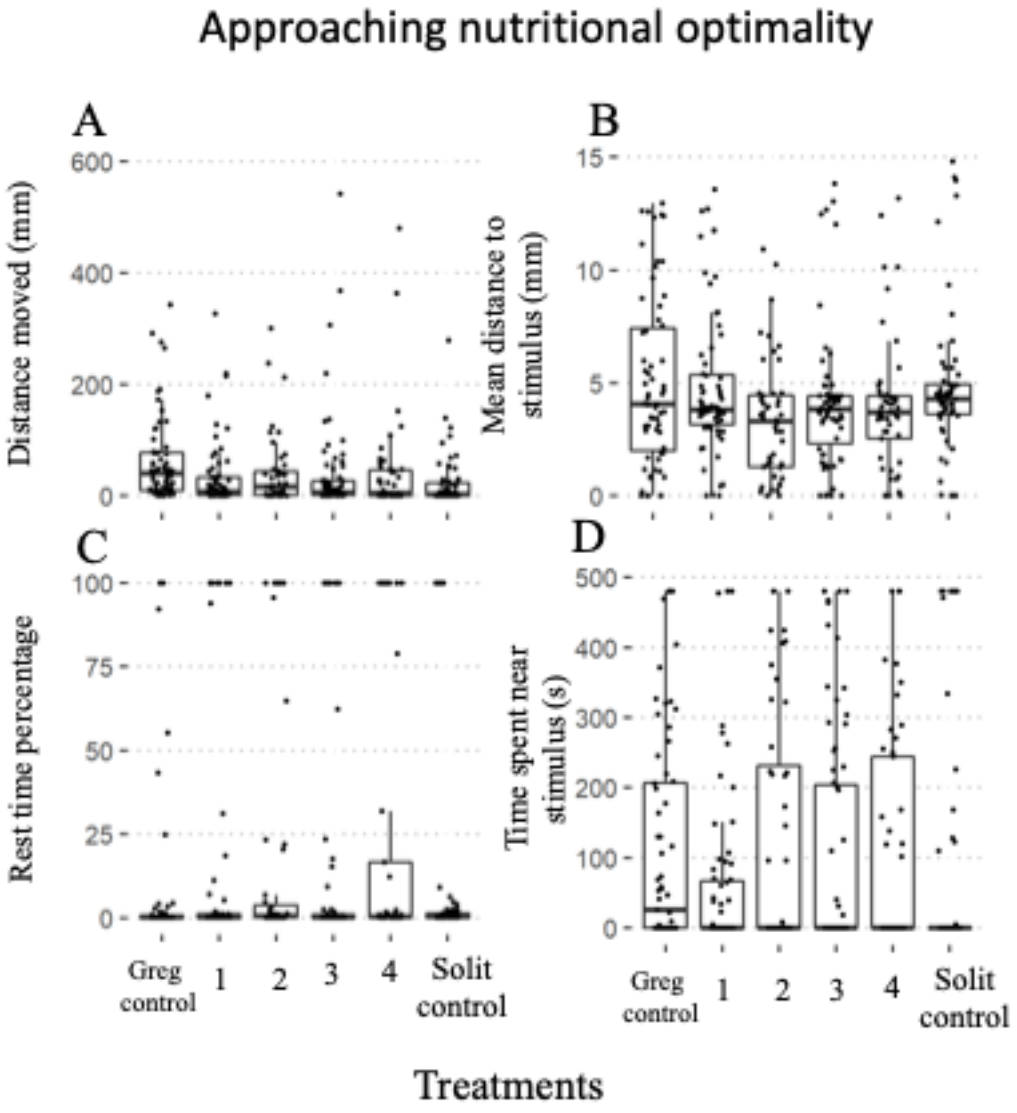

Figure A.3: The Four Behavior Variables Tracked for the All Treatments in Experiment B. Greg: Gregarious. Solit: Solitarious. 1 = Most Suboptimal Homogeneous Distribution, 4 = Most Optimal Homogeneous Distribution.

APPENDIX B

WOODY VEGETATION REMNANTS WITHIN PASTURES INFLUENCE LOCUST DISTRIBUTION: TESTING BOTTOM-UP AND TOP-DOWN CONTROL

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Woody vegetation remnants within pastures influence locust distribution: Testing bottom-up and top-down control

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ABSTRACT

Agriculture is a major factor in landscape fragmentation, altering nutrient cycling and animal and plant populations through increasing habitat edge density. Most research on insect herbivores in agroecosystems has focused on the top-down effects of predators moving throughout the habitat mosaic. Few studies have focused on the top-down and bottom-up factors modulating the distribution of insect herbivore populations between natural and agricultural patches. For example, despite an understanding that Australian plague locusts (Chortoicetes terminifera) avoid tree patches, the underlying mechanisms remain unknown. Here, we explored how wooded remnants within pastures affect locust density and the potential top-down and bottom-up mechanistic explanations. We tested three hypotheses: 1) grasses near wooded areas are nutritionally suboptimal, 2) predator density is higher near wooded areas, and 3) temperatures are cooler underneath trees. We measured locust density, grass nutrient content, predator abundance, temperature, and ground cover along 50 m transects from wooded areas to open grassy areas. We ran those transects in three fields and had four transects per field. We confirmed locust avoidance for trees at a 20 m periphery, however none of the variables tested independently explained this trend. Grass nutrient content was similar underneath wooded areas and in open patches. Predator abundance did not differ between the two habitats. The ground was warmer under wooded areas than in grassy areas potentially due to woody vegetation negating windchill. Further, we found that locust density was negatively correlated with plant protein content and was highest in areas with approximately 20 % bare ground cover. Both plant protein and ground cover are important for grasshopper performance and reproduction. It is likely a complex interaction between these variables and others that drive the distribution of this species and other insect herbivores in agroecosystems. The small-scale mechanisms driving the response of insect herbivores to landscape changes is critical to understanding and predicting population dynamics at large-scales.

1. Introduction

Anthropogenic fragmentation of landscapes has considerable impacts on many aspects of biodiversity (Fahrig, 2003). One of the major contributors to fragmentation is agriculture, which alters nutrient cycling (Hobbs, 1993) and the distribution and connectivity of animal populations (Fischer and Lindenmayer, 2007). In particular, this fragmentation leads to patchy landscapes with increased edge effects (Ries et al., 2004). For insect herbivore population regulation, most research has focused on the top-down effects of predators moving throughout habitat mosaics (Rand et al., 2006). Few studies have looked at the effects of both top-down and bottom-up forces on insect herbivore populations distributed between natural remnants and agricultural patches. In this study, we explored how woody vegetation remnants within grazed pastures affect the density and distribution of a common insect herbivore, the Australian plague locust (*Chortoicetes terminifera*, Walker 1875), and tested several potential top-down and bottom-up effect mechanisms to explain these patterns.

The presence of remnant vegetation, hereafter referred to as wooded areas, in an agricultural landscape may influence insect herbivore density through changes in predator abundance, microclimates, and/or soil chemical composition, which in turn affects host plant nutrient content. Host plant nutrient content is important for insect herbivores (Behmer, 2009; Raubenheimer et al., 2009; White, 1993) on multiple scales: from physiology (Cease et al., 2017; Simpson and Raubenheimer, 2012, 1993) to population regulation (Cease et al.,

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2012; Joern et al., 2012; Joern and Behmer, 1997). For instance, from a bottom-up perspective, trees have been termed 'islands of fertility' because they deposit nutrients under their canopies via dead leaf accumulation, atmospheric dust collection via rainstorms, and by acting as nutrient pumps from deep soil nutrient layers (Kellman, 1979; Scholes and Archer (1997); Szott et al., 1991). In the understory of widely spaced trees in Kenya, plants contained higher amounts of phosphorous, potassium, calcium, and mineralizable nitrogen than plants in open grassy areas (Belsky et al., 1993). This suggests that subsequent differences in host plant nutrient content may explain differences in insect herbivore distribution between wooded areas and open grassy patches.

The extent of wooded areas in agroecosystems is commonly cited to play a role in stable, long-term insect herbivore control (Bianchi et al., 2006; Schellhorn et al., 2008; Thomson and Hoffmann, 2010). These remnants provide suitable habitat for predators providing top-down control of insect herbivore populations (Rencken, 2006). For example, there was more parasitism on rape pollen beetles (*Meligethes aeneus*) in fields with six-year as compared to one-year old field margin in rapeseed agroecosystems in northern Germany (Thies and Tscharntke, 1999). This is also true for woody vegetation remnants within agricultural ecosystem. Ground-dwelling arthropod predators (spiders, centipedes, and ground beetles) in central Italy are influenced by proximity to the grassy area edge up to 15 m away from the forest, while in the forest they were not affected by the edge proximity (Lacasella et al., 2015). Grassy area arthropod community occurrence was lower compared to forest arthropod communities next to the forest edge, potentially due to tree shade creating a less preferable microclimates (Cadenasso et al., 1997).

Indeed, differences in microclimates can also drive insect population patterns in agricultural landscapes both directly and indirectly. Microhabitat selection plays an important role in the thermoregulation, which has direct physiological consequences (Angilletta (2009); Huey, 1991) and likely impacts insect herbivore distribution within an agricultural landscape (e.g. Maeno et al., 2019). Indirectly, microclimates can influence the overall balance of top-down and bottom-up effects. For example, when temperature increased, the top-down (mosquito larva) control of protozoa and bacteria populations within pitcher plants increased whereas bottom-up (ant carcasses) control remained relatively constant (Hoekman, 2010). Since nutrient regulation in insect herbivores is tied to temperature (e.g. Miller et al., 2009; Coggan et al., 2011), bottom-up control importance can also fluctuate. However, the indirect impacts of microclimates through top-down and bottom-up control of insect herbivores have not been extensively studied (Cross et al., 2015). Microclimates likely have numerous direct and indirect impacts of insect herbivore distributions between natural remnant and agricultural patches.

Grasshoppers are often the dominant herbivore in rangelands (Branson et al., 2006) and play an important part in ecosystem functioning (Belovsky and Slade, 1993; Gandar, 1982; Schmitz, 1994). Although it was initially argued that grasshopper populations were primarily predator regulated (Dempster, 1963), we now know that the effects of predation may not be as straightforward as previously thought (e.g. Joern and Gaines, 1990; Belovsky and Slade, 1993). Grasshopper populations are influenced by microclimates (Chappell and Whitman, 1990; Maeno et al., 2019; May, 1979), resource limitation (Bernays and Chapman, 1973; Chapman and Joern, 1990; Jonas and Joern, 2008), and host plant nutrients (Cease et al., 2012; Joern et al., 2012; Word et al., 2019). Understanding both top-down and bottom-up effects on populations is important to the overall regulation of grasshoppers, however this has yet to be shown in agroecosystems.

In this study, we explored the relationship among Australian plague locusts, trees, grass nutrient content, invertebrate predator abundance, and ground temperature using transects established within wooded areas, at the edge of wooded areas, 20 m away from the wooded areas, and in open grassy areas. These variables are intercorrelated (e.g. Miller et al., 2009; Hawlena et al., 2012), therefore our hypotheses are non-mutually exclusive. Based on the 'island of fertility' hypothesis (Scholes and Archer (1997)), we predicted grasses near or in the wooded areas would have higher nitrogen content (and corresponding higher protein) compared with the same species growing in open grassy areas. Many studies have demonstrated the importance of macro-nutrient ratios on food selection (Simpson and Raubenheimer, 2012), and we know that Australian plague locusts prefer a carbohydrate-biased diet (Clissold et al., 2006; Cease et al. unpub. data.), we thus predicted Australian plague locust density would be highest in the grassy areas where plants should have a lower protein:carbohydrate ratio. We predicted that the abundance of predators, would have little effect on Australian plague locusts density based on previous research showing limited direct impact of predator abundance (Farrow, 1982a, 1982b, 1979a). We predicted that bottom-up forces would have stronger effects on herbivore populations than top-down forces. Furthermore, since it is generally cooler in the shade and *C. terminifera* prefers high temperatures 38 – 40 °C (Klass et al., 2007), we predicted there would be a positive correlation between grasshopper density and temperature.

2. Methods

2.1. Field surveys

2.1.1. Wooded-grassy area transects selection

We conducted this study in New South Wales, Australia, at the Trangie Agricultural Research Centre on December 12–28, 2016 and October 10–28, 2017. We selected three open native pastures (Fig. S1) with at least one substantial wooded area measuring > 50 m in diameter. All pastures used rotational grazing of both cattle and sheep and there was no history of cultivation.

Within each of the three fields, we placed four, 50 m transects to survey the gradient from wooded to grassy areas coined: wooded area, edge, 20 m from edge (henceforward called 20 m), and grassy area. We placed the wooded area, edge, and 20 m transects parallel to each other but disconnected the grassy area transect to avoid sparsely distributed trees. To ensure suitable host plants were available for locusts across our survey gradients, we selected wooded areas that had understory grass communities. We defined open grassy area as a perpendicular 50 m transect with no trees or shrubs located within 100 m of the transect.

2.1.2. Locust density

For this study, we focused on Australian plague locusts, *C. terminifera*, which is within a subset of grasshoppers that exhibit phase polyphenism (Simpson and Sword, 2009), and is of economic importance in agricultural areas (Cullen et al., 2017). We determined locust density in two parts, using an approach modified from earlier "ring count" methods (Joern, 2005; Joern et al., 2012; Onsager, 1977): (1) we recorded overall grasshopper density via transects and (2) we calculated the proportion of *C. terminifera* out of all grasshoppers via sweep net sampling (Evans et al., 1983). To count how many grasshoppers were on the transects, a single observer (D. Lawton) walked back and forth on either side of, and ten meters away from, a given 50 m transect, recording every grasshopper spotted within 0.5 m on each side of the walking path (i.e. 1 m width x50 m length). Because adults disperse by flight several meters in advance of the observer, and nymphs have no wings and tend to jump when the observer was within a couple meters, the observer looked up to focus on adults during the first pass on one side (50 m^2 area) and looked down to focus on nymphs during the second pass on the other side (50 m^2 area). Nymphs were recorded as either 1st-3rd instar, 4th-5th instar. This allowed us to estimate grasshopper adult and nymph density in a 50 m^2 area. After the visual assessment, we collected locusts via sweep net for 30 min around the transect area (~ 1000 m^2). All sweep net samples were frozen for 48 h and then sorted. We recorded all grasshoppers as either *C. terminfera* or other grasshopper species, sorted them into life stage groups, noted the

sex, and weighed each group. Locust (*C. terminifera*) density was then estimated by multiplying the proportion of *C. terminifera* by the total number of grasshoppers counted in the 50 m^2 transects.

We repeated these surveys at each transect in the three fields, three times in 2016 and two times in 2017. To account for imperfect detection and unintended variation, all density data were collected by the same observer (D. Lawton). Temperature, relative humidity, and wind speed averages during sweep net sampling can be found in table S1.

2.2. Bottom-up effects

2.2.1. Ground cover and plant nutrient content

In both years, we recorded ground cover (bare ground, cryptogam, litter, manure, coarse woody debris) and the three most abundant non-woody plant genus along each transects using the point intercept method (Bauer, 1943). Since litter accounted for the majority of non-bare ground cover (96 % +/- 0.58 % SEM) in each transect, with cryptogam, coarse woody debris, and manure accounting for the remaining small proportion (3.4 % +/- SEM: 0.49 %), we grouped all non-bare ground variables into a single cover category (Fig. S2). We then used the percentage of bare ground as the primary variable for statistical analyses. Leaves of the most abundant grass and forb genus were collected, kept in a cooler with ice until they were placed in an oven and dried at 60 °C for three days. We ground leaves using a Retsch MM 400 ball mill for 30 s at 200 rpm. To measure leaf carbohydrate and protein content, we used the Bradford protein and phenol-sulfuric carbohydrate assays (Bradford, 1976; Dubois et al., 1956) following the protocol in Clissold et al. (2006). Since carbohydrate and protein contents were highly correlated (Pearson's r, r: 0.76, p-value: < < 0.001) and would violate statistical assumptions of independence between the predictor variables, we used protein proportion of total macronutrient content [protein / (protein + carbohydrate)] for appropriate statistical analyses.

2.2.2. Locust host plant choice test

To test if locusts preferred plants growing in the open grassy area (potentially lower nitrogen) *vs.* under the wooded area, we collected a readily accepted host plant, curly windmill grass (*Enteropogon acicularis*) (Key, 1945) from both areas in December 2016 within field 1 and 2. After collection, we wrapped plant stems in a wet paper towel and immediately brought them back to the lab. The same day, we collected 24 locust (12 males and 12 females) adults. We placed locusts in plastic containers (26 × 20 × 5 cm) with holes for aeration, a perch, water tube, and secured a single grass blade from each transect into a tube of water using cotton. Trials were conducted between 10 am – 6 pm December 17th, 2016. The average temperature was 28.1 °C (SEM: 0.492). The first blade to be considerably consumed (> 1 cm) was considered the preferred plant. If any locust did not eat either blade of grass after 8 h, the trial was ended and excluded from the analysis.

2.3. Top-down effects

2.3.1. Pitfall traps

In 2017, we used pitfall traps to record invertebrate predator abundance (Woodcock, 2005). For each transect we dug five traps evenly spaced (10 m apart), using PVC pipe sections (10 cm height X 7.5 cm width) with plastic cups (260 mL) inside flush to the ground and a plastic cover (13 mm above surface) nailed into the ground to prevent soil or rain from entering the trap. We filled the traps with a 50 % propylene glycol solution and added a drop of dish soap to break the surface tension and kill the insects. After 48 h, we collected the trap contents, washed the specimens with ethanol, and identified arthropods to family.

2.3.2. Effects of predators on grasshopper distribution

The meat ant (*Iridomyrmex purpureus*; Smith, 1858) has been suggested as a major predator of Australian plague locusts (Farrow, 1982a). Meat ants typically stay within 50 m from their nest (Greenslade, 1976). To assess how the presence of meat ants affected grasshopper community distribution, we surveyed grasshopper abundance near 10 nests. For each nest, we swept for grasshoppers along 20 m transects located at 5, 10, and 20 m from the nest center in two cardinal directions (east/west or north/south). Grasshoppers were then frozen and sorted by species, sex, and age.

2.4. Temperature

We used iButtons (Thermochron, Maxim Integrated) to collect temperature data from the wooded to grassy area gradients. In 2016 we selected one field (field 2) and placed three iButtons at each transect at the following heights: 10 cm aboveground and at ground level. This allowed us to analyze the temperature differences for the full thermal profile of locust behavior (e.g. sitting on the surface of the soil and roosting on plant). In 2017, for logistical reasons we were only able to record one height along all transects. We selected ground temperature as it is important for behavioral thermoregulation (Chappell and Whitman, 1990). When transects were shaded by trees, we placed the iButtons in tree canopy gaps where they received partial sun. In all cases, iButtons were placed under dead standing litter to avoid direct exposure to sunlight.

2.5. Statistical analyses

All data were tested for normality and homoscedasticity. We performed a three-way ANOVA (dependents: transect, field, year) to determine how locust density change through space and time. We performed MANOVAs on grass nutrient content (dependents: protein and carbohydrate content; independents: year, field, transect, and genus) to determine how protein and carbohydrates changed through time and space. We performed Scheirer-Ray-Hare tests (a non-parametric version of the two way ANOVA) (Scheirer et al., 1976) on predators abundance (ants and predators recovered from the pitfall traps) with transect and field as independent factors. We constructed generalized additive mixed models (GAMM) to determine which predictor variables best explained locust distribution across years and to test the effect of transect on ground temperature. Due to sample size and methodological design, we were unable to model the interactive effects between transect and independent variables on locust abundance. All GAMMs were constructed using mgcv (Wood, 2017), validated with mgcViz (Fasiolo et al., 2019) packages and selected via null space penalization (Marra and Wood, 2011; Wood et al., 2016). We performed post hoc analyses on significant independent variables determined by GAMMs. All statistics were conducted in the Tidyverse framework (Wickham, 2017) within the R statistical environment (Team, 2018).

3. Results

3.1. Locust density and abundance

Locust density and abundance was lower in wooded areas than in all other locations, besides the edge transect for locust density (Fig. 1, Table 1; Table S2). Field 3 had a higher locust density and abundance than fields 1 and 2 (Fig. S3, Table S3). We found no difference in locust density and abundance between years (Table 1). There was an interactive effect between transect location and field on locust density and abundance: there were more individuals in the grassy area of field 3 than in any other area surveyed (Fig. S3, Table S4, Table S5). We found no other interactive effects among transect location, field, or year (Table 1).

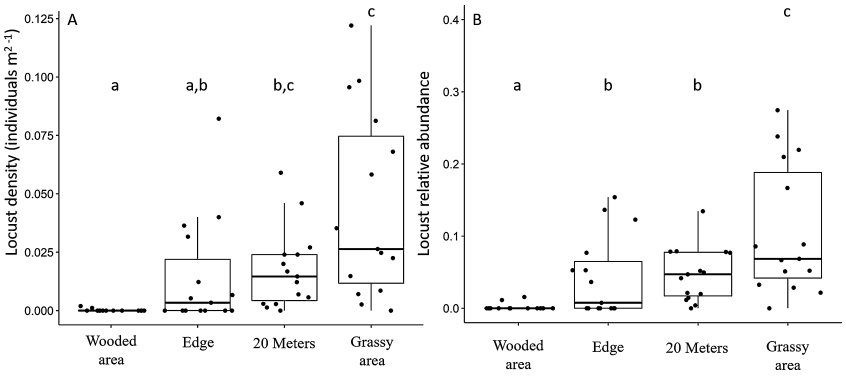

Fig. 1. Australian plague locust density (A) and abundance (B) along a wooded to grassy area gradient. Raw data represented by dots. Letters represent significance.

3.2. Grass nutrient content and host plant choice test

Grass nutrients differed between years and genus but not between transect or field (Table 2, Fig. 2). In 2017, grasses contained more protein and carbohydrates than grasses in 2016 (Table 2, Fig. 2B). Similarly, grasses from different genera differed significantly in both protein and carbohydrate content (Table S6, Fig. S4). However, none of the variables tested (dependents: field, transect location, plant genus, year; covariate: total macronutrient content) affected protein: carbohydrate ratio (Table S7), and the differences observed were driven by differences in total macronutrient contents. Corroborating this pattern, locusts did not exhibit preference for curly windmill leaves (*Enteropogon articulus*) collected under wooded areas *vs.* leaves from the grassy areas (X^2: 0.44, p-value: 0.50).

Table 2
MANOVA results of predictor effects on grass carbohydrate and protein content.

Effect	Pillai's Trace	F	df	P-value
Field	0.155	0.922	444	0.460
Transect	0.215	0.884	644	0.515
Genus	0.855	3.286	1044	0.003
Year	0.538	12.233	221	< < 0.001
Transect * genus	0.330	0.483	1844	0.952
Transect * Year	0.168	0.671	644	0.673
Genus * Year	0.216	2.891	221	0.078

3.3. Temperature gradient

We fitted a GAMM (family: scaled t, link: log) to the 2016 data (Fig. S5) with temperature as the response variable, the predictor variables being height (above ground or ground) and hour of day, and transect as a random effect (Table 3, Fig. 3A). This led to a final model with an adjusted R^2 value of 0.657 (deviance explained: 0.507). Height was a significant factor in the overall GAMM (Table 3). During the day, ground temperature was higher than above ground (Fig. 3A, Table 3). We also fitted a GAMM (family: scaled t, link: log) to the 2017 data (Fig. S6) with ground temperature (the only temperature measured that year) as the response variable, the predictors variables being transect and hour of day, and field as a random effect (Table 4, Fig. 3B). This led to a final model with an adjusted R^2 value of 0.627 (deviance explained: 0.444). Transect was a significant factor in the overall GAMM (Table 4). Daily temperature was higher in the wooded area transects than on the edge and grassy area transects (Table S8). Daily temperature in the 20 m transect was higher than edge and grassy area transects. Daily temperature in the grassy area transects was higher than the edge transects.

3.4. Predator abundance

Because meat ants were the most abundant predator and known to eat locust, we analyzed them separately from the rest of the arthropod predators collected from pitfall traps. There was no effect of transect location on meat ant abundance (Scheirer-Ray-Hare test: H: 7.403, df: 3, p-value: 0.060; Fig. 4A), although there was a general pattern with ants typically being more abundant near the edge and in the grassy area. Similar to locust populations, field 3 harbored more meat ants than field 2 (H: 15.969, df: 2, p-value: < 0.001; Table S9). We found an interactive effect of field and transect location on meat ant abundance (H: 20.501, df: 6, p-value: 0.002): there were more meat ants in field 3 at edge, 20 m, and grassy area transects than fields 1 or 2 (Fig. S7, Table S10). In a separate survey (see section 2.2), we found that locust abundance was not affected by the proximity to meat ant hills (Kruskal-Wallis: X^2: 0.685, df: 2, p: 0.710) within grassy areas. The abundance of other ant species did not vary along the wooded to grassy area gradient

Table 1
Three-way ANOVA of locust density along a wooded to grassy area gradient.

	Locust density			Locust abundance		
Variable	F	degrees freedom	P-value	F	degrees freedom	P-value
Transect	18.837	3	< < **0.001**	25.923	3	< < **0.001**
Field	18.456	2	< < **0.001**	31.118	2	< < **0.001**
Year	2.079	1	0.158	2.287	1	0.139
Transect*Field	7.178	6	< < **0.001**	8.234	6	< < **0.001**
Transect*Year	0.447	3	0.721	0.388	3	0.762
Field*Year	0.045	2	0.956	0.866	2	0.429
Transect*Field*Year	1.014	6	0.431	1.422	6	0.226

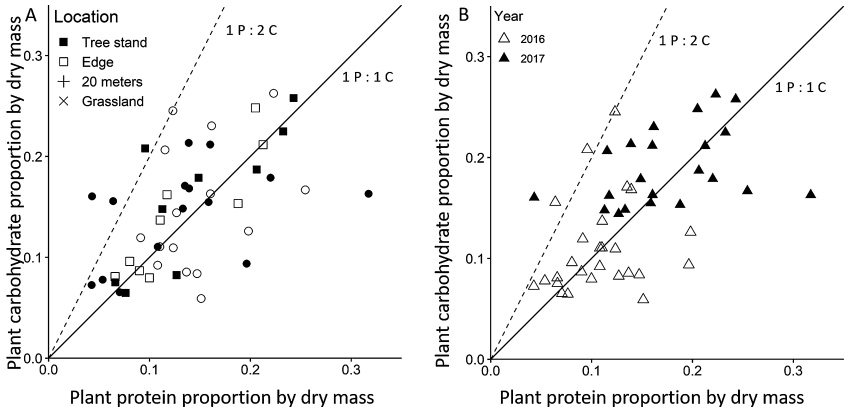

Fig. 2. Grass carbohydrate and protein content by transect (A) and by year (B). Solid lines are 1:1 and dashed lines are 1:2 protein:carbohydrate ratios.

Table 3
Generalized additive mixed model results for the effect of height by hour of day on temperature in 2016.

Parametric coefficients	Estimate	Error	p-value
Intercept	26.864	0.296	< < 0.001
Ground	1.375	0.072	< < 0.001
Smooth Terms	edf	F	p-value
Hour * above ground	17.94	1266	< < 0.001
Hour * ground	19.13	1696	< < 0.001
Transect (random effect)	2.96	65.5	< < 0.001

Table 4
Generalized additive mixed model results for the effect of transect by hour of day on temperature in 2017.

Parametric coefficients	Estimate	Error	p-value
Intercept	3.204	0.035	< < 0.001
Edge	−0.095	0.008	< < 0.001
20 m	0.030	0.007	< < 0.001
Grassy area	−0.057	0.008	< < 0.001
Smooth Terms	edf	F	p-value
Hour * Wooded area	17.368	6667	< < 0.001
Hour * Edge	9.925	1158	< < 0.001
Hour * 20 m	14.422	6997	< < 0.001
Hour * Grassy area	11.822	3553	< < 0.001
Field (random effect)	1.992	506	< < 0.001

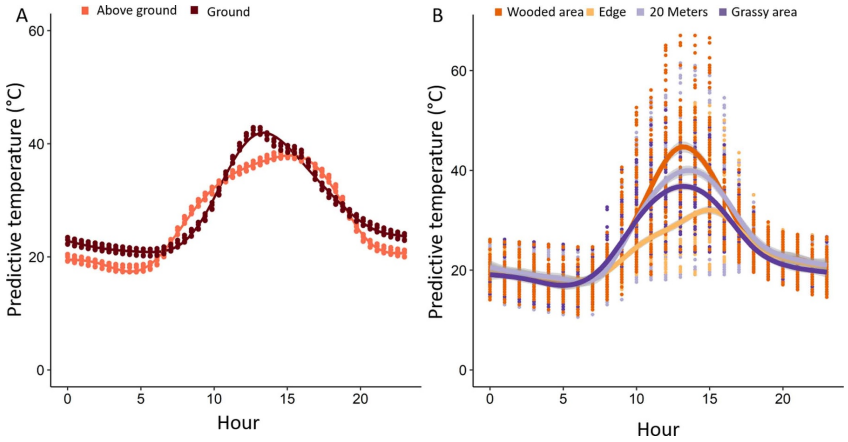

Fig. 3. Daily GAM predictive temperature for height in 2016 (A) and transect in 2017 (B). Dotted lines represent 95 % CI. Points are predictive values from the GAMM model with the smoothed relationship for each transect represented as a line. Shaded areas represent 95 % CI.

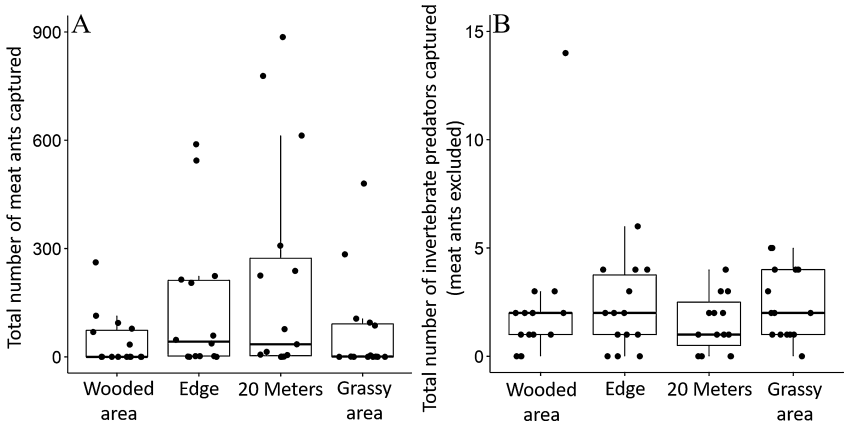

Fig. 4. Predators collected at each transect for meat ants (A) and other invertebrate predators (ants excluded) (B). Points represent data for an individual pitfall trap.

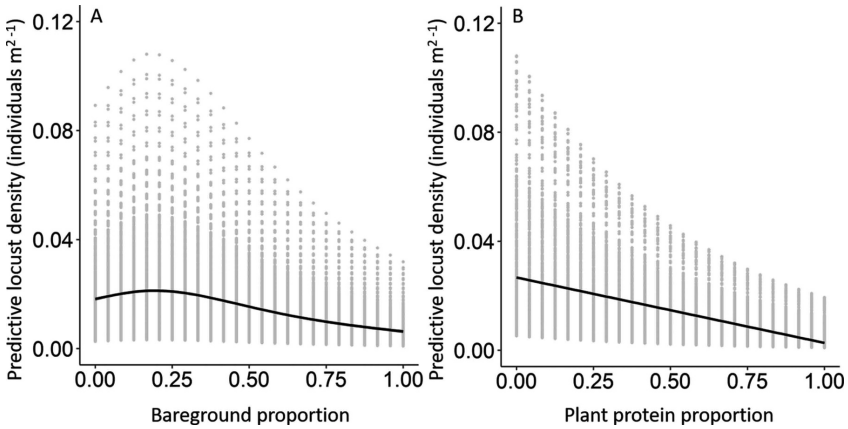

Fig. 5. Model predictive Australian plague locust density response to proportion of bare ground (A) and plant protein (B). Dots represent model prediction and lines represent line of best fit.

Table 5
Generalized additive model for the effect environmental variables on locust density on a gradient from wooded to grassy areas.

Parametric coefficients	Estimate	Error	p-value
Intercept	0.779	0.405	0.055
Year	−0.087	0.083	0.292
Plant protein proportion	−1.718	0.692	0.013
Edge	0.362	0.165	0.028
20 m	0.681	0.172	< < 0.001
Grassy area	1.118	0.152	< < 0.001
Smooth Terms	edf	X^2	p-value
% Bare ground	1.771	12.010	0.008
Field (random effect)	1.893	41.840	< < 0.001

(Table S11) and were on average 12 folds less abundant than meat ants (Table S12). Therefore, we excluded ants in further analyses. We identified arthropods present in the pitfall traps at family level and reported predaceous ones only (Table S12). We found that predator abundance did not significantly differ along transect location or among fields (Fig. 4B).

3.5. Overall model

We fitted a GAMM (family: scaled t family, link: log) to the data (Fig. S8). Due to methodological differences between years, we were unable to include temperature and predator abundance into the final model. Our response variable was locust density; predictors were transect, percent bare ground, and protein proportion, and field was included as a random effect. Protein proportion was first included as a nonlinear variable; however, it was not selected as a nonlinear variable under null space parameterization (estimated degrees of freedom ≈ 1) (Marra and Wood, 2011). Therefore, we included protein proportion as a linear predictor. This led to a model with an adjusted R^2 of 0.656 (deviance explained: 0.509). Locust density was highest at 20 % bare ground and decreased thereafter (Fig. 5A, Table 5). Locust density was positively correlated with distance away from wooded area transects

and negatively correlated with protein (as a proportion of total macronutrients) (Fig. 5B, Table 5).

4. Discussion

We found that Australian plague locusts avoided wooded areas by at least 20 m (Fig. 1). This result corroborates earlier surveys on non-swarming *C. terminifera* populations (Clark, 1950) and on swarming populations (Deveson, 2017; Key, 1945; Veran et al., 2015). Australian landowners and locust managers have reported watching Australian plague locust marching bands avoid wooded areas and/or tree shade (Ted Deveson, pers. comm). Over decadal time scales, deforestation has been correlated with the appearance of Australian plague locust outbreaks and subsequent migratory swarms (Deveson, 2017; Deveson and Walker, 2005; Farrow, 1979b). However, despite the important influence of wooded areas on Australian plague locust populations, the mechanisms underpinning these patterns have not been previously tested. In this study, we proposed three top-down and bottom-up hypotheses to explain this species' aversion to wooded areas: 1) grass nutrient gradient, 2) predation, and/or 3) thermoregulation. We did not find support for any of these hypotheses as standalone variables to explain why Australian plague locusts avoided wooded areas. However, host plant nutrient content and ground cover, independent of the wooded to grassy area gradient, were significant predictors of Australian plague locust abundance when considered in a mixed model.

4.1. Wooded to grassy area gradient

4.1.1. Plant nutrient content

Grass protein and carbohydrate contents and ratios were not significantly different across the wooded to grassy area gradient (Fig. 2A, Table 2). This lack of an apparent 'island of fertility' (Scholes and Archer, 1997) effect by trees in this system (fragmented eucalypt woodland within grazing pasture) may be due to several factors. Since plant nutrient content varies across space and time, this could have been from only having two time points. However, since we did see a change in total nutrient content between years and not between protein and carbohydrates independent from location (Fig. 2B), we do not expect this to be the case. Further, our results run counter to previous studies that have indicated livestock camp sites in wooded areas increases soil and grass fertility (Robinson et al., 1983; Taylor et al., 1984). It could be that nitrogen is accumulating under trees but is not translated to protein content in plants. Grass nutrient content is also affected by phenological stages (Arzani et al., 2004), species-specific soil nutrient responses (Bradshaw et al., 1964), and inter-specific competition for light, nutrients, and water (Craine and Dybzinski, 2013). The similar nutritional value of host plants collected from wooded vs. grassy area is corroborated by Australian plague locust individuals showing no preference between these plants (see section 3.2). Overall, the majority of plants were protein biased as compared to the preferred 1 protein: 2 carbohydrates (P:C) ratio of this locust species despite the noticeable variation in plant nutrient content (Fig. 2) suggesting that overall this landscape is nutritionally suboptimal for this species.

4.1.2. Temperature

Ground temperature was different among transects. Wooded areas had the highest ground temperature and edge had the lowest (Fig. 3B). This may be due to trees precluding wind-chill and preventing heat to be dissipated. Further, litter likely mediates the ground temperature as most grassy areas and 20 m transect locations had high proportions of litter as compared to the wooded area and edge locations (Fig. S2). These results suggest that ground temperature alone is likely not an important variable explaining Australian plague locust distribution in this agroecosystem. When given the choice, Australian plague locusts will thermoregulate to achieve body temperatures between 38 – 40 °C (Klass et al., 2007) - a temperature range found 20 m from wooded areas, where Australian plague locusts are not abundant (Fig. 3). However, the ground temperature recorded by iButtons is likely not representative of the full array of thermal niches available to grasshoppers, who are adept at thermoregulating by moving among microclimates and positioning their body according to solar radiation (Chappell and Whitman, 1990). By thermoregulating, many grasshopper species are able to maintain a constant body temperature that is 10 °C or greater than ambient temperature (e.g. Chappell, 1983; Whitman, 1987). For example, a desert locust (*Schistocerca gregaria*; Forsskål, 1775) population in Mauritania changed microhabitats (i.e. bare ground vs short or tall vegetation) throughout the day corresponding to the daily thermo-photocycle (Maeno et al., 2019). Similarly, if Australian plague locusts are able to reach an acceptable body temperature within grassy areas, larger-scale temperature gradients (i.e. at the level of hectares) may not be important in determining locust distribution.

4.1.3. Invertebrate predators

Invertebrate predator abundance did not explain the distribution of Australian plague locusts in this field study. There was no effect of transect location on ant or other predator abundance (Fig. 5). Even though pitfall traps provide an indicative measure of abundance, it is possible that catches are influenced by invertebrate activity (Waters et al., 2017) and other biases such as trap spacing (Ward et al., 2001) and fluid choice (Schmidt et al., 2006). The eastern Australian landscape is dominated by large meat ant nests (Andersen, 1993) which, along with lycosid spiders, have been suggested as the main predators of Australian plague locusts (Farrow, 1982a). However, the proximity to meat ant nests also had no impact on locust nymph abundance.

The effects of predation on herbivore populations is a complex issue, including direct and indirect or non-consumptive effects (e.g. Griffin and Thaler, 2006; Murakami and Nakano, 2002; Schmitz and Suttle, 2001), which were not measured in this study. Vertebrates, such as birds and reptiles, as well as spiders, have been identified as grasshopper predators (Bock et al., 1992; Chase, 1996; Joern, 1992, 1986; Joern and Gaines, 1990; Schmitz et al., 1997). However, field studies on outbreaking Australian plague locust populations suggest that predation, including birds, has limited impact on locust distribution and density (Farrow, 1982a). In our study, locust density was very low overall (< 0.13 per m^2) and this may impact predation rates. Interestingly we found higher abundance of both Australian plague locusts and ants in field 3, suggesting that top-down control may not be a major factor regulating population dynamics in this system. However, to our knowledge, no studies have directly measured the impact of predation on low density Australian plague locust populations.

4.2. Overall model

The overall model showed that multiple factors were needed to best describe Australian plague locust density (Fig. 5, Table 1). In addition to an aversion to wooded areas, Australian plague locust density was negatively correlated with plant protein (proportion of total macronutrient concentration) and was highest in habitats with ~20 % bare ground cover (Fig. 5). Interactive effects of temperature and predator presence on nutrient selection have previously been demonstrated for other grasshopper species (Hawlena et al., 2012; Miller et al., 2009), providing more evidence that our three hypotheses are not necessarily mutually exclusive. This could explain our non-significant results along the wooded to grassy area gradient, but the significant effects of bare ground and protein proportion in the final model.

The balance of macronutrients has strong impacts on fitness correlates, such as growth and survival, for organisms ranging from slime molds to humans (Simpson and Raubenheimer, 2012). For insect herbivores, the balance of proteins and carbohydrates is particularly important (Behmer, 2009). Australian plague locust populations collected

from Mendooran and Guntawang (near our Trangie study site) self-selected a 1:2 P:C diet (Cease et al. unpublished data). In comparison, the majority of host plants collected in this study had ratios closer to 1:1 P:C, regardless of year, field, or transect (Fig. 3, Table 2). This discrepancy between dietary preference and host plant nutrients suggests that the Australian plague locust populations we studied were carbohydrate (not protein) limited, explaining their higher abundance near high carbohydrate, low protein vegetation (Fig. 5, Table 1). Our results are in line with previous research suggesting that Australian plague locusts are carbohydrate-limited based on their reduced capacity to extract carbohydrates relative to proteins from host plant tissues (Clissold et al., 2006). The ratio of litter to bare ground is important for thermoregulation (Chappell and Whitman, 1990), oviposition (Clark, 1965; Stauffer et al., 2019), predator avoidance (Lagos, 2017), and food (Uvarov, 1977). The ratio of ~20 % bare ground and ~80 % litter, where Australian plague locusts were most abundant (Fig. 1 and 5), is likely a good balance to allow individuals to meet their physiological and ecological needs.

4.3. Conclusions

We showed that Australian plague locusts avoid wooded areas, corroborating previous research (Clark, 1950; Deveson, 2017; Key, 1945; Veran et al., 2015). However, we did not find support for the three hypotheses tested (temperature, plant nutrients, or predators) to explain this aversion. Perhaps other factors, such as light intensity or vertebrate predators (Belovsky and Slade, 1993; Chapman, 1954) may be important and/or a complex interaction of multiple factors may be necessary to explain Australian plague locust's aversion to wooded areas. These factors are all influenced by land use patterns and it is likely that there are interactive effects among multiple factors on grasshopper populations. For example, a study using a 350 km transect and 200 − 400 mm precipitation gradient in Inner Mongolia showed that livestock grazing decreased grasshopper community diversity in low, but not high, precipitation sites (Hao et al., 2015).

At a national scale, wooded area aversion can be seen in the Australian Plague Locust Commissions monthly surveys (Deveson and Hunter, 2002). This suggests that the pattern of locusts avoiding trees may be consistent across scales, which is not common in ecological processes (Levin, 1992). Arid lands are in constant flux due to agriculture, invasive weeds, shrubby encroachment, and unpredictable rain, among other factors, drastically changing the landscape. Understanding the small-scale mechanisms driving the responses of grasshoppers and other major dryland herbivores to these changing landscapes is critical to understanding and predicting large-scale population dynamics.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agee.2020.106931.

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APPENDIX C

SUPPLEMENTARY DATA FOR CHAPTER 4

Table C.1: Median Ground Cover Categories for Field in All Locations. Categories Are as Follows: 0 = 0%, 1 = 1% - 5%, 2 = 6% - 10%, 3 = 11% - 25%, 4 = 26% - 50%, 5 = 51% - 75%, 6 = 76% - 100%

Region	Field	Vegetation	Rock	Litter	Dung
Coonamble	A	3	0	3	1
	B	4	0	3	0
Ivanhoe	A	4	2	4	0
Trangie	A	4	0	4	1
	B	4	0	4	1

Table C.2: Averaged Plant Cover by Location. Each Location Was Sampled 10 (Coomable, Trangie Early, Trangie Late) or 5 (Ivanhoe) Times. We Then Averaged the Plots Together and Reported Standard Error. Since the Grasshoppers in This Study Do Not Eat Forbs, We Combined All Forbs Together Into a 'Other Forbs' Group.

Location	Species	Average percent cover	Standard error
Coonamble	*Cenchrus ciliaris*	8.00%	0.00
Coonamble	*Dactyloctenium radulans*	3.00%	0.00
Coonamble	*Diplachne fusca*	8.00%	0.00
Coonamble	*Enteropogon acicularis*	14.11%	3.51
Coonamble	other forbs	6.75%	3.75
Coonamble	*Paspalidium jubiflorum*	5.50%	2.50
Coonamble	*Stipa scabra*	5.50%	2.50
Ivanhoe	other forbs	3.00%	0.00
Ivanhoe	*Stipa scabra*	5.00%	1.22
Trangie early	*Enteropogon acicularis*	3.00%	0.00
Trangie early	*Stipa spp*	3.00%	0.00
Trangie early	*unknown grass*	3.00%	0.00
Trangie late	*Enteropogon acicularis*	12.38%	2.20
Trangie late	other forbs	10.14%	4.74
Trangie late	*Sida spp*	3.00%	0.00
Trangie late	*Stipa spp*	3.00%	0.00
Trangie late	*Stipa variables*	13.00%	5.00
Trangie late	unknown grass	3.00%	0.00

Table C.3: Environmental Conditions When Sampling Grasshopper Abundances. It Was Raining During Locust Abundance Sampling in Coonamble Field 2.

Location	Field	Temperature (C)		Relative Humidity (%)		Wind speed (mps)	
		average	SEM	average	SEM	average	SEM
Coonamble	1	27.9	0.677	56.7	1.4	0.5	0.22
	2	27.7	0.3	100	0	0.72	0.16
Trangie Early	1	27.8	0.455	41.8	1.37	1.7	0.12
	2	32.4	0.548	34.2	1.24	2	0.32
Trangie Late	1	28.1	1.88	41.5	3.32	1.7	0.2
	2	26.5	1.1	44.7	2.67	2.26	0.19
Ivanhoe	1	32.1	0.348	39	0.38	1.9	0.19

Table C.4: Grasshopper Density (M2-1) at Each Location by Species and Age. CT: Chortocietes Terminifera, OA: Oedaleus Australis, AT: Aiolopus Thalassinus Dubios, OG: Other Grasshoppers

Location	CT adult	CT 5th	CT 1-4th	OA adult	OA 5th	OA 1-3rd	AT 5th	AT 5th	AT 1-3rd	OG adult	OG nymphs
Coonamble	0.002	0	0	0.079	0.008	0.022	0.007	0.002	0.011	0.009	0.027
Ivanhoe	0.026	0	0.016	0.002	0	0	0.002	0	0	0	0
Trangie early	0.001	0	0.021	0	0	0	0	0	0	0.004	0.499
Trangie late	0.003	0.001	0.002	0	0	0	0.004	0.012	0.364	0.003	0.052

Table C.5: Intake Target Experiment Summary of Total Grasshopper Started, the Numbers That Died or Survived, and the Mean and Percentage Body Weight Change.

Location	Species	Total	Died	Survived	Averaged body weight change (g)	Averaged percent body weight change
Coonamble	*C. terminifera*	23	5	18	-0.010	-0.058%
	O. australis	24	9	15	-0.033	-0.159%
	A. thalassinus	15	3	12	-0.022	-0.123%
Ivanhoe	*C. terminifera*	26	7	19	-0.041	-0.169%
	O. australis	11	7	4	0.005	0.039%
Trangie early	*C. terminifera*	13	7	6	-0.112	-0.373%
Trangie late	*A. thalassinus*	24	3	21	-0.015	-0.078%
	C. terminifera	28	5	23	-0.046	-0.153%

Table C.6: Intake Target Experiment Day Temperature, Relative Humidity, and Light Intensity

Location	Mean Temperature (C)	SEM Temperature	Mean Relative Humidity (%)	SEM Relative Humidity	Mean Light Intensity (lumens/ft^2)	SEM Light Intensity
Trangie early	30.19	0.200	30.37	0.4267	293.2	10.87
Trangie late	32.45	0.208	28.87	0.6134	250.5	7.590
Coonamble	31.44	0.197	41.52	0.6713	292.2	14.59
Ivanhoe	27.08	0.148	35.54	0.4147	355.0	10.67

Table C.7: Model Selection via Akaike Information Criterion for C. Terminifera. The S(Weight) Notation Denotes a Smoothing (e.g. Nonlinear) Parameter Was Estimated.

Model	Response Variables	Independent Variables				AIC
1	Carbohydrates	Location	Sex	Treatment	s(Weight)	-708.426
	Protein	Location	Sex	Treatment	s(Weight)	
2	Carbohydrates	Location	Sex	Treatment	s(Weight)	-706.581
	Protein	Location	Sex	Treatment	Weight	
3	Carbohydrates	Location	Sex	Treatment	s(Weight)	-708.427
	Protein	Location	Sex	Treatment		
4	Carbohydrates	Location	Sex	Treatment		-700.733
	Protein	Location	Sex	Treatment		
5	Carbohydrates	1				-678.54

Table C.8: Model Selection via Akaike Information Criterion for A. Thalassinus. The S(Weight) Notation Denotes a Smoothing (e.g. Nonlinear) Parameter Was Estimated.

Model	Response Variables	Independent Variables				AIC
1	Carbohydrates	Location	Sex	Treatment	s(Weight)	-457.339
	Protein	Location	Sex	Treatment	s(Weight)	
2	Carbohydrates	Location	Sex	Treatment	s(Weight)	-455.331
	Protein	Location	Sex	Treatment	Weight	
3	Carbohydrates	Location	Sex	Treatment	s(Weight)	-457.34
	Protein	Location	Sex	Treatment		
4	Carbohydrates	Location	Sex	Treatment		-445.748
	Protein	Location	Sex	Treatment		
5	Carbohydrates	1				-444.121
	Protein	1				

Table C.9: Model Selection via Akaike Information Criterion for O. Australis. The s(Weight) Notation Denotes a Smoothing (e.g. Nonlinear) Parameter Was Estimated.

Model	Response Variables	Independent Variables				AIC
1	Carbohydrates	Location	Sex	Treatment	s(Weight)	-271.775
	Protein	Location	Sex	Treatment	Weight	
2	Carbohydrates	Location	Sex	Treatment	Weight	-270.249
	Protein	Location	Sex	Treatment	s(Weight)	
3	Carbohydrates	Location	Sex	Treatment	s(Weight)	-268.254
	Protein	Location	Sex	Treatment		
4	Carbohydrates	Location	Sex	Treatment		-272.055
	Protein	Location	Sex	Treatment		
5	Carbohydrates	1				-277.223

Table C.10: TukeyHSD Posthoc Test to Determine the Abundance Differences Between Locations. Significance Shown in Bold.

Species	Location comparison		p-value
Aiolopus thlassinus	Coonamble	Ivanhoe	0.853
		Trangie	**0.000**
	Ivanhoe	Trangie	**0.000**
Chortoicetes terminifera	Coonamble	Ivanhoe	**0.000**
		Trangie	0.880
	Ivanhoe	Trangie	**0.000**
Oedaleus australis	Coonamble	Ivanhoe	**0.002**
		Trangie	**0.000**
	Ivanhoe	Trangie	0.996
Other grasshopper species	Coonamble	Ivanhoe	0.227
		Trangie	0.750
	Ivanhoe	Trangie	0.077

Figure C.1: Example Photo of the 2017 Conditions in Trangie, NSW. Overall, Biomass Was Low With High Standing Litter Content. The Black Rope Represents the 5 X 5 M Quadrat.

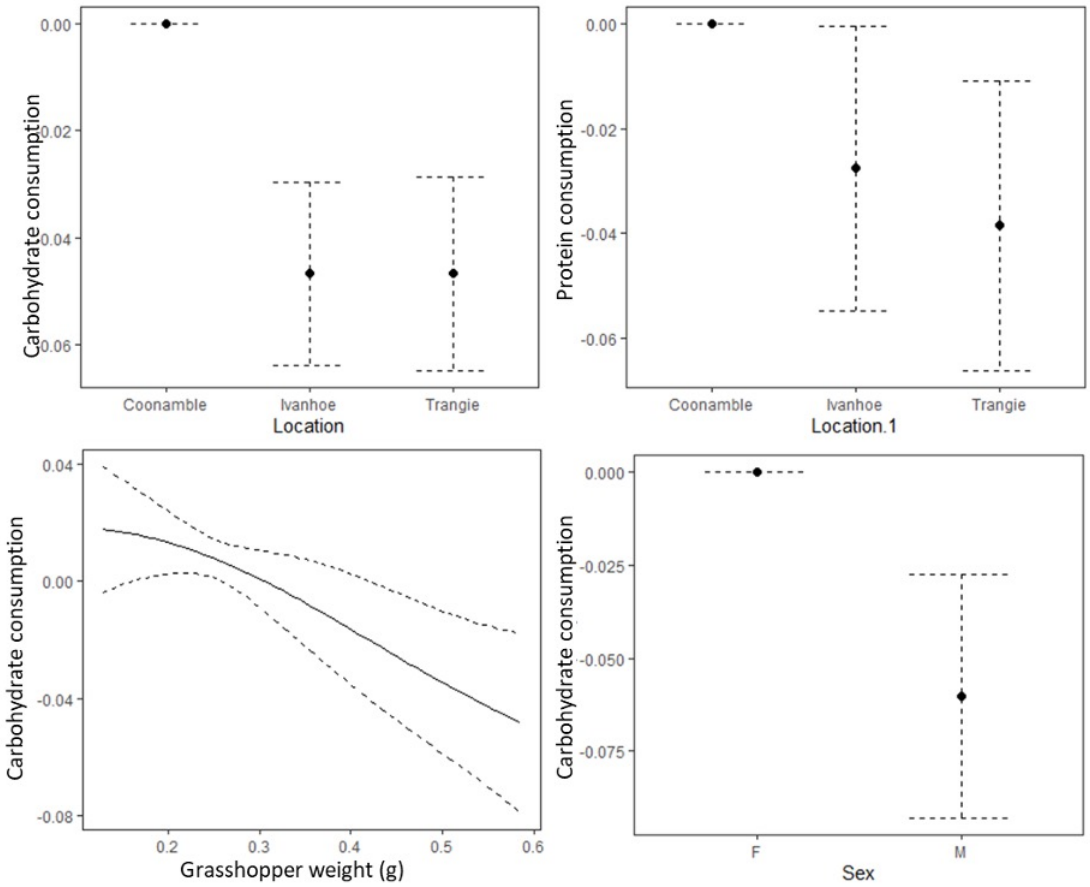


Figure C.2: Significant Predictors Effect on Carbohydrate and Protein Consumption for C. Terminifera.

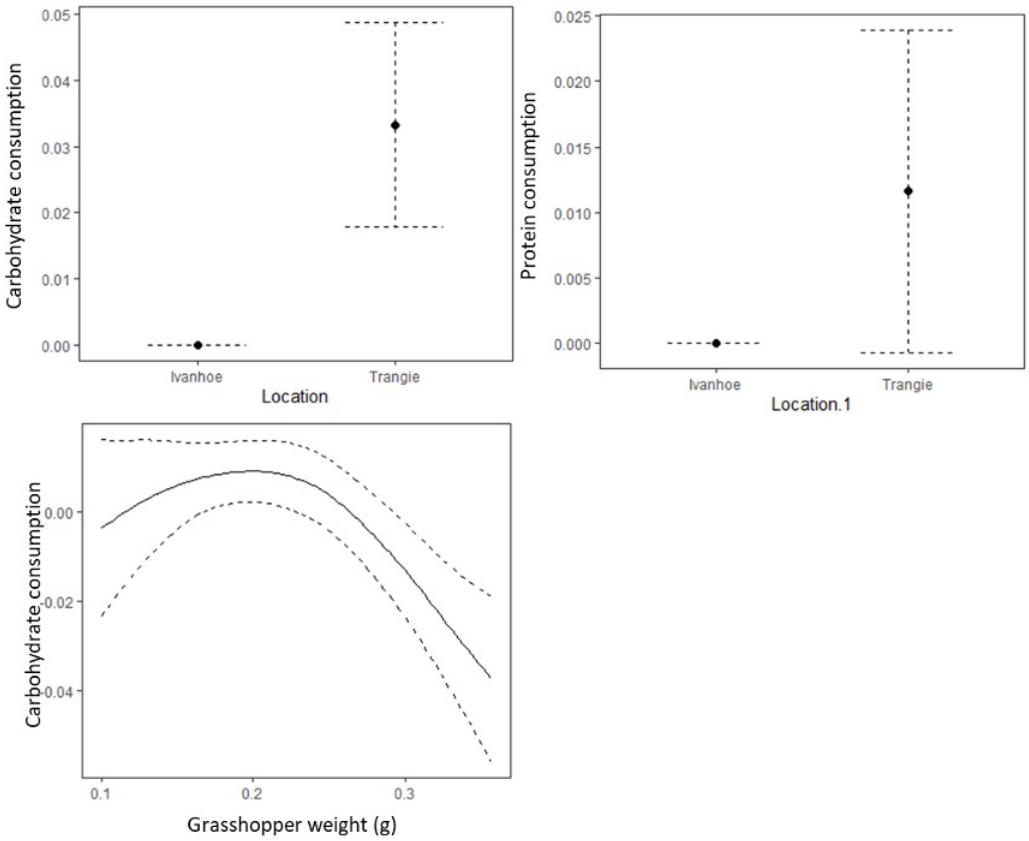


Figure C.3: Significant Predictors Effect on Carbohydrate and Protein Consumption for A. Thalassinus.

APPENDIX D

SUPPLEMENTARY DATA FOR CHAPTER 5

Table D.1: Basis Dimensions Check for Australian Plague Locust (APL) and Desert Locust (DL) Model GS. Significance Shown in Bold. EDF = Estimated Degrees Freedom. K' = Knots

Model GS	APL				DL			
Variables	k'	edf	k-index	p-value	k'	edf	k-index	p-value
te(days_diff,NDVI_mean)	24.00	19.47	1.00	0.80	24	5.95	0.95	0.27
t2(days_diff,NDVI_mean,Major_rain_zones,Bioregn,Season)	1251.00	740.66	NA	NA	760	511.15	NA	NA
s(Latitude,Longitude)	49.00	48.76	0.85	**0.00**	49	48.96	0.88	**0.00**

Table D.2: Basis Dimensions Check for Australian Plague Locust (APL) and Desert Locust (DL) Model S. Significance Shown in Bold. EDF = Estimated Degrees Freedom. K' = Knot

Model S	APL				DL			
Variables	k'	edf	k-index	p-value	k'	edf	k-index	p-value
t2(days_diff,NDVI_mean,Major_rain_zones,Bioregn,Season)	4875	765.12	NA	NA	3200	527.97	NA	NA
s(Latitude,Longitude)	49	46.60	0.80	**0.00**	49	48.96	0.87	**0.00**

Table D.3: Basis Dimensions Check for Australian Plague Locust (APL) Model GI. Significance Shown in Bold. EDF = Estimated Degrees Freedom. K' = Knot

APL - Model GI	k'	edf	k-index	p-value
s(Bioregn)	13	10.19	NA	NA
s(Season)	3	1.97	NA	NA
s(Latitude,Longitude)	49	46.68	0.84	**0.00**
te(days_diff,NDVI_mean):Major_rain_zonesArid	24	13.53	0.95	0.38
te(days_diff,NDVI_mean):Major_rain_zonesSummer	24	14.50	0.95	0.31
te(days_diff,NDVI_mean):Major_rain_zonesSummer Dominant	24	9.69	0.95	0.34
te(days_diff,NDVI_mean):Major_rain_zonesUniform	24	21.54	0.96	0.61
te(days_diff,NDVI_mean):Major_rain_zonesWinter	24	16.34	0.94	0.30
te(days_diff,NDVI_mean):BioregnBrigalow Belt South	24	8.23	0.95	0.36
te(days_diff,NDVI_mean):BioregnBroken Hill Complex	24	8.48	0.95	0.32
te(days_diff,NDVI_mean):BioregnChannel Country	24	16.45	0.94	0.27
te(days_diff,NDVI_mean):BioregnCobar Peneplain	24	15.26	0.95	0.47
te(days_diff,NDVI_mean):BioregnDarling Riverine Plains	24	4.55	0.95	0.30
te(days_diff,NDVI_mean):BioregnFlinders Lofty Block	24	22.04	0.94	0.26
te(days_diff,NDVI_mean):BioregnMitchell Grass Downs	24	13.74	0.95	0.40
te(days_diff,NDVI_mean):BioregnMulga Lands	24	17.75	0.94	0.25
te(days_diff,NDVI_mean):BioregnMurray Darling Depression	24	22.27	0.95	0.38
te(days_diff,NDVI_mean):BioregnNSW South Western Slopes	24	15.12	0.95	0.36
te(days_diff,NDVI_mean):BioregnRiverina	24	13.26	0.95	0.55
te(days_diff,NDVI_mean):BioregnSimpson Strzelecki Dunefields	24	9.71	0.94	0.30
te(days_diff,NDVI_mean):BioregnStony Plains	24	10.82	0.95	0.48
te(days_diff,NDVI_mean):SeasonSpring	24	13.23	0.95	0.39
te(days_diff,NDVI_mean):SeasonSummer	24	10.89	0.95	0.43
te(days_diff,NDVI_mean):SeasonFall	24	16.65	0.95	0.35

Table D.4: Basis Dimensions Check for Desert Locust (DL) Model GI. Significance Shown in Bold. EDF = Estimated Degrees Freedom. K' = Knot

DL - Model GI	k'	edf	k-index	p-value
s(Ecoregion)	16	14.05	NA	NA
s(Season)	4	2.95	NA	NA
s(Latitude,Longitude)	49	48.92	0.84	**0.00**
te(days_diff,NDVI_mean):ZoneInvasion	24	17.22	0.96	0.73
te(days_diff,NDVI_mean):ZoneRecession	24	14.41	0.94	0.20
te(days_diff,NDVI_mean):ECO_NAMEArabian Desert and East Sahero-Arabian xeric shrublands	24	4.89	0.96	0.54
te(days_diff,NDVI_mean):ECO_NAMEArabian Peninsula coastal fog desert	24	6.04	0.96	0.59
te(days_diff,NDVI_mean):ECO_NAMEEthiopian xeric grasslands and shrublands	24	9.91	0.96	0.57
te(days_diff,NDVI_mean):ECO_NAMEGulf of Oman desert and semi-desert	24	8.19	0.96	0.65
te(days_diff,NDVI_mean):ECO_NAMENorth Saharan steppe and woodlands	24	4.07	0.95	0.31
te(days_diff,NDVI_mean):ECO_NAMENorthwestern thorn scrub forests	24	11.93	0.96	0.54
te(days_diff,NDVI_mean):ECO_NAMERed Sea coastal desert	24	5.27	0.95	0.53
te(days_diff,NDVI_mean):ECO_NAMERed Sea Nubo-Sindian tropical desert and semi-desert	24	5.99	0.96	0.71
te(days_diff,NDVI_mean):ECO_NAMESahara desert	24	5.89	0.96	0.59
te(days_diff,NDVI_mean):ECO_NAMESahelian Acacia savanna	24	12.66	0.95	0.54
te(days_diff,NDVI_mean):ECO_NAMESomali Acacia-Commiphora bushlands and thickets	24	15.01	0.95	0.57
te(days_diff,NDVI_mean):ECO_NAMESouth Iran Nubo-Sindian desert and semi-desert	24	5.92	0.96	0.78
te(days_diff,NDVI_mean):ECO_NAMESouth Saharan steppe and woodlands	24	7.62	0.96	0.72
te(days_diff,NDVI_mean):ECO_NAMESouthwestern Arabian foothills savanna	24	5.31	0.96	0.71
te(days_diff,NDVI_mean):ECO_NAMEThar desert	24	8.69	0.96	0.68
te(days_diff,NDVI_mean):ECO_NAMEWest Saharan montane xeric woodlands	24	2.63	0.96	0.71
te(days_diff,NDVI_mean):SeasonFall	24	12.59	0.96	0.73
te(days_diff,NDVI_mean):SeasonSpring	24	11.14	0.96	0.66
te(days_diff,NDVI_mean):SeasonSummer	24	21.09	0.95	0.31
te(days_diff,NDVI_mean):SeasonWinter	24	1.30	0.94	0.24

Table D.5: Basis Dimensions Check for Australian Plague Locust (APL) Model I. Significance Shown in Bold. EDF = Estimated Degrees Freedom. K' = Knot

APL - Model I	k'	edf	k-index	p-value
te(days_diff,NDVI_mean):Major_rain_zonesArid	24	14.68	0.97	0.82
te(days_diff,NDVI_mean):Major_rain_zonesSummer	24	12.84	0.97	0.86
te(days_diff,NDVI_mean):Major_rain_zonesSummer Dominant	24	10.62	0.97	0.87
te(days_diff,NDVI_mean):Major_rain_zonesUniform	24	20.32	0.97	0.85
te(days_diff,NDVI_mean):Major_rain_zonesWinter	24	9.88	1.00	0.99
te(days_diff,NDVI_mean):BioregnBrigalow Belt South	24	8.38	0.96	0.63
te(days_diff,NDVI_mean):BioregnBroken Hill Complex	24	5.30	0.99	0.98
te(days_diff,NDVI_mean):BioregnChannel Country	24	15.02	0.98	0.87
te(days_diff,NDVI_mean):BioregnCobar Peneplain	24	15.69	0.98	0.90
te(days_diff,NDVI_mean):BioregnDarling Riverine Plains	24	14.88	0.97	0.84
te(days_diff,NDVI_mean):BioregnFlinders Lofty Block	24	14.29	0.97	0.85
te(days_diff,NDVI_mean):BioregnMitchell Grass Downs	24	14.33	0.98	0.87
te(days_diff,NDVI_mean):BioregnMulga Lands	24	18.47	0.99	0.99
te(days_diff,NDVI_mean):BioregnMurray Darling Depression	24	22.84	0.97	0.82
te(days_diff,NDVI_mean):BioregnNSW South Western Slopes	24	16.23	0.98	0.83
te(days_diff,NDVI_mean):BioregnRiverina	24	7.31	0.99	0.99
te(days_diff,NDVI_mean):BioregnSimpson Strzelecki Dunefields	24	9.95	0.97	0.87
te(days_diff,NDVI_mean):BioregnStony Plains	24	10.28	0.99	0.97
te(days_diff,NDVI_mean):SeasonSpring	24	20.61	1.00	1.00
te(days_diff,NDVI_mean):SeasonSummer	24	18.54	0.99	0.96
te(days_diff,NDVI_mean):SeasonFall	24	18.38	0.97	0.82
s(Latitude,Longitude)	49	46.72	0.78	**0.00**

Table D.6: Basis Dimensions Check for Australian Plague Locust (APL) Model I. Significance Shown in Bold. EDF = Estimated Degrees Freedom. K' = Knot

DL - Model I	k'	edf	k-index	p-value
te(days_diff,NDVI_mean):ZoneInvasion	24	17.63	0.95	0.33
te(days_diff,NDVI_mean):ZoneRecession	24	8.06	0.94	0.20
te(days_diff,NDVI_mean):ECO_NAMEArabian Desert and East Sahero-Arabian xeric shrublands	24	7.55	0.95	0.40
te(days_diff,NDVI_mean):ECO_NAMEArabian Peninsula coastal fog desert	24	6.36	0.95	0.36
te(days_diff,NDVI_mean):ECO_NAMEEthiopian xeric grasslands and shrublands	24	12.04	0.94	0.29
te(days_diff,NDVI_mean):ECO_NAMEGulf of Oman desert and semi-desert	24	8.48	0.94	0.33
te(days_diff,NDVI_mean):ECO_NAMENorth Saharan steppe and woodlands	24	4.32	0.93	**0.04**
te(days_diff,NDVI_mean):ECO_NAMENorthwestern thorn scrub forests	24	12.74	0.94	0.21
te(days_diff,NDVI_mean):ECO_NAMERed Sea coastal desert	24	8.91	0.94	0.18
te(days_diff,NDVI_mean):ECO_NAMERed Sea Nubo-Sindian tropical desert and semi-desert	24	6.53	0.95	0.48
te(days_diff,NDVI_mean):ECO_NAMESahara desert	24	8.67	0.95	0.31
te(days_diff,NDVI_mean):ECO_NAMESahelian Acacia savanna	24	14.17	0.94	0.18
te(days_diff,NDVI_mean):ECO_NAMESomali Acacia-Commiphora bushlands and thickets	24	22.73	0.94	0.15
te(days_diff,NDVI_mean):ECO_NAMESouth Iran Nubo-Sindian desert and semi-desert	24	5.97	0.94	0.25
te(days_diff,NDVI_mean):ECO_NAMESouth Saharan steppe and woodlands	24	9.75	0.95	0.27
te(days_diff,NDVI_mean):ECO_NAMESouthwestern Arabian foothills savanna	24	5.57	0.94	0.29
te(days_diff,NDVI_mean):ECO_NAMEThar desert	24	8.09	0.94	0.22
te(days_diff,NDVI_mean):ECO_NAMEWest Saharan montane xeric woodlands	24	3.28	0.94	0.21
te(days_diff,NDVI_mean):SeasonFall	24	16.46	0.93	**0.04**
te(days_diff,NDVI_mean):SeasonSpring	24	13.29	0.93	0.06
te(days_diff,NDVI_mean):SeasonSummer	24	20.69	0.92	**0.01**
te(days_diff,NDVI_mean):SeasonWinter	24	9.38	0.93	**0.04**
s(Latitude,Longitude)	49	48.92	0.82	**0.00**

Table D.7: Basis Dimensions Check for Australian Plague Locust (APL) and Desert Locust (DL) Model G. Significance Shown in Bold. EDF = Estimated Degrees Freedom. K' = Knot

Model G	APL				DL			
Variables	k'	edf	k-index	p-value	k'	edf	k-index	p-value
te(days_diff,NDVI_mean)	24	23.32	0.98	0.88	24	18.77	0.94	0.34
s(Latitude,Longitude)	49	46.78	0.80	**0.00**	49	48.93	0.82	**0.00**
s(Major_rain_zones)	5	3.97	NA	NA	2	1.00	NA	NA
s(Bioregn)	13	11.92	NA	NA	16	14.94	NA	NA
s(Season)	3	2.00	NA	NA	4	3.00	NA	NA

Table D.8: Basis Dimensions Check for Australian Plague Locust (APL) and Desert Locust (DL) Model N. Significance Shown in Bold. EDF = Estimated Degrees Freedom. K' = Knot

Model N	APL				DL			
Variables	k'	edf	k-index	p-value	k'	edf	k-index	p-value
te(days_diff,NDVI_mean)	24	23.38	0.95	0.56	24	18.86	0.94	0.52
s(Latitude,Longitude)	49	46.69	0.83	**0.00**	49	48.94	0.81	**0.00**

Table D.9: Out of Sample Deviance per Each Unique Level of Zone, Bioregion, and Season for All Australian Plague Locust Models. The Lower the Number, the Better Predictive the Model Is for That Unique Level.

APL out-of-sample deviance			Model deviances					
Zone	Bioregn	Season	Intercept only	Model G	Model GS	Model S	Model I	Model N
Arid	Broken Hill Complex	Fall	1428	1408	1371	1367	1412	1563
Arid	Broken Hill Complex	Spring	2749	2713	2697	2703	2771	2857
Arid	Broken Hill Complex	Summer	833	890	768	784	912	1024
Arid	Channel Country	Fall	5355	4432	3944	3968	4053	4283
Arid	Channel Country	Spring	1283	1022	193	197	591	475
Arid	Channel Country	Summer	3971	3835	3680	3707	3677	3791
Arid	Darling Riverine Plains	Spring	576	436	380	395	421	405
Arid	Flinders Lofty Block	Fall	313	383	74	78.8	397	512
Arid	Flinders Lofty Block	Spring	3565	3374	3135	3121	3323	3879
Arid	Mitchell Grass Downs	Fall	523	354	318	343	343	319
Arid	Mitchell Grass Downs	Summer	878	600	483	511	567	614
Arid	Mulga Lands	Fall	2538	2054	1664	1693	1832	1940
Arid	Mulga Lands	Spring	1240	983	460	471	744	605
Arid	Mulga Lands	Summer	3923	3359	2913	2901	3030	3238
Arid	Murray Darling Depression	Spring	3121	2973	2730	2740	3086	3187
Arid	Murray Darling Depression	Summer	260	205	174	178	191	187
Arid	Simpson Strzelecki Dunefields	Fall	724	595	491	543	498	533
Arid	Simpson Strzelecki Dunefields	Spring	279	237	196	203	219	197
Arid	Stony Plains	Fall	1015	1026	832	836	868	1078
Arid	Stony Plains	Summer	829	710	662	665	689	752
Summer	Brigalow Belt South	Spring	2025	1503	1112	1107	1399	1458
Summer	Brigalow Belt South	Summer	2005	2094	1712	1752	1981	1938
Summer	Darling Riverine Plains	Fall	2704	2570	2175	2171	2366	2528
Summer	Darling Riverine Plains	Spring	1820	1687	1428	1467	1597	1501
Summer	Darling Riverine Plains	Summer	1178	1172	1143	1151	1257	1273
Summer	Mitchell Grass Downs	Summer	3564	2201	1910	1930	1976	2663
Summer	Mulga Lands	Fall	172	213	151	154	208	367
Summer	Mulga Lands	Spring	323	354	227	229	338	320
Summer	Mulga Lands	Summer	1344	1217	1082	1082	1085	1337
Summer Dominant	Mitchell Grass Downs	Summer	816	797	704	731	735	815
Uniform	Brigalow Belt South	Fall	83.7	143	58.8	63.9	102	292
Uniform	Brigalow Belt South	Spring	1593	1110	1017	1029	1049	1102
Uniform	Brigalow Belt South	Summer	106	149	93.3	97.9	123	241
Uniform	Cobar Peneplain	Fall	642	644	535	537	571	840
Uniform	Cobar Peneplain	Spring	5352	5059	4607	4621	4683	5572
Uniform	Cobar Peneplain	Summer	513	484	125	124	266	724
Uniform	Darling Riverine Plains	Fall	3039	3157	2636	2659	3080	3017
Uniform	Darling Riverine Plains	Spring	5867	5641	5439	5490	5490	5673
Uniform	Darling Riverine Plains	Summer	1132	1180	1005	1012	1116	1533
Uniform	Mulga Lands	Fall	62.9	52.2	46.1	41	53.9	57.7
Uniform	Mulga Lands	Spring	153	154	137	137	185	160
Uniform	Murray Darling Depression	Fall	550	505	471	484	487	550
Uniform	Murray Darling Depression	Spring	1924	1703	1655	1682	1777	1794
Uniform	NSW South Western Slopes	Fall	486	456	348	363	407	717
Uniform	NSW South Western Slopes	Spring	7207	6770	6470	6481	6719	6747
Uniform	NSW South Western Slopes	Summer	1200	1058	981	973	1054	1208
Uniform	Riverina	Fall	641	614	427	433	625	620
Uniform	Riverina	Spring	2373	1994	1765	1770	1897	2093
Uniform	Riverina	Summer	375	300	96.2	102	219	494
Winter	Broken Hill Complex	Spring	219	196	178	185	191	199
Winter	Cobar Peneplain	Spring	132	114	105	85.2	106	114
Winter	Darling Riverine Plains	Spring	350	321	325	340	331	318
Winter	Flinders Lofty Block	Spring	14597	14768	14481	14461	14631	14955
Winter	Flinders Lofty Block	Summer	1153	1021	815	820	1114	1431
Winter	Murray Darling Depression	Fall	640	688	353	367	710	1039
Winter	Murray Darling Depression	Spring	25175	24356	23246	23310	23691	25119
Winter	Murray Darling Depression	Summer	1212	938	899	914	966	1128
Winter	NSW South Western Slopes	Fall	226	162	91.7	92.8	171	226
Winter	NSW South Western Slopes	Spring	1166	1082	1001	1011	1055	1078
Winter	NSW South Western Slopes	Summer	1464	1652	1237	1252	1553	1564
Winter	Riverina	Fall	860	760	412	427	643	1145
Winter	Riverina	Spring	8028	6661	6294	6278	6548	7318
Winter	Riverina	Summer	3233	3570	3081	3115	3456	4027

Table D.10: Out of Sample Deviance per Each Unique Level of Zone, Bioregion, and Season for All Desert Locust Models. The Lower the Number, the Better Predictive the Model Is for That Unique Level.

DL out-of-sample deviance			Model deviances					
Zone	ECO_NAME	Season	Intercept only	G	GS	S	I	N
Invasion	North Saharan steppe and woodlands	Spring	2309	496	461	489	484	981
Invasion	Sahelian Acacia savanna	Summer	5721	4543	4354	3972	4378	5522
Recession	Arabian Desert and East Sahero-Arabian xeric shrublands	Spring	7265	6891	6865	6984	6792	6915
Recession	Arabian Peninsula coastal fog desert	Fall	6536	6061	5913	5994	5874	6199
Recession	Arabian Peninsula coastal fog desert	Spring	1496	1048	988	990	1030	1102
Recession	Arabian Peninsula coastal fog desert	Winter	8422	7375	6883	6898	7325	7904
Recession	Ethiopian xeric grasslands and shrublands	Fall	6419	6465	6039	6011	6508	6132
Recession	Ethiopian xeric grasslands and shrublands	Winter	11397	10114	10026	10048	10056	10947
Recession	Gulf of Oman desert and semi-desert	Fall	1949	1864	1559	1722	1670	2063
Recession	North Saharan steppe and woodlands	Fall	15335	14687	13700	13757	14437	15429
Recession	North Saharan steppe and woodlands	Spring	22580	16185	14787	15295	15876	15993
Recession	North Saharan steppe and woodlands	Winter	19093	17419	15793	15916	17263	17415
Recession	Northwestern thorn scrub forests	Fall	2662	2085	2075	2056	2010	2330
Recession	Red Sea coastal desert	Winter	5663	5500	5353	5374	5395	5715
Recession	Red Sea Nubo-Sindian tropical desert and semi-desert	Fall	2449	2372	1811	1838	1943	2589
Recession	Red Sea Nubo-Sindian tropical desert and semi-desert	Spring	7412	6653	6540	6547	6600	6645
Recession	Red Sea Nubo-Sindian tropical desert and semi-desert	Summer	3162	3127	2988	2960	3025	3196
Recession	Red Sea Nubo-Sindian tropical desert and semi-desert	Winter	10807	9340	8733	8756	8982	9665
Recession	Sahara desert	Spring	5953	5879	6023	6018	5712	6014
Recession	Sahara desert	Winter	2975	2519	2235	2214	2537	2427
Recession	Sahelian Acacia savanna	Fall	40318	38840	37814	37803	38821	39304
Recession	Sahelian Acacia savanna	Spring	3810	3872	3523	3477	3659	3971
Recession	Sahelian Acacia savanna	Summer	22364	20397	18024	17953	19974	20968
Recession	Sahelian Acacia savanna	Winter	12792	12060	11884	11829	11786	11750
Recession	Somali Acacia-Commiphora bushlands and thickets	Fall	2433	2198	2255	2252	2104	2083
Recession	Somali Acacia-Commiphora bushlands and thickets	Summer	1608	1642	1655	1665	1615	1500
Recession	South Iran Nubo-Sindian desert and semi-desert	Spring	9825	9705	9302	9201	9511	9729
Recession	South Saharan steppe and woodlands	Fall	9317	9163	8818	8793	9075	9436
Recession	South Saharan steppe and woodlands	Spring	1963	1768	1914	1822	1766	1705
Recession	South Saharan steppe and woodlands	Winter	4230	3860	3839	3797	3865	3901
Recession	Southwestern Arabian foothills savanna	Fall	9034	8305	7663	7696	8083	9141
Recession	Southwestern Arabian foothills savanna	Spring	3278	2878	2785	2790	2858	2925
Recession	Southwestern Arabian foothills savanna	Summer	3355	3706	3594	3584	3703	3836
Recession	Southwestern Arabian foothills savanna	Winter	16191	14182	12987	12988	13692	14310
Recession	Thar desert	Fall	30814	27659	26478	26258	27348	28010
Recession	Thar desert	Spring	6649	4877	2210	2190	4436	4046
Recession	Thar desert	Summer	33767	34295	32770	32784	33583	34306
Recession	West Saharan montane xeric woodlands	Spring	1870	1632	1509	1571	1621	1639

Table D.11: Model GI Results for Australian Plague Locust (APL) Outbreaks. Significance Shown in Bold. EDF = Estimated Degrees Freedom.

APL - Model GI	EDF	DF	X^2	P-value
s(Bioregn)	10.19	12	368.47	**0.00**
s(Season)	1.97	2	231.52	**0.00**
s(Latitude,Longitude)	46.68	49	16237.47	**0.00**
te(days_diff,NDVI_mean):Major_rain_zonesArid	13.53	24	55.31	**0.00**
te(days_diff,NDVI_mean):Major_rain_zonesSummer	14.50	24	105.32	**0.00**
te(days_diff,NDVI_mean):Major_rain_zonesSummer Dominant	9.69	24	226.01	**0.00**
te(days_diff,NDVI_mean):Major_rain_zonesUniform	21.54	24	262.51	**0.00**
te(days_diff,NDVI_mean):Major_rain_zonesWinter	16.34	24	116.13	**0.00**
te(days_diff,NDVI_mean):BioregnBrigalow Belt South	8.23	24	80.03	**0.00**
te(days_diff,NDVI_mean):BioregnBroken Hill Complex	8.48	24	122.25	**0.10**
te(days_diff,NDVI_mean):BioregnChannel Country	16.45	24	397.11	**0.00**
te(days_diff,NDVI_mean):BioregnCobar Peneplain	15.26	24	136.99	**0.00**
te(days_diff,NDVI_mean):BioregnDarling Riverine Plains	4.55	24	8.76	**0.00**
te(days_diff,NDVI_mean):BioregnFlinders Lofty Block	22.04	24	881.90	**0.00**
te(days_diff,NDVI_mean):BioregnMitchell Grass Downs	13.74	24	523.42	**0.00**
te(days_diff,NDVI_mean):BioregnMulga Lands	17.75	24	600.33	**0.00**
te(days_diff,NDVI_mean):BioregnMurray Darling Depression	22.27	24	444.00	**0.00**
te(days_diff,NDVI_mean):BioregnNSW South Western Slopes	15.12	24	59.58	**0.00**
te(days_diff,NDVI_mean):BioregnRiverina	13.26	24	200.28	**0.00**
te(days_diff,NDVI_mean):BioregnSimpson Strzelecki Dunefields	9.71	24	105.86	**0.00**
te(days_diff,NDVI_mean):BioregnStony Plains	10.82	24	267.22	**0.00**
te(days_diff,NDVI_mean):SeasonSpring	13.23	24	78.88	**0.00**
te(days_diff,NDVI_mean):SeasonSummer	10.89	24	209.06	**0.00**
te(days_diff,NDVI_mean):SeasonFall	16.65	24	132.92	**0.00**

Table D.12: Model GI Results for Desert Locust (DL) Outbreaks. Significance Shown in Bold. EDF = Estimated Degrees Freedom.

DL - Model GI	EDF	DF	X^2	P-value
s(ECO_NAME)	14.05	16.00	1042.59	**0.00**
s(Season)	2.95	4.00	194.27	**0.00**
s(Latitude,Longitude)	48.92	49.00	70427.13	**0.00**
te(days_diff,NDVI_mean):ZoneInvasion	17.22	24.00	1015.30	**0.00**
te(days_diff,NDVI_mean):ZoneRecession	14.41	24.00	308.79	**0.00**
te(days_diff,NDVI_mean):ECO_NAMEArabian Desert and East Sahero-Arabian xeric shrublands	4.89	24.00	60.50	**0.00**
te(days_diff,NDVI_mean):ECO_NAMEArabian Peninsula coastal fog desert	6.04	24.00	784.16	**0.00**
te(days_diff,NDVI_mean):ECO_NAMEEthiopian xeric grasslands and shrublands	9.91	24.00	493.09	**0.00**
te(days_diff,NDVI_mean):ECO_NAMEGulf of Oman desert and semi-desert	8.19	20.00	9926.27	0.13
te(days_diff,NDVI_mean):ECO_NAMENorth Saharan steppe and woodlands	4.07	24.00	18.63	**0.00**
te(days_diff,NDVI_mean):ECO_NAMENorthwestern thorn scrub forests	11.93	24.00	196.21	**0.00**
te(days_diff,NDVI_mean):ECO_NAMERed Sea coastal desert	5.27	21.00	2439.53	**0.00**
te(days_diff,NDVI_mean):ECO_NAMERed Sea Nubo-Sindian tropical desert and semi-desert	5.99	22.00	36743.91	**0.00**
te(days_diff,NDVI_mean):ECO_NAMESahara desert	5.89	21.00	165336.10	**0.00**
te(days_diff,NDVI_mean):ECO_NAMESahelian Acacia savanna	12.66	24.00	556.36	**0.00**
te(days_diff,NDVI_mean):ECO_NAMESomali Acacia-Commiphora bushlands and thickets	15.01	24.00	1317.04	**0.00**
te(days_diff,NDVI_mean):ECO_NAMESouth Iran Nubo-Sindian desert and semi-desert	5.92	22.00	2289.54	**0.00**
te(days_diff,NDVI_mean):ECO_NAMESouth Saharan steppe and woodlands	7.62	24.00	7034.18	**0.00**
te(days_diff,NDVI_mean):ECO_NAMESouthwestern Arabian foothills savanna	5.31	24.00	195.82	**0.00**
te(days_diff,NDVI_mean):ECO_NAMEThar desert	8.69	24.00	1393.88	**0.00**
te(days_diff,NDVI_mean):ECO_NAMEWest Saharan montane xeric woodlands	2.63	20.00	45.55	**0.00**
te(days_diff,NDVI_mean):SeasonFall	12.59	24.00	2765.61	**0.00**
te(days_diff,NDVI_mean):SeasonSpring	11.14	24.00	41600.88	**0.00**
te(days_diff,NDVI_mean):SeasonSummer	21.09	24.00	1587.17	**0.00**
te(days_diff,NDVI_mean):SeasonWinter	1.30	24.00	29.71	**0.00**

Table D.13: Model I Results for Australian Plague Locust Outbreaks. Significance Shown in Bold. EDF = Estimated Degrees Freedom.

APL - Model I	EDF	DF	X^2	P-value
te(days_diff,NDVI_mean):Major_rain_zonesArid	14.68	24	71.85	**0.00**
te(days_diff,NDVI_mean):Major_rain_zonesSummer	12.84	24	86.52	**0.00**
te(days_diff,NDVI_mean):Major_rain_zonesSummer Dominant	10.62	24	211.69	**0.00**
te(days_diff,NDVI_mean):Major_rain_zonesUniform	20.32	24	217.72	**0.00**
te(days_diff,NDVI_mean):Major_rain_zonesWinter	9.88	24	63.37	**0.00**
te(days_diff,NDVI_mean):BioregnBrigalow Belt South	8.38	24	28.05	**0.00**
te(days_diff,NDVI_mean):BioregnBroken Hill Complex	5.30	24	29.66	**0.00**
te(days_diff,NDVI_mean):BioregnChannel Country	15.02	24	308.96	**0.00**
te(days_diff,NDVI_mean):BioregnCobar Peneplain	15.69	24	162.43	**0.00**
te(days_diff,NDVI_mean):BioregnDarling Riverine Plains	14.88	24	54.12	**0.00**
te(days_diff,NDVI_mean):BioregnFlinders Lofty Block	14.29	24	198.03	**0.00**
te(days_diff,NDVI_mean):BioregnMitchell Grass Downs	14.33	24	243.80	**0.00**
te(days_diff,NDVI_mean):BioregnMulga Lands	18.47	24	395.38	**0.00**
te(days_diff,NDVI_mean):BioregnMurray Darling Depression	22.84	24	568.54	**0.00**
te(days_diff,NDVI_mean):BioregnNSW South Western Slopes	16.23	24	102.61	**0.00**
te(days_diff,NDVI_mean):BioregnRiverina	7.31	24	45.94	**0.00**
te(days_diff,NDVI_mean):BioregnSimpson Strzelecki Dunefields	9.95	24	125.82	**0.00**
te(days_diff,NDVI_mean):BioregnStony Plains	10.28	24	166.41	**0.00**
te(days_diff,NDVI_mean):SeasonSpring	20.61	24	170.22	**0.00**
te(days_diff,NDVI_mean):SeasonSummer	18.54	24	285.55	**0.00**
te(days_diff,NDVI_mean):SeasonFall	18.38	24	213.61	**0.00**
s(Latitude,Longitude)	46.72	49	15945.35	**0.00**

Table D.14: Model I Results for Desert Locust Outbreaks. Significance Shown in Bold. EDF = Estimated Degrees Freedom.

DL - Model I	EDF	DF	X^2	P-value
te(days_diff,NDVI_mean):ZoneInvasion	17.63	24.00	529.89	**0.00**
te(days_diff,NDVI_mean):ZoneRecession	8.06	24.00	219.23	**0.00**
te(days_diff,NDVI_mean):ECO_NAMEArabian Desert and East Sahero-Arabian xeric shrublands	7.55	23.00	215.01	**0.00**
te(days_diff,NDVI_mean):ECO_NAMEArabian Peninsula coastal fog desert	6.36	24.00	136.54	**0.00**
te(days_diff,NDVI_mean):ECO_NAMEEthiopian xeric grasslands and shrublands	12.04	24.00	1349.49	**0.00**
te(days_diff,NDVI_mean):ECO_NAMEGulf of Oman desert and semi-desert	8.48	23.00	576.67	**0.00**
te(days_diff,NDVI_mean):ECO_NAMENorth Saharan steppe and woodlands	4.32	24.00	19.58	**0.00**
te(days_diff,NDVI_mean):ECO_NAMENorthwestern thorn scrub forests	12.74	24.00	191.61	**0.00**
te(days_diff,NDVI_mean):ECO_NAMERed Sea coastal desert	8.91	24.00	300.11	**0.00**
te(days_diff,NDVI_mean):ECO_NAMERed Sea Nubo-Sindian tropical desert and semi-desert	6.53	24.00	444.48	**0.00**
te(days_diff,NDVI_mean):ECO_NAMESahara desert	8.67	20.00	246.32	**0.00**
te(days_diff,NDVI_mean):ECO_NAMESahelian Acacia savanna	14.17	24.00	579.07	**0.00**
te(days_diff,NDVI_mean):ECO_NAMESomali Acacia-Commiphora bushlands and thickets	22.73	24.00	1736.88	**0.00**
te(days_diff,NDVI_mean):ECO_NAMESouth Iran Nubo-Sindian desert and semi-desert	5.97	23.00	521.50	**0.00**
te(days_diff,NDVI_mean):ECO_NAMESouth Saharan steppe and woodlands	9.75	24.00	164.20	**0.00**
te(days_diff,NDVI_mean):ECO_NAMESouthwestern Arabian foothills savanna	5.57	24.00	142.27	**0.00**
te(days_diff,NDVI_mean):ECO_NAMEThar desert	8.09	24.00	1085.48	**0.00**
te(days_diff,NDVI_mean):ECO_NAMEWest Saharan montane xeric woodlands	3.28	21.00	28.64	**0.00**
te(days_diff,NDVI_mean):SeasonFall	16.46	24.00	584.85	**0.00**
te(days_diff,NDVI_mean):SeasonSpring	13.29	24.00	402.40	**0.00**
te(days_diff,NDVI_mean):SeasonSummer	20.69	24.00	793.91	**0.00**
te(days_diff,NDVI_mean):SeasonWinter	9.38	24.00	92.80	**0.00**
s(Latitude,Longitude)	48.92	49.00	70198.54	**0.00**

Table D.15: Model G Results for Australian Plague Locust (APL) and Desert Locust (DL) Outbreaks. Significance Shown in Bold. EDF = Estimated Degrees Freedom.

	APL - Model G				DL - Model G			
Variable	EDF	DF	X^2	P-value	EDF	DF	X^2	P-value
te(days_diff,NDVI_mean)	23.32	24	28397.89	**0.00**	18.77	24.00	18443.29	**0.00**
s(Latitude,Longitude)	46.78	49	15641116.29	**0.00**	48.93	49.00	189184020.95	**0.00**
s(Major_rain_zones)	3.97	4	2433.62	**0.00**	1.00	2.00	6202.61	**0.00**
s(Bioregn)	11.92	12	1909.53	**0.00**	14.94	16.00	10809.77	**0.00**
s(Season)	2.00	2	8919.23	**0.00**	3.00	4.00	4220.16	**0.00**

Table D.16: Model N Results for Australian Plague Locust (APL) and Desert Locust (DL) Outbreaks. Significance Shown in Bold. EDF = Estimated Degrees Freedom.

	APL - Model N				DL - Model N			
Variable	edf	ref.df	X^2	p.value	edf	ref.df	X^2	p.value
te(days_diff,NDVI_mean)	23.38	24	12942.16	**0.00**	18.86	24.00	13245.80	**0.00**
s(Latitude,Longitude)	46.69	49	58220.24	**0.00**	48.94	49.00	107491.19	**0.00**

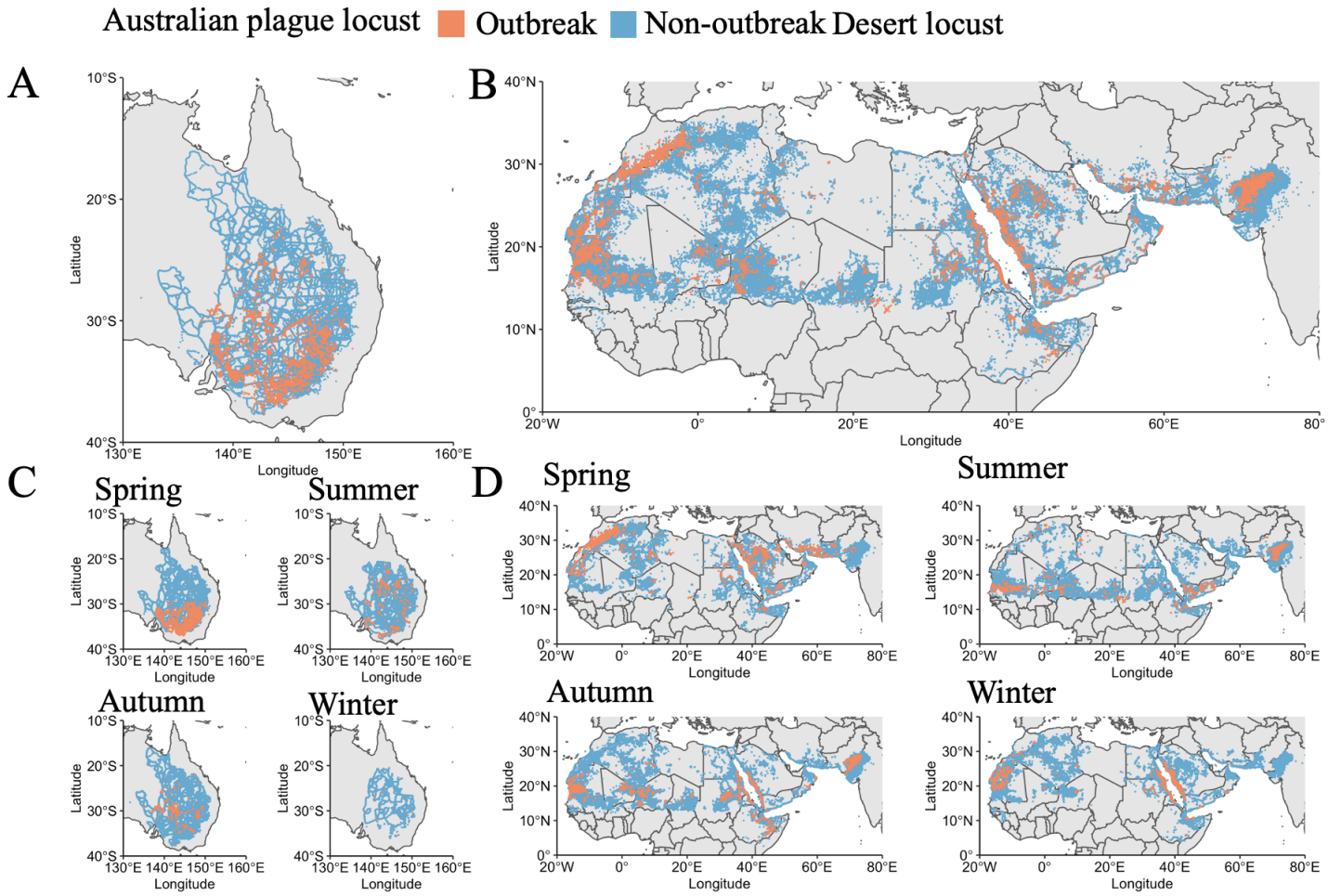


Figure D.1: Observation Maps for Both the Australian Plague Locust (a & C) and Desert Locust (B & D) Overall and Broken Into Season. Red Points Are Outbreaks and Blue Points Are Non-Outbreaks.

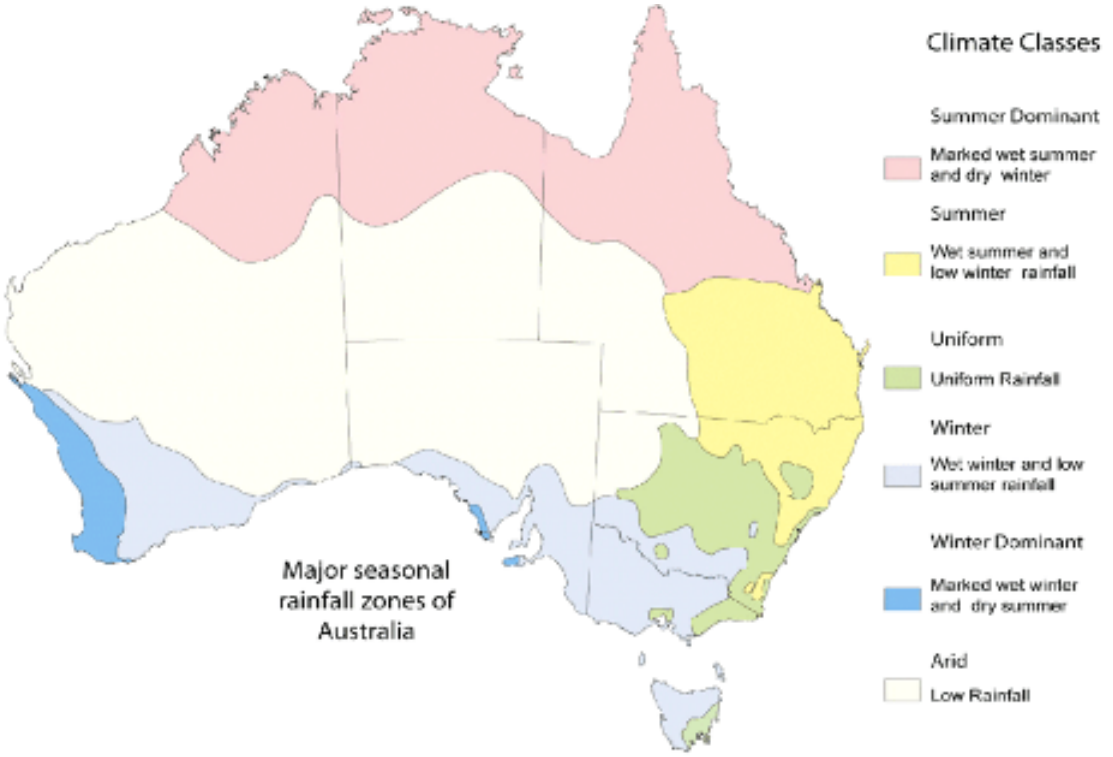


Figure D.2: Major Rainfall Zones Used in the Australian Plague Locust Model. Taken From: Http://www.bom.gov.au; Product Code: IDCJCM0000

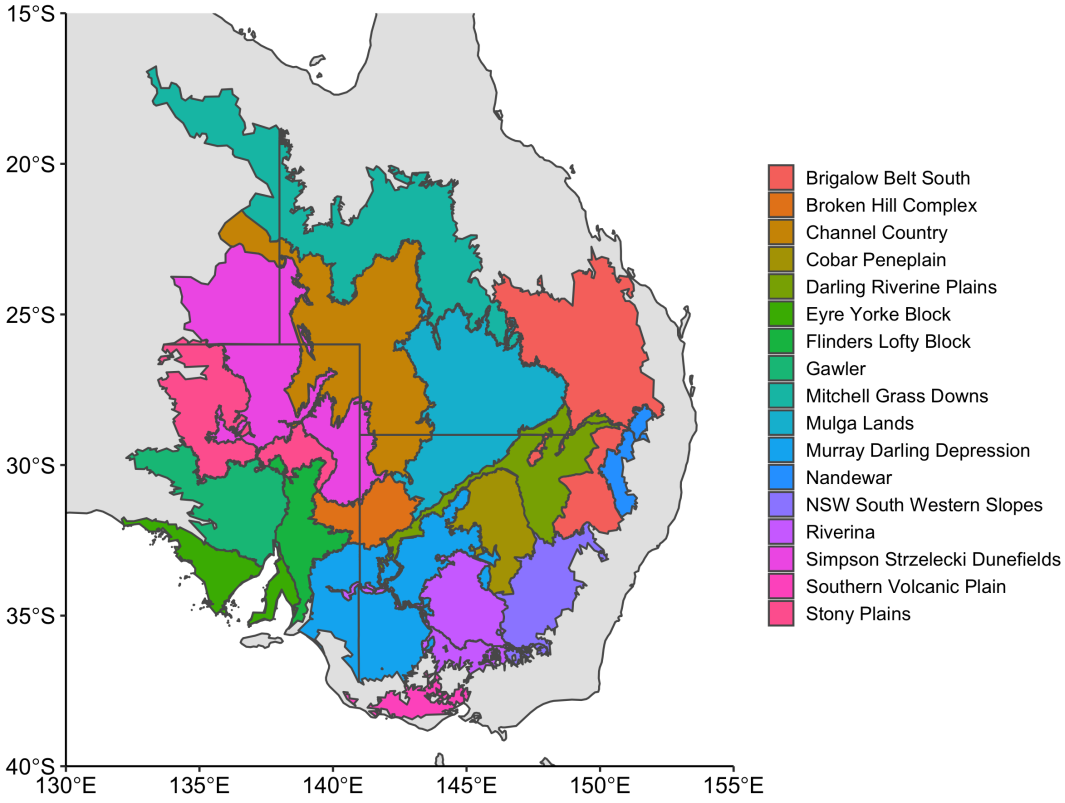


Figure D.3: Bioregions Used in the Australian Plague Locust Model.

Figure D.4: Invasion (Blue) and Recession (Orange) Zones Used in the Desert Locust Model.

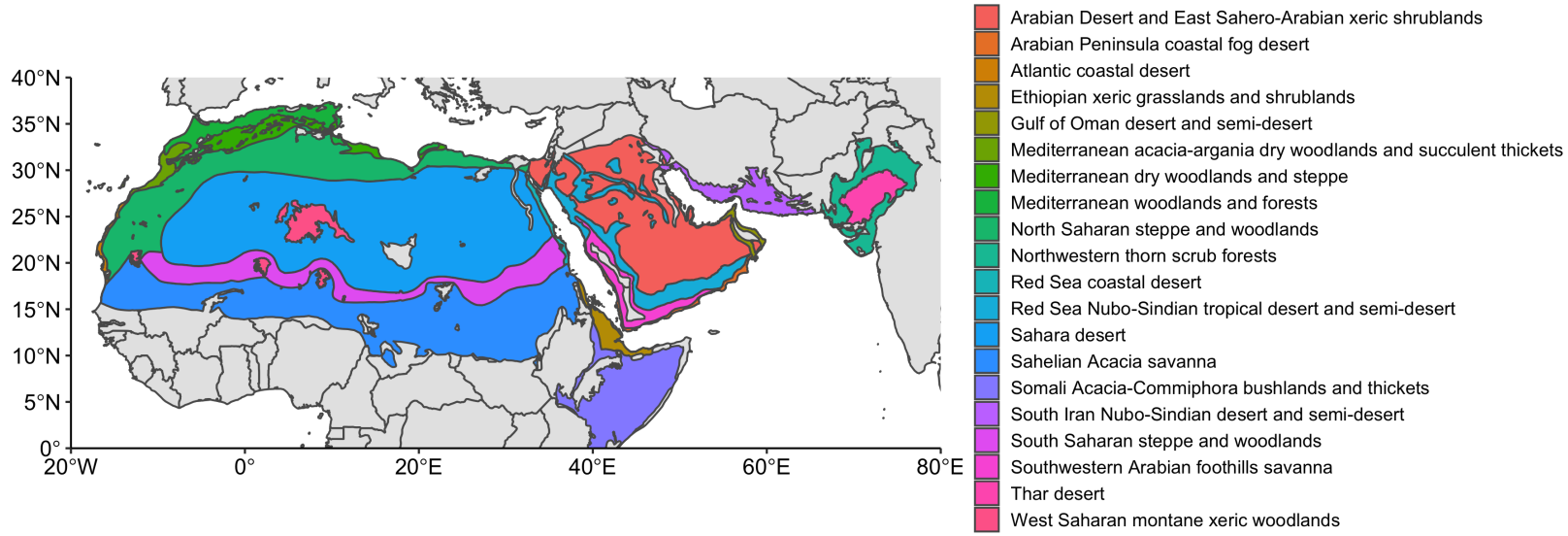


Figure D.5: Ecoregions Used in the Desert Locust Model.

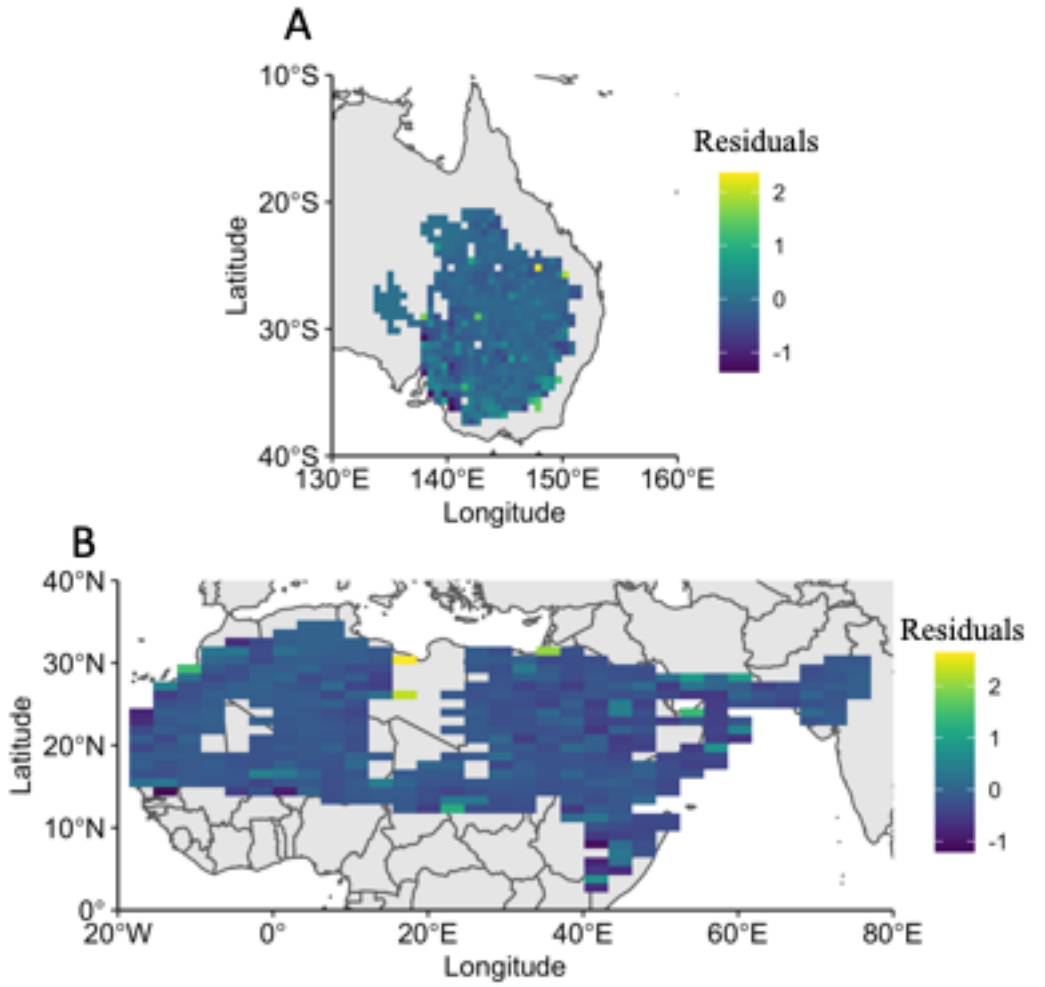


Figure D.6: Map of Residuals for the Australian Plague Locust (a) and Desert Locust (B) Models Demonstrating the Residual Spatial Autocorrelation After Modeling. Since This Variable Remained Constant Between Models the Residuals Will Name Roughly the Same.

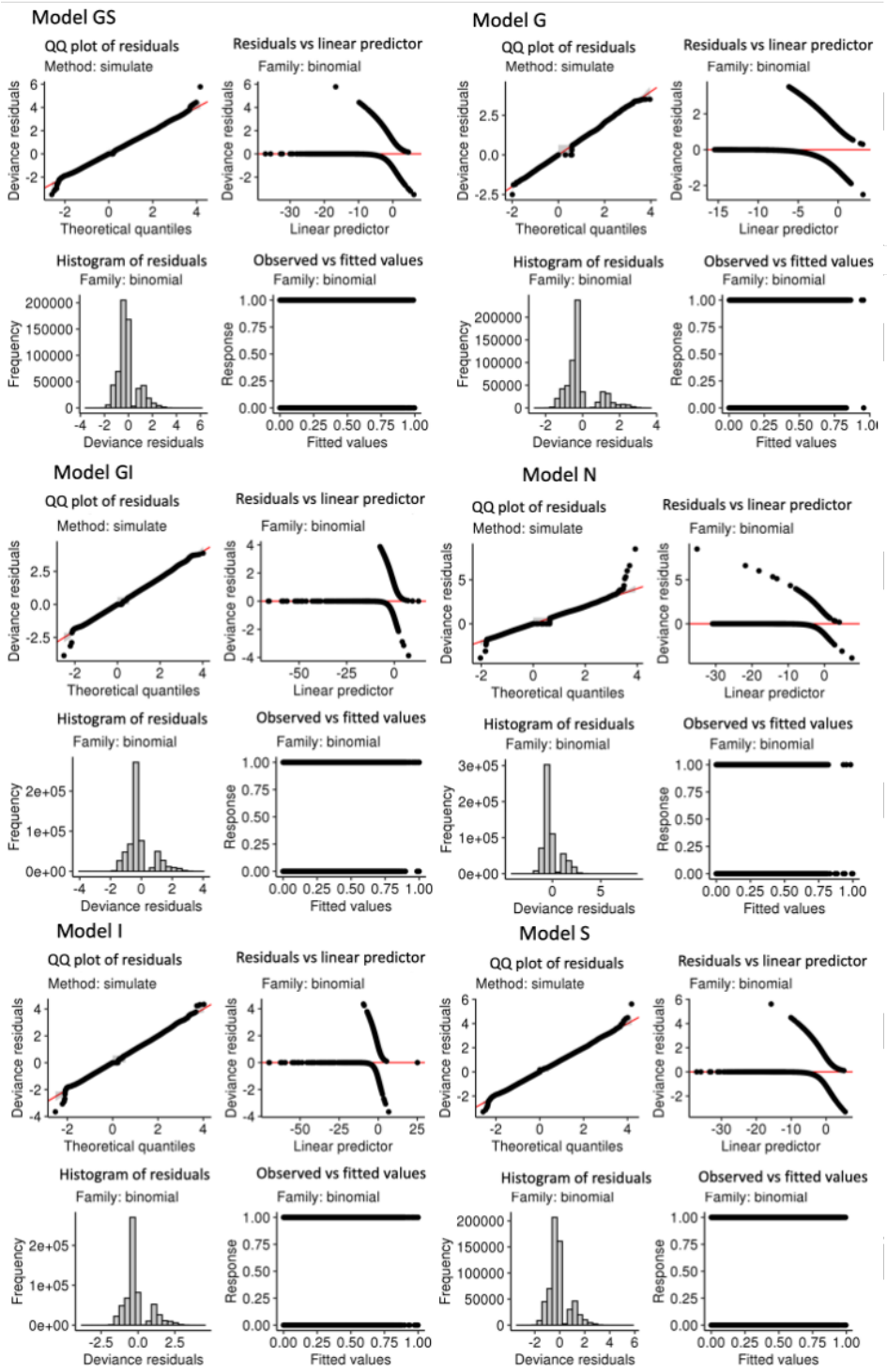


Figure D.7: Model Diagnostic Plots of Each Hierarchical Model for Australian Plague Locust.

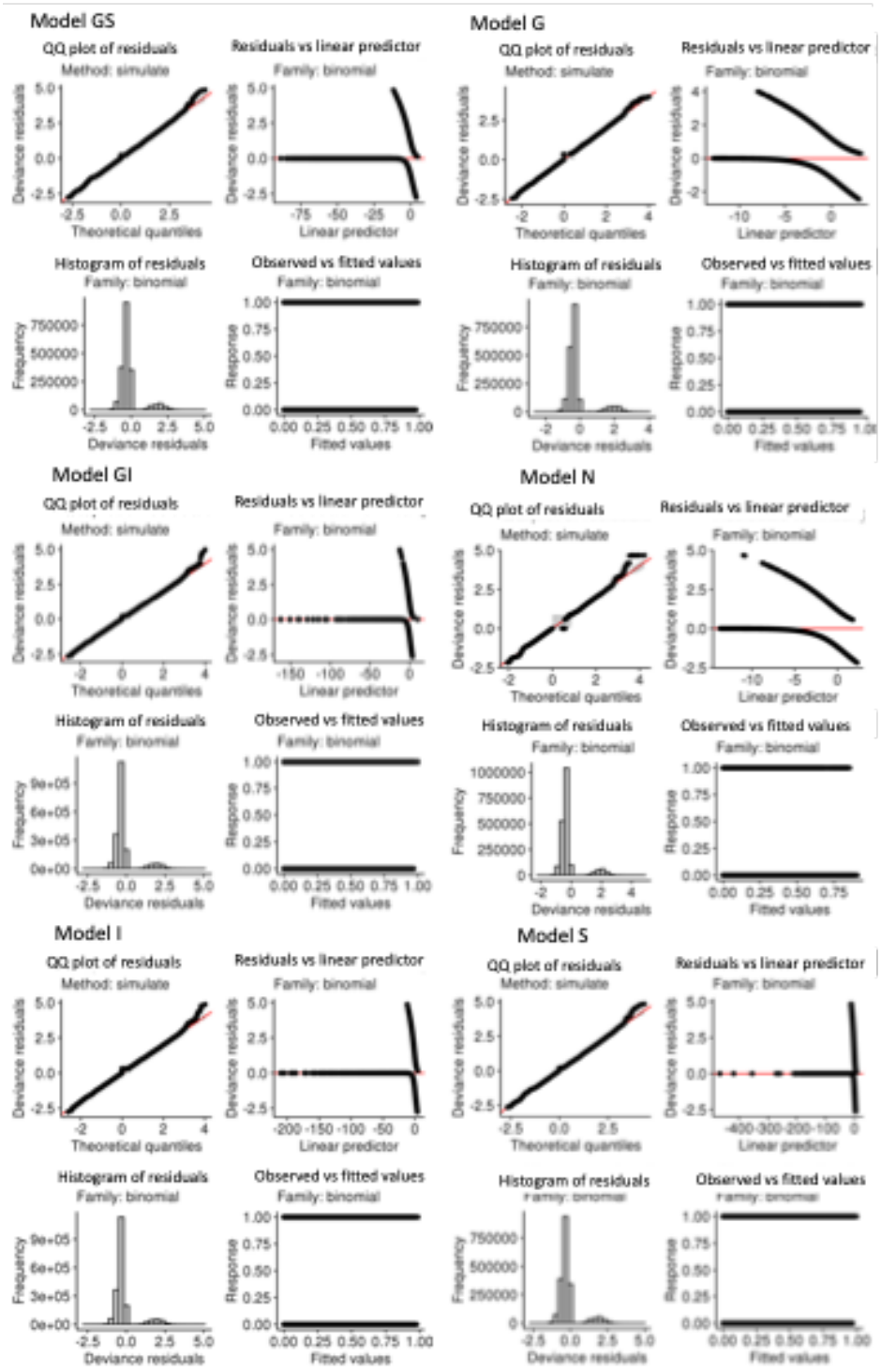


Figure D.8: Model Diagnostic Plots of Each Hierarchical Model for Desert Locust.

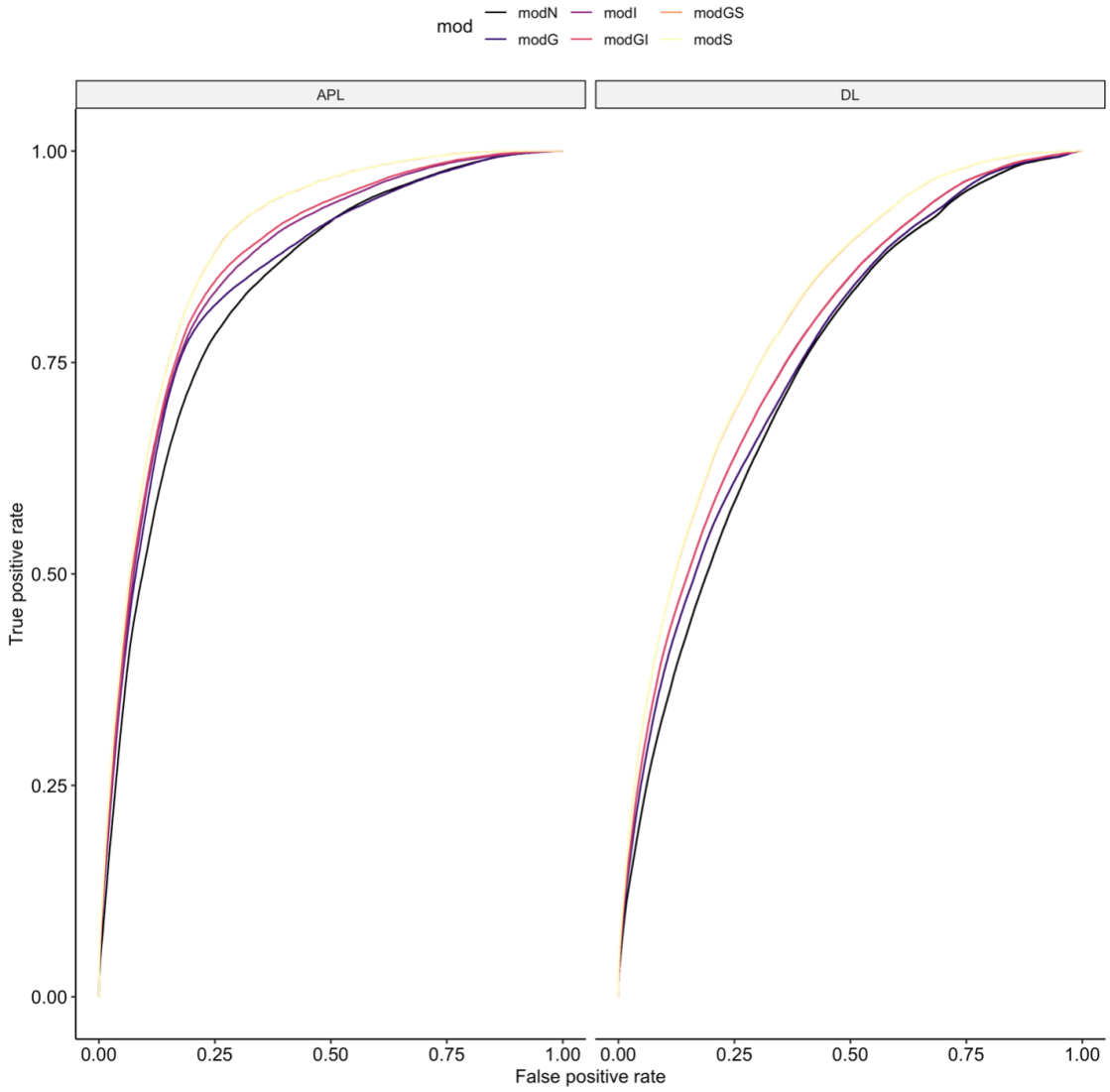
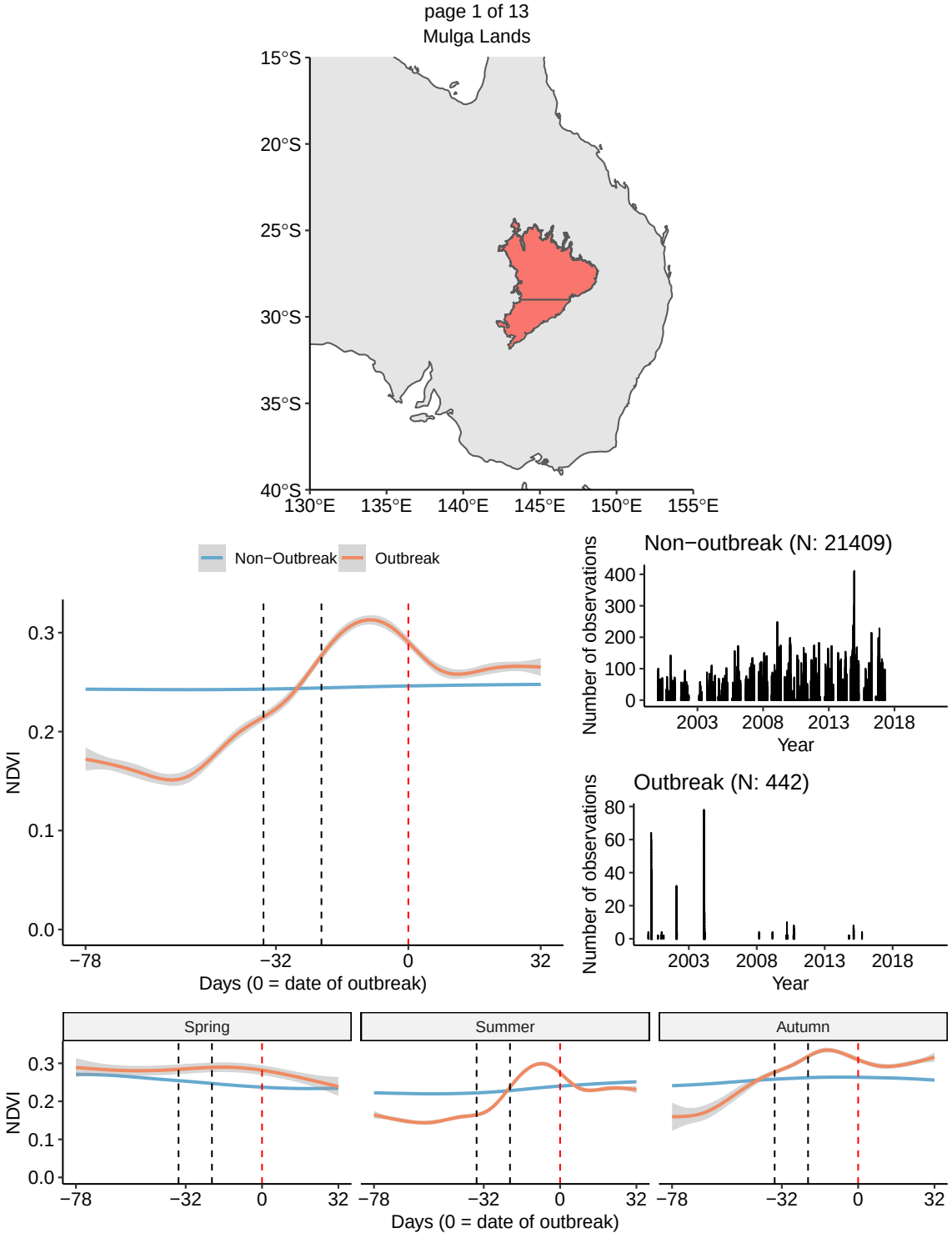


Figure D.9: ROC Curves for Each Hierarchical Model for Australian Plague Locust (APL) and Desert Locust (DL). Model Descriptions Can Be Seen in Figure 2.

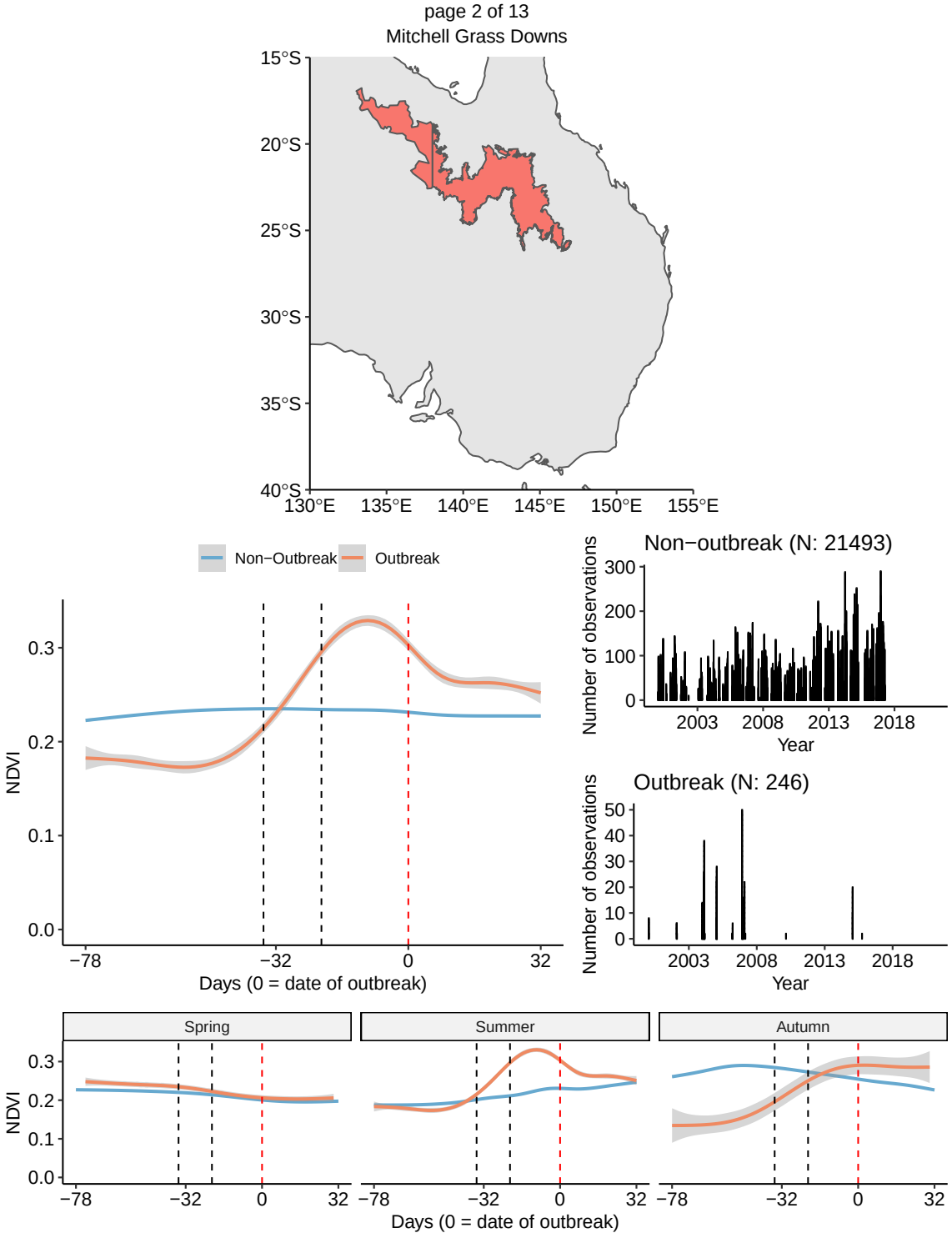
APPENDIX E

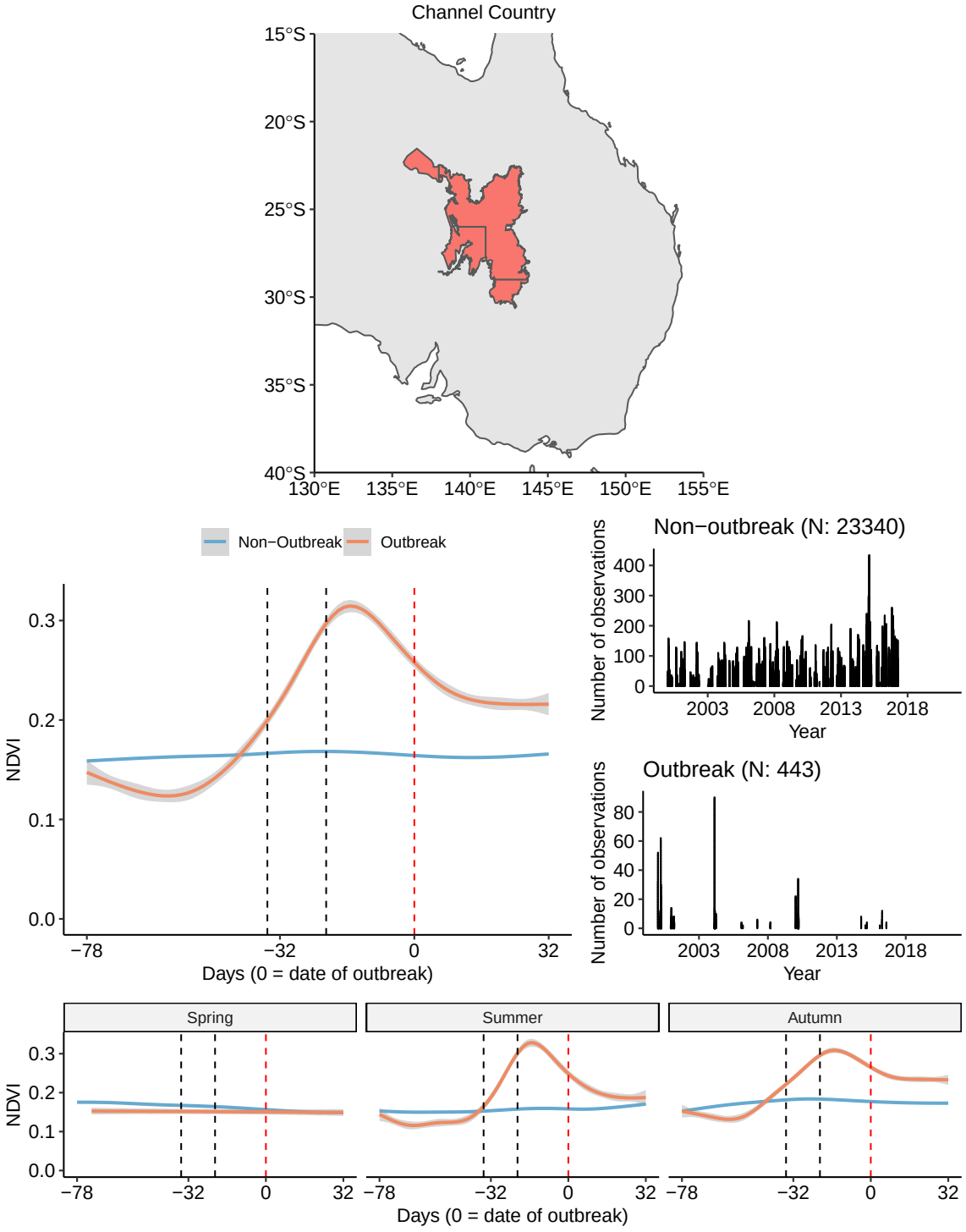
SUPPLEMENTARY FIGURE 10 FOR CHAPTER 5

Mulga Lands

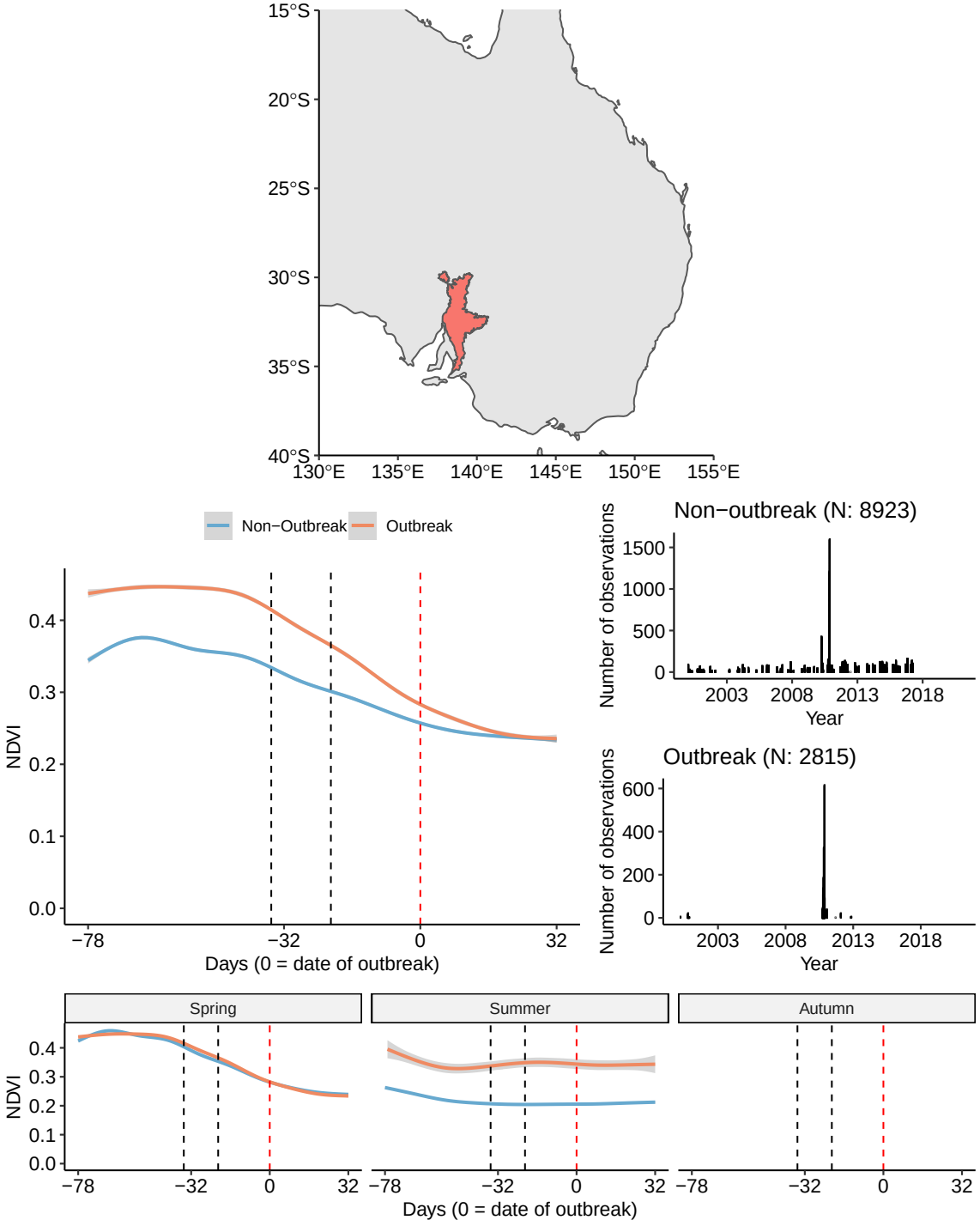

15°S
20°S
25°S
30°S
35°S
40°S
130°E
135°E
140°E
145°E
150°E
155°E
Non−Outbreak
Outbreak
NDVI
0.0
0.1
0.2
0.3
−78
−32
0
32
Days (0 = date of outbreak)
Non−outbreak (N: 21409)
Number of observations
0
100
200
300
400
2003
2008
2013
2018
Year
Outbreak (N: 442)
0
20
40
60
80
Spring
Summer
Autumn

Mitchell Grass Downs

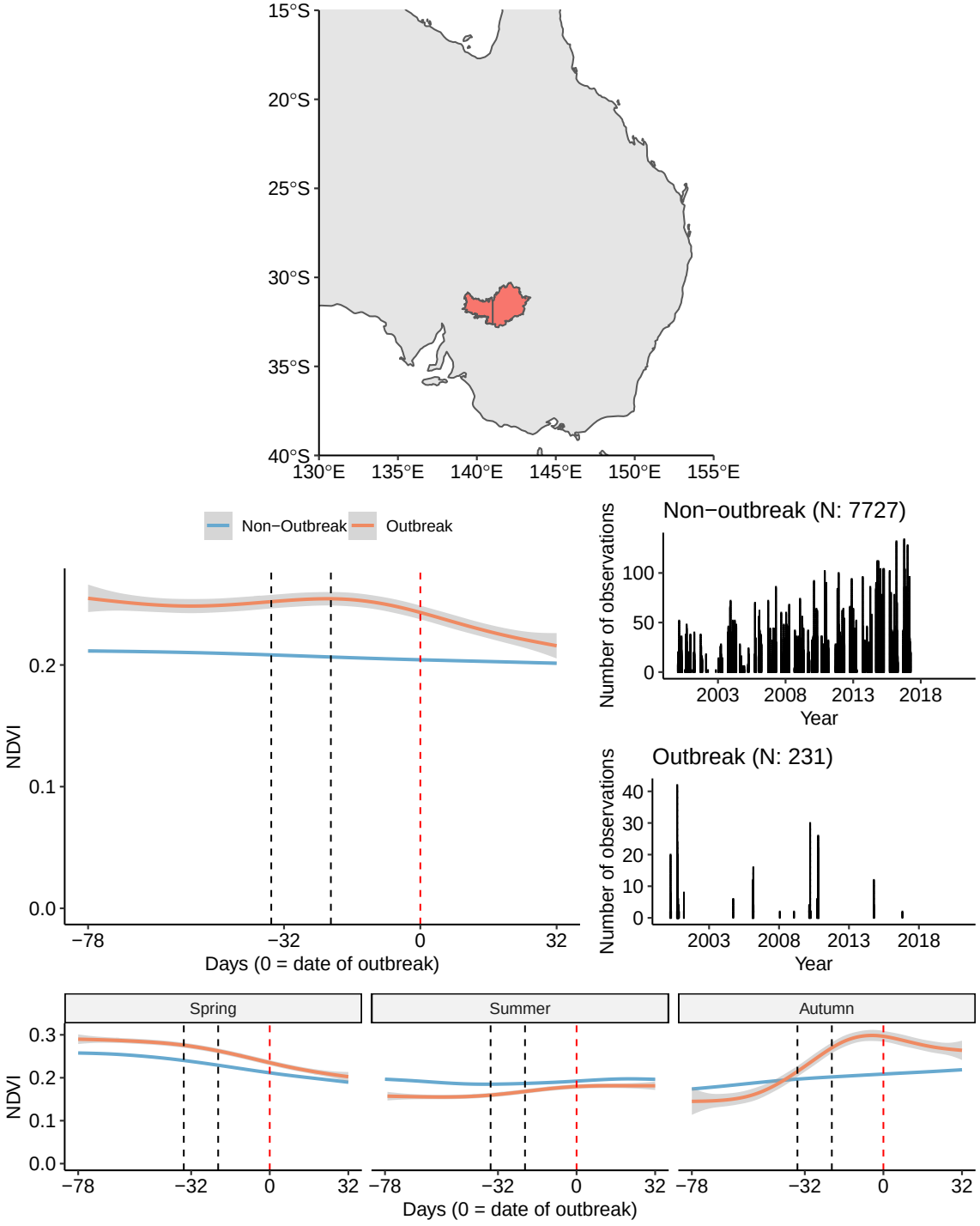



Channel Country
15°S
20°S
25°S
30°S
35°S
40°S
130°E
135°E
140°E
145°E
150°E
155°E
Non−Outbreak
Outbreak
NDVI
0.3
0.2
0.1
0.0
−78
−32
0
32
Days (0 = date of outbreak)
Non−outbreak (N: 23340)
Number of observations
400
300
200
100
0
2003
2008
2013
2018
Year
Outbreak (N: 443)
80
60
40
20
0
Spring
Summer
Autumn

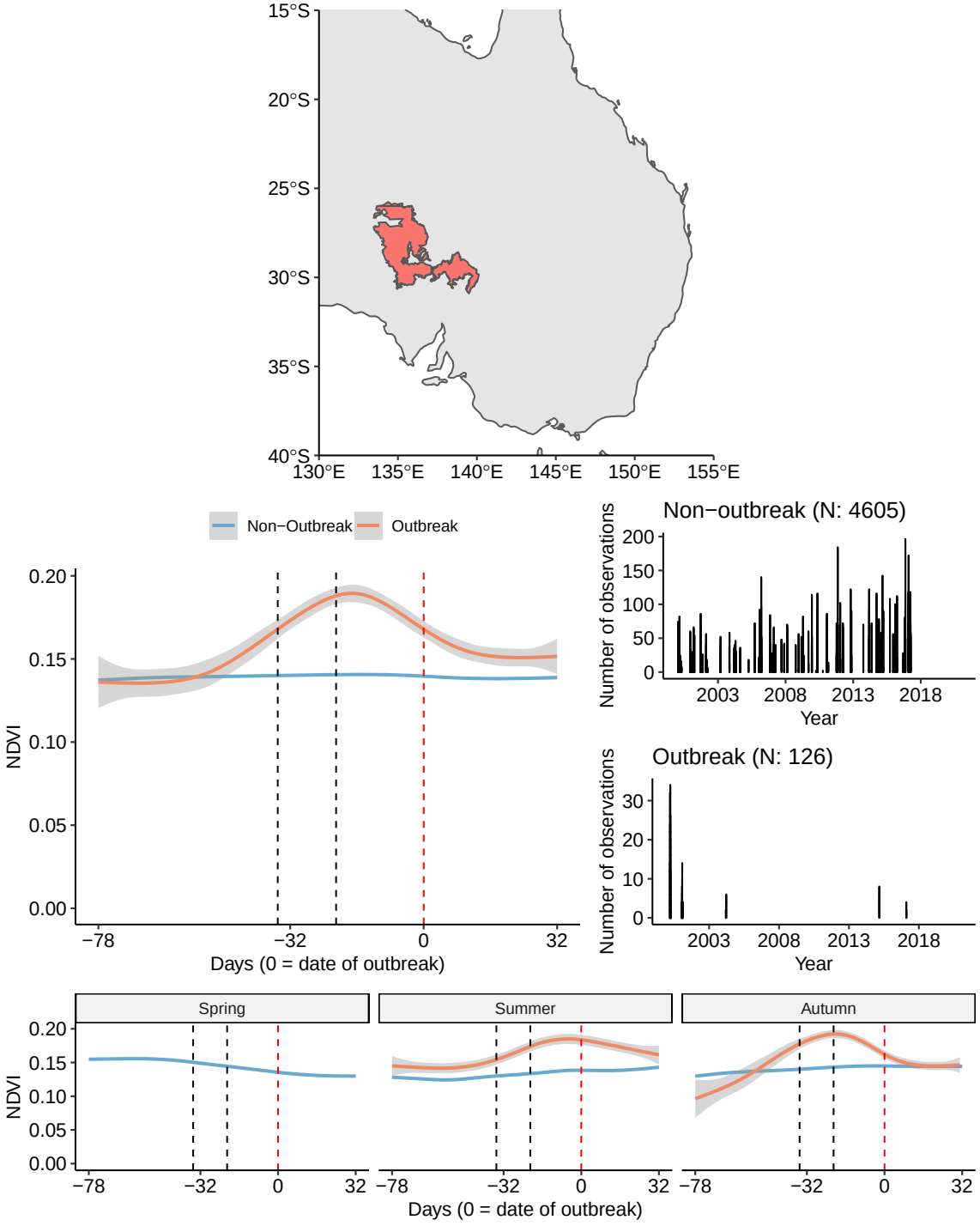
Flinders Lofty Block



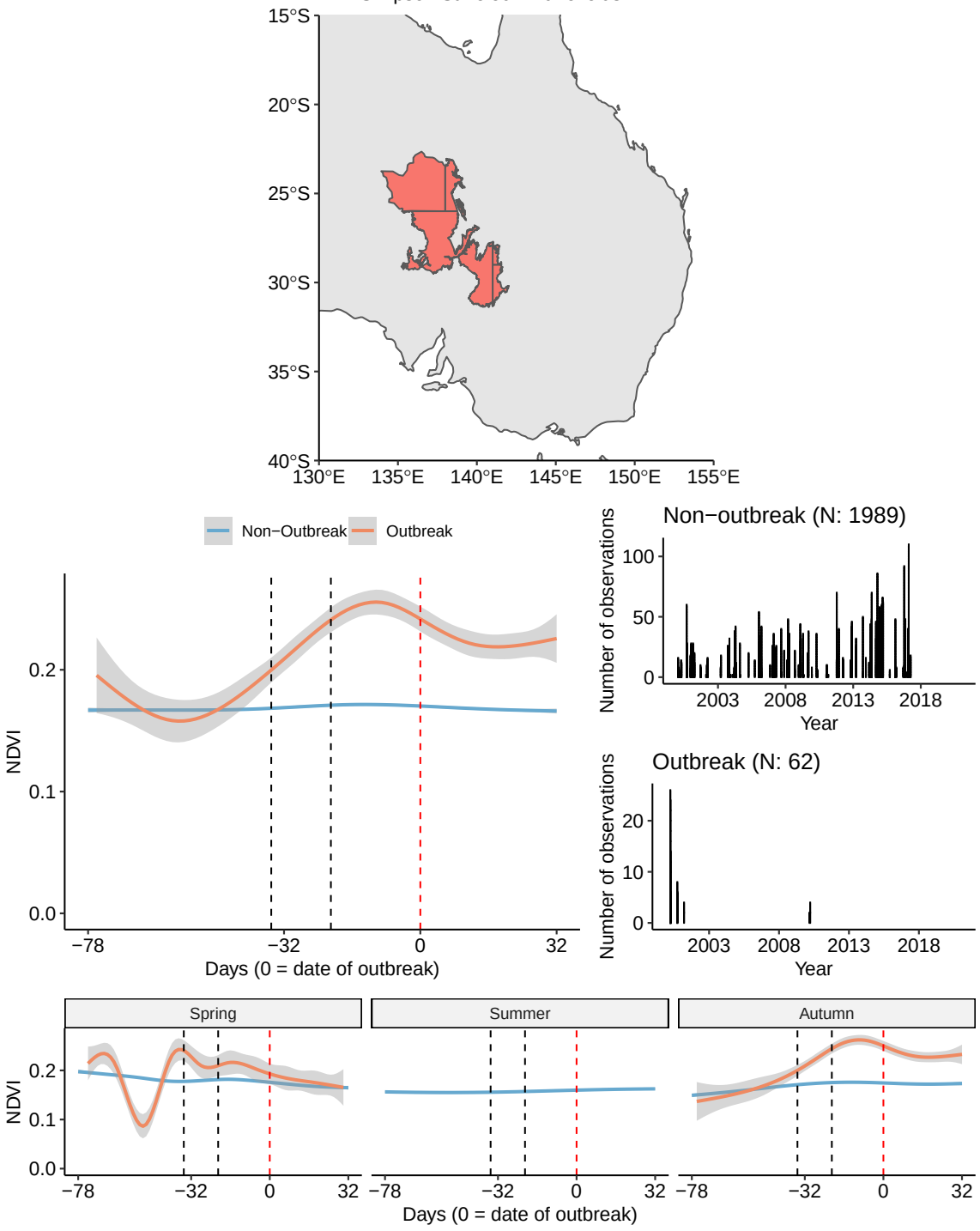
Broken Hill Complex



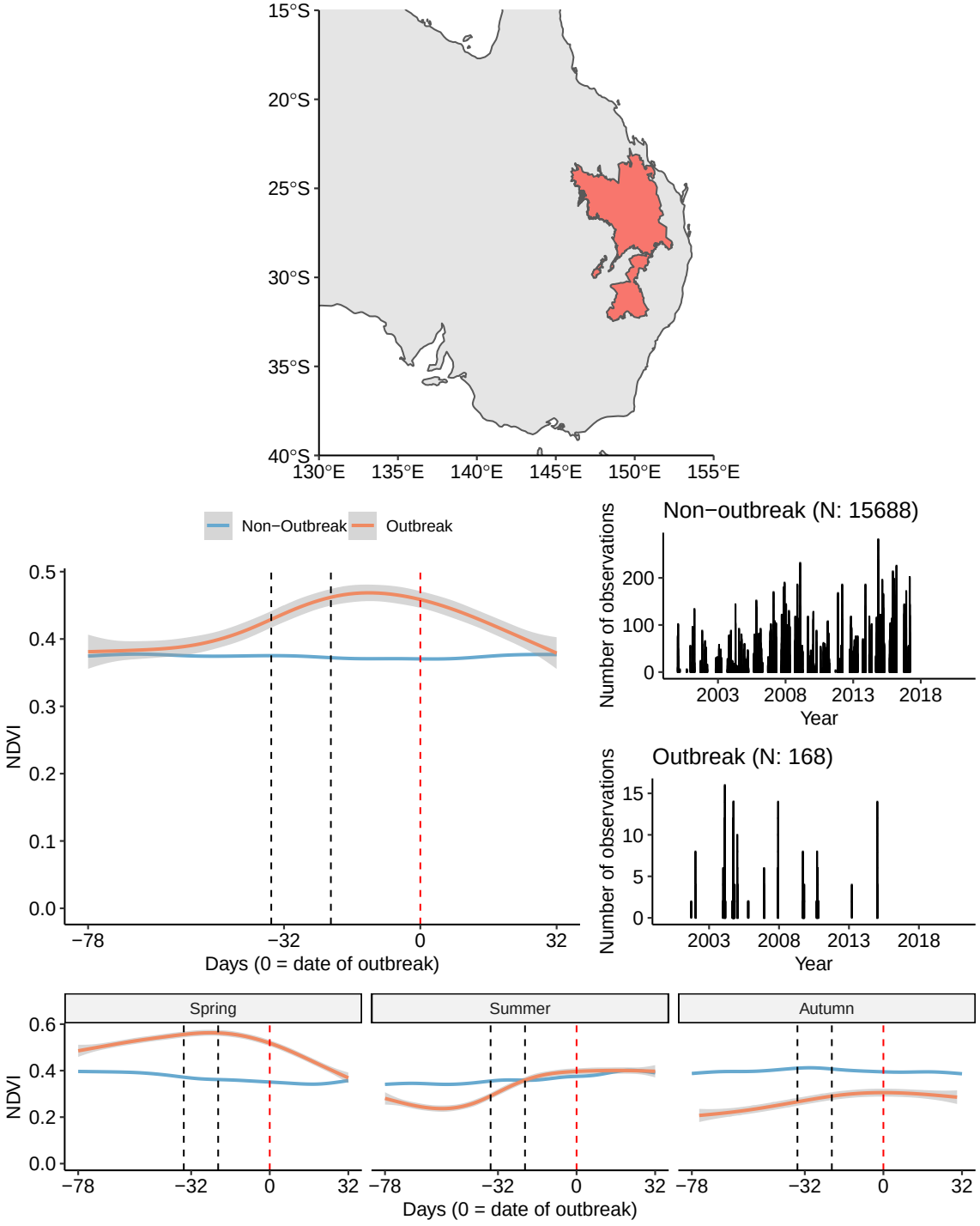
Stony Plains



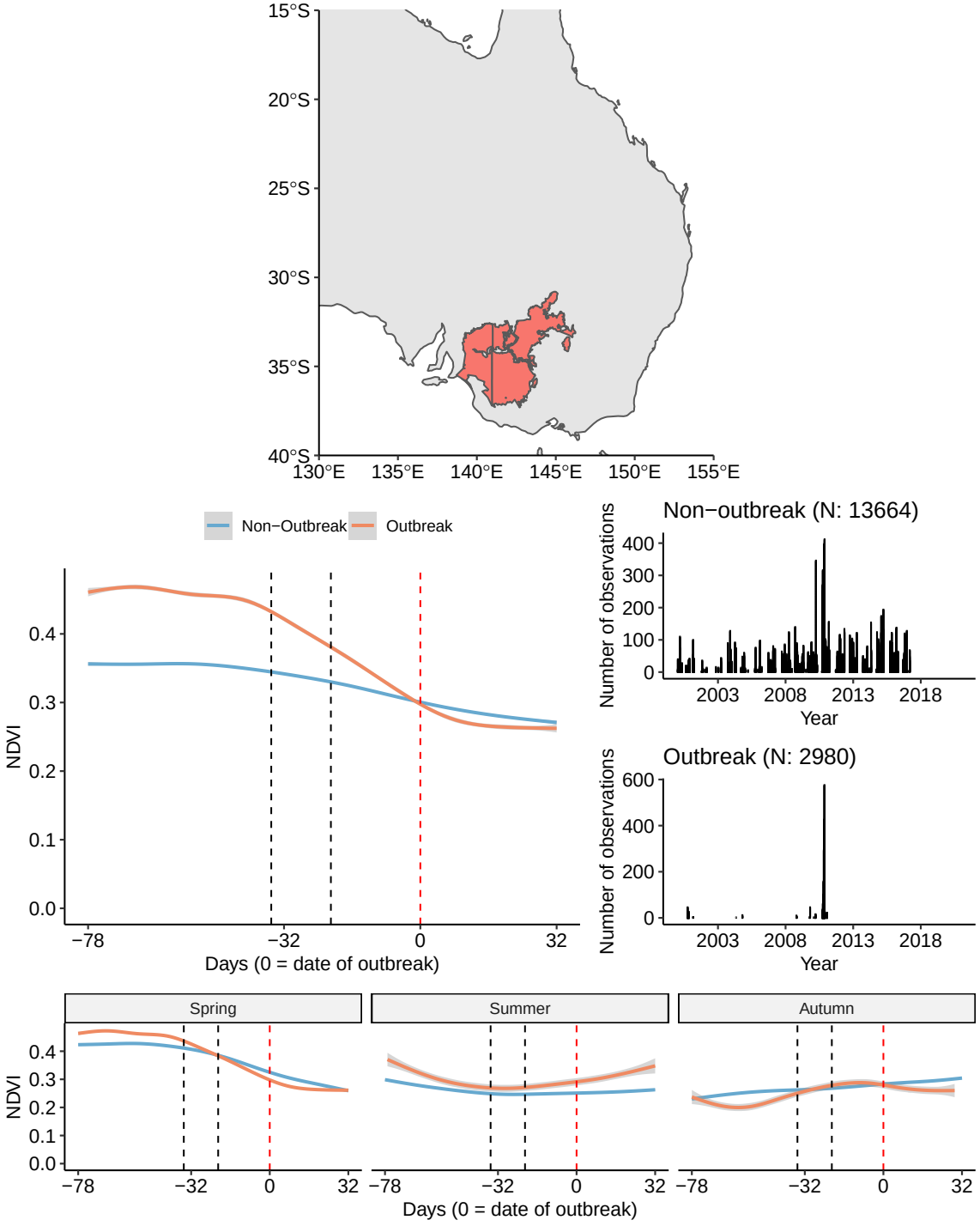
Simpson Strzelecki Dunefields



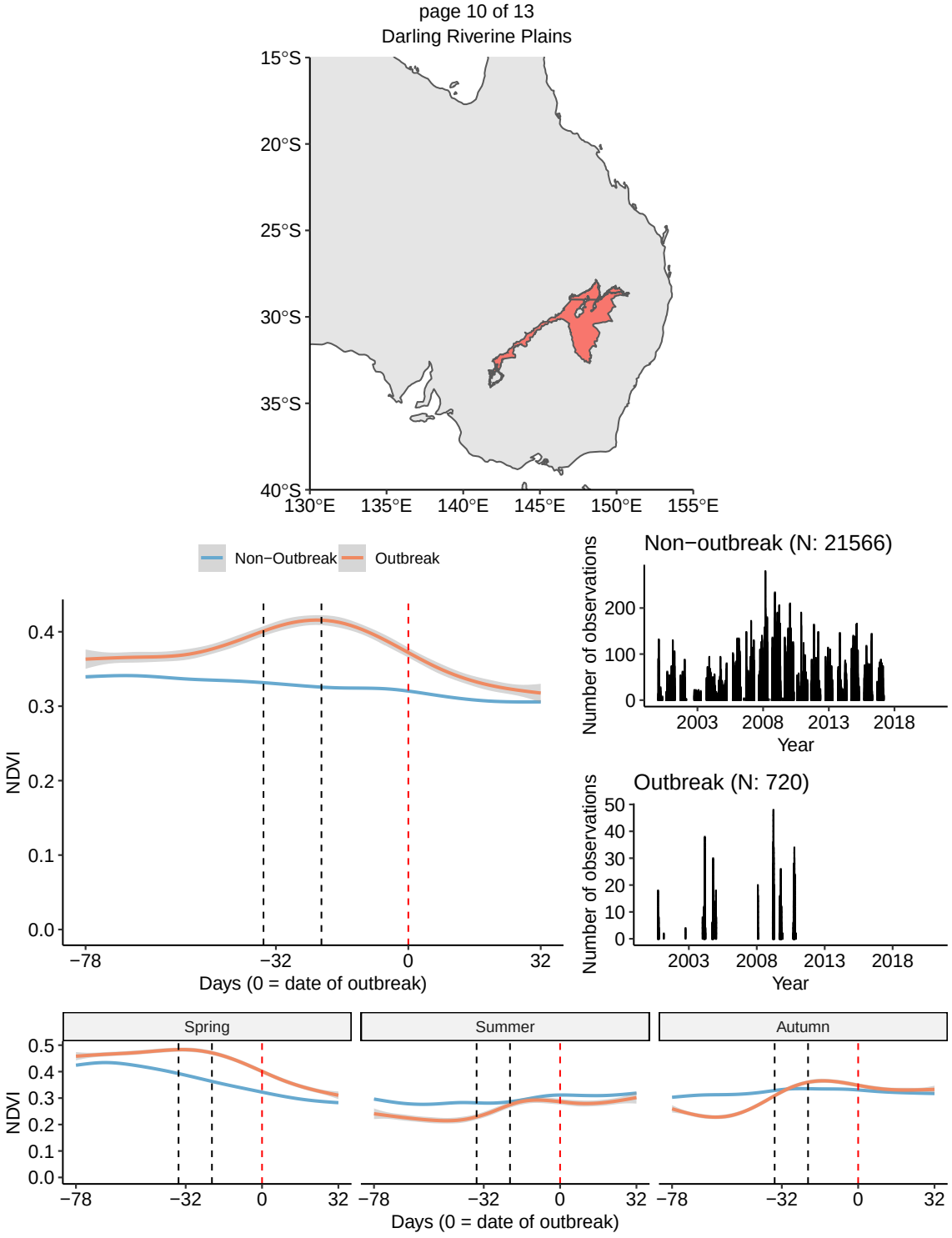
Brigalow Belt South

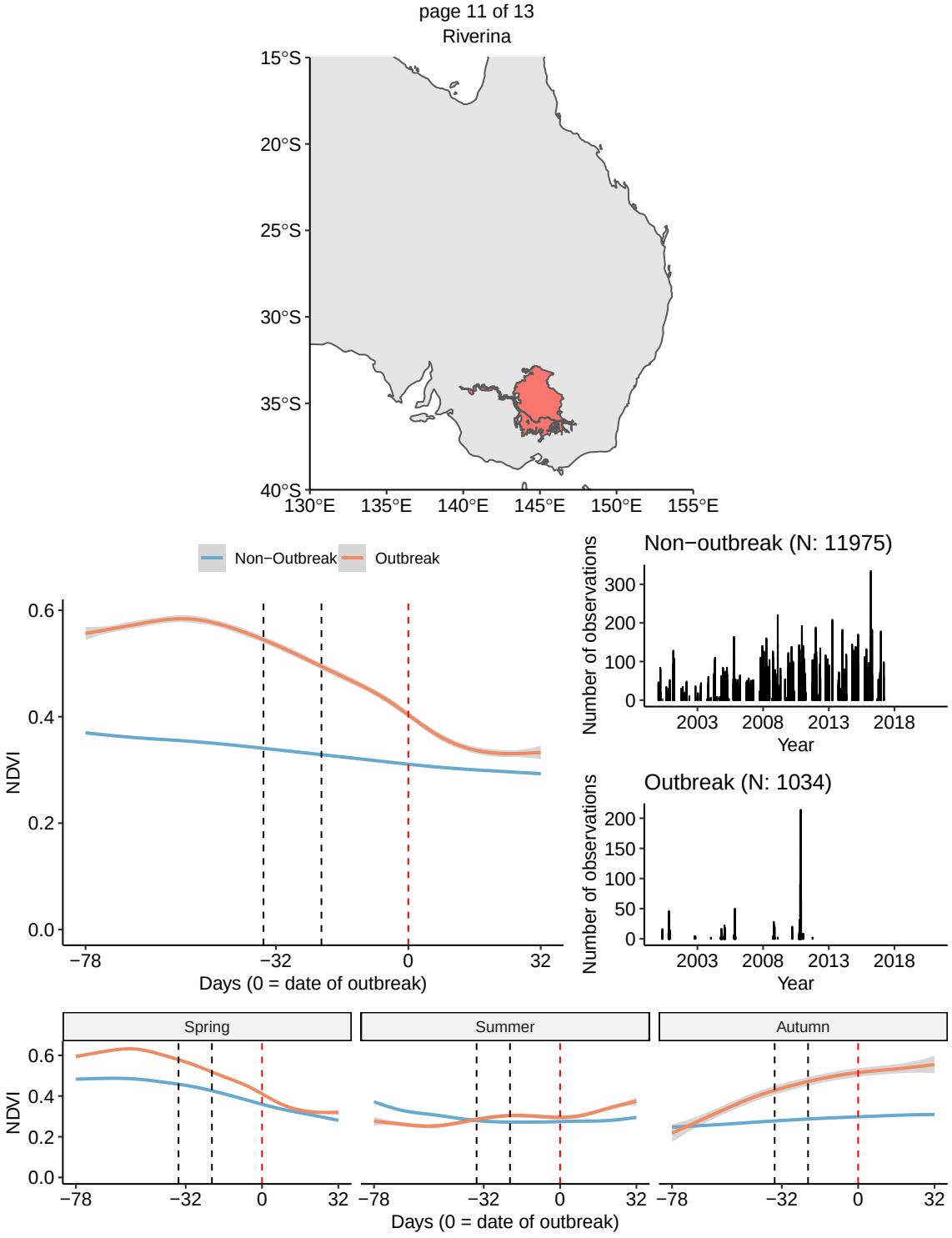


Murray Darling Depression

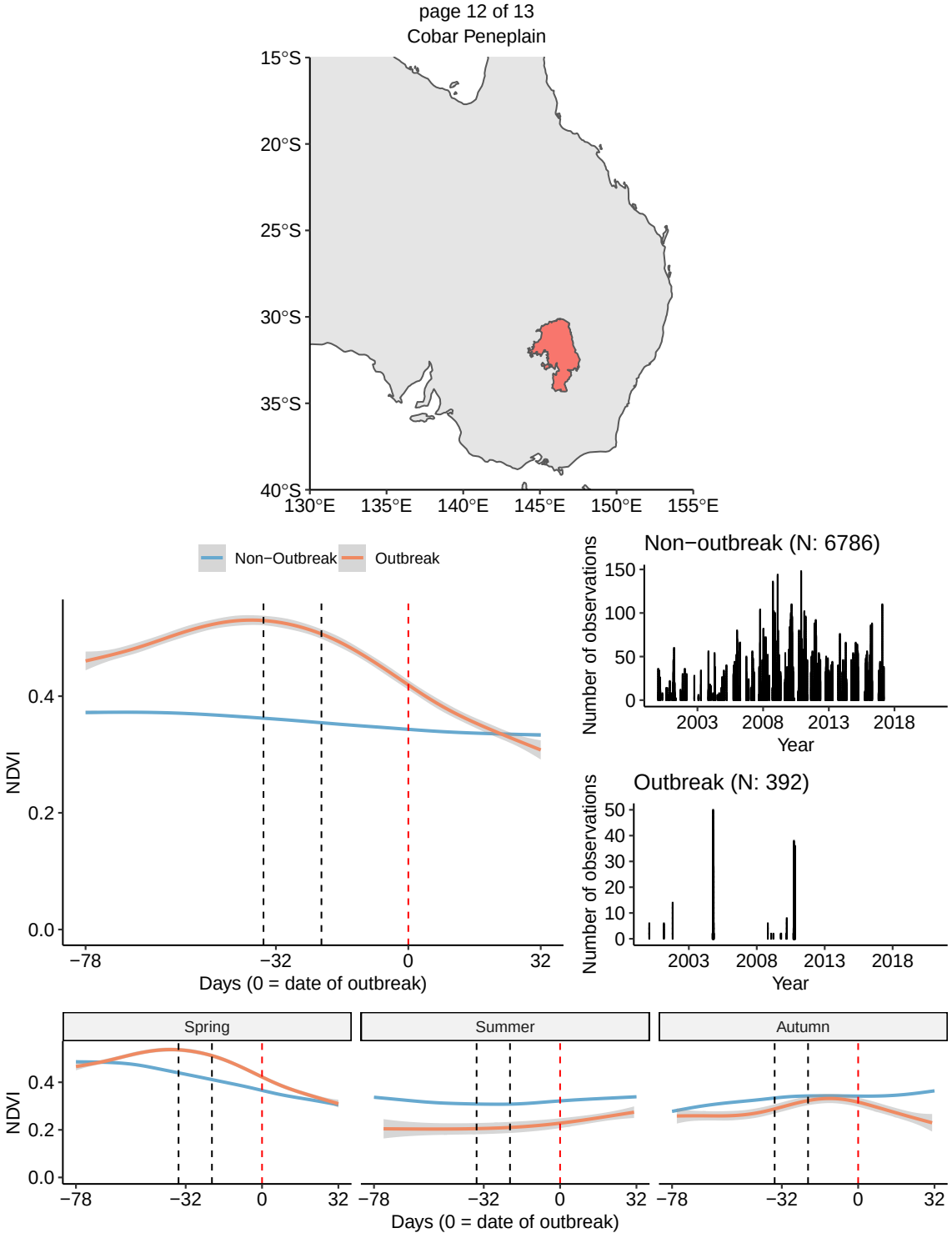


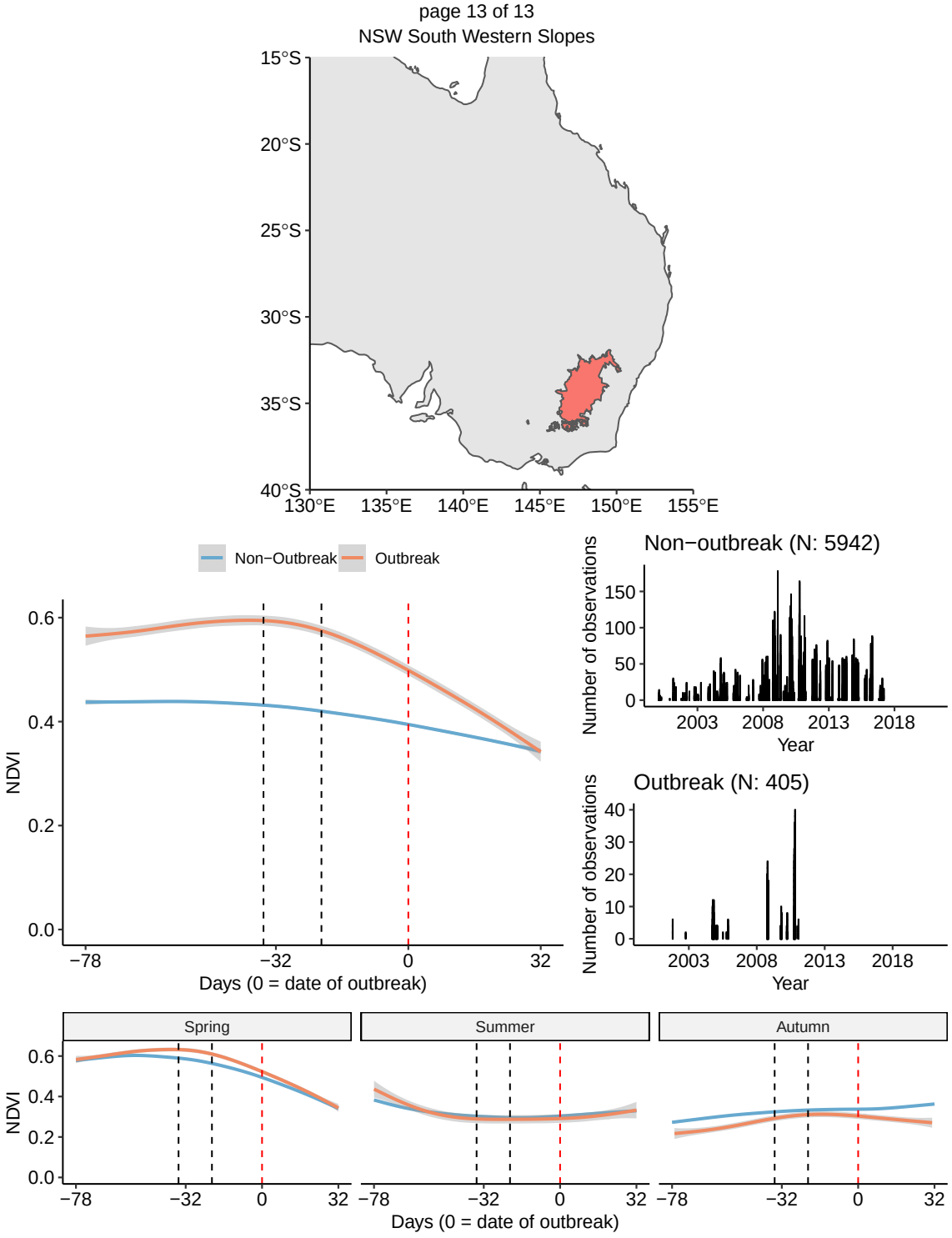
Darling Riverine Plains




Riverina
15°S
20°S
25°S
30°S
35°S
40°S
130°E
135°E
140°E
145°E
150°E
155°E
Non−Outbreak
Outbreak
NDVI
0.6
0.4
0.2
0.0
−78
−32
0
32
Days (0 = date of outbreak)
Non−outbreak (N: 11975)
Number of observations
300
200
100
0
2003
2008
2013
2018
Year
Outbreak (N: 1034)
200
150
100
50
0
Spring
Summer
Autumn

Cobar Peneplain

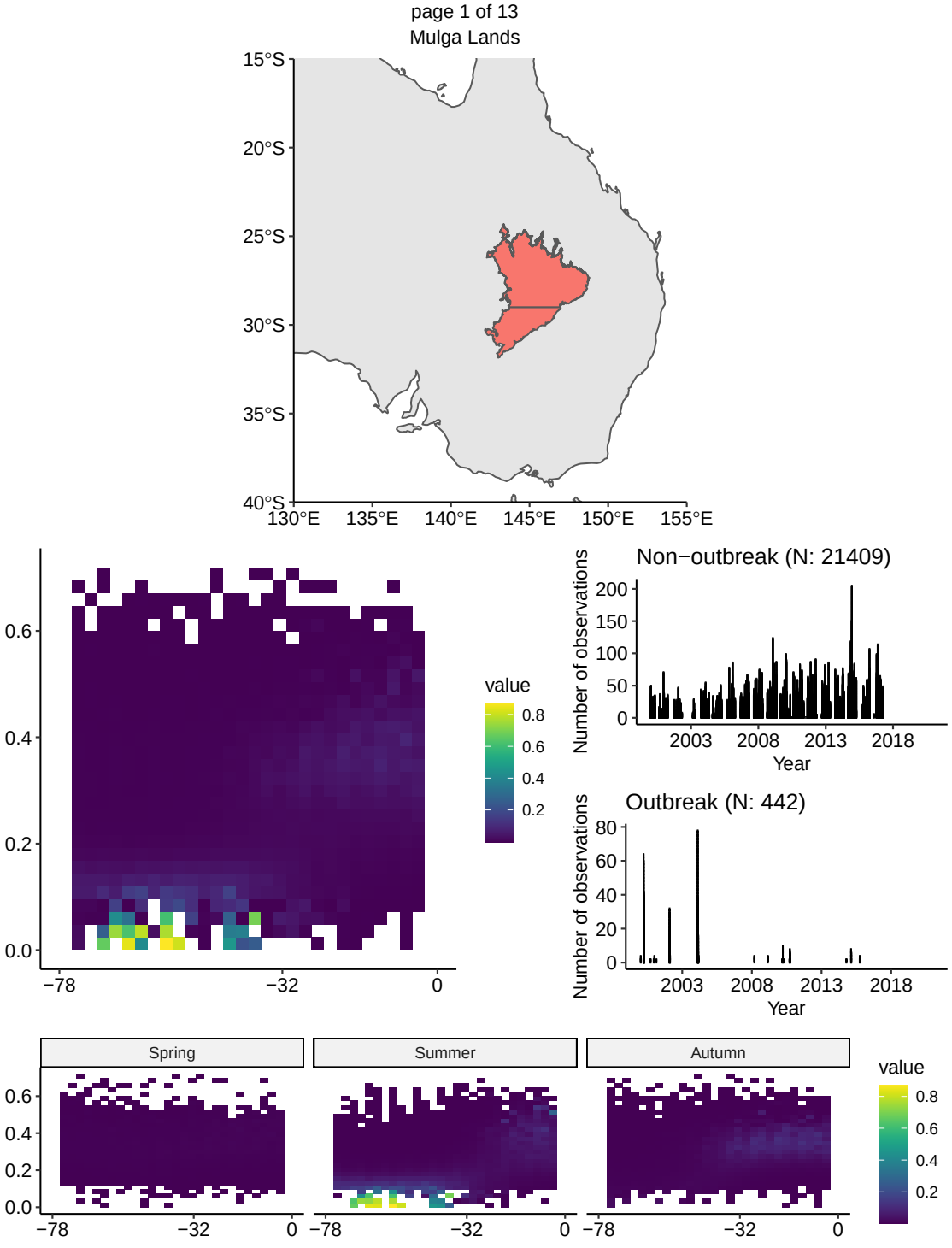



NSW South Western Slopes
15°S
20°S
25°S
30°S
35°S
40°S
130°E
135°E
140°E
145°E
150°E
155°E
Non−Outbreak
Outbreak
NDVI
0.6
0.4
0.2
0.0
−78
−32
0
32
Days (0 = date of outbreak)
Non−outbreak (N: 5942)
Number of observations
150
100
50
0
2003
2008
2013
2018
Year
Outbreak (N: 405)
40
30
20
10
0
Spring
Summer
Autumn

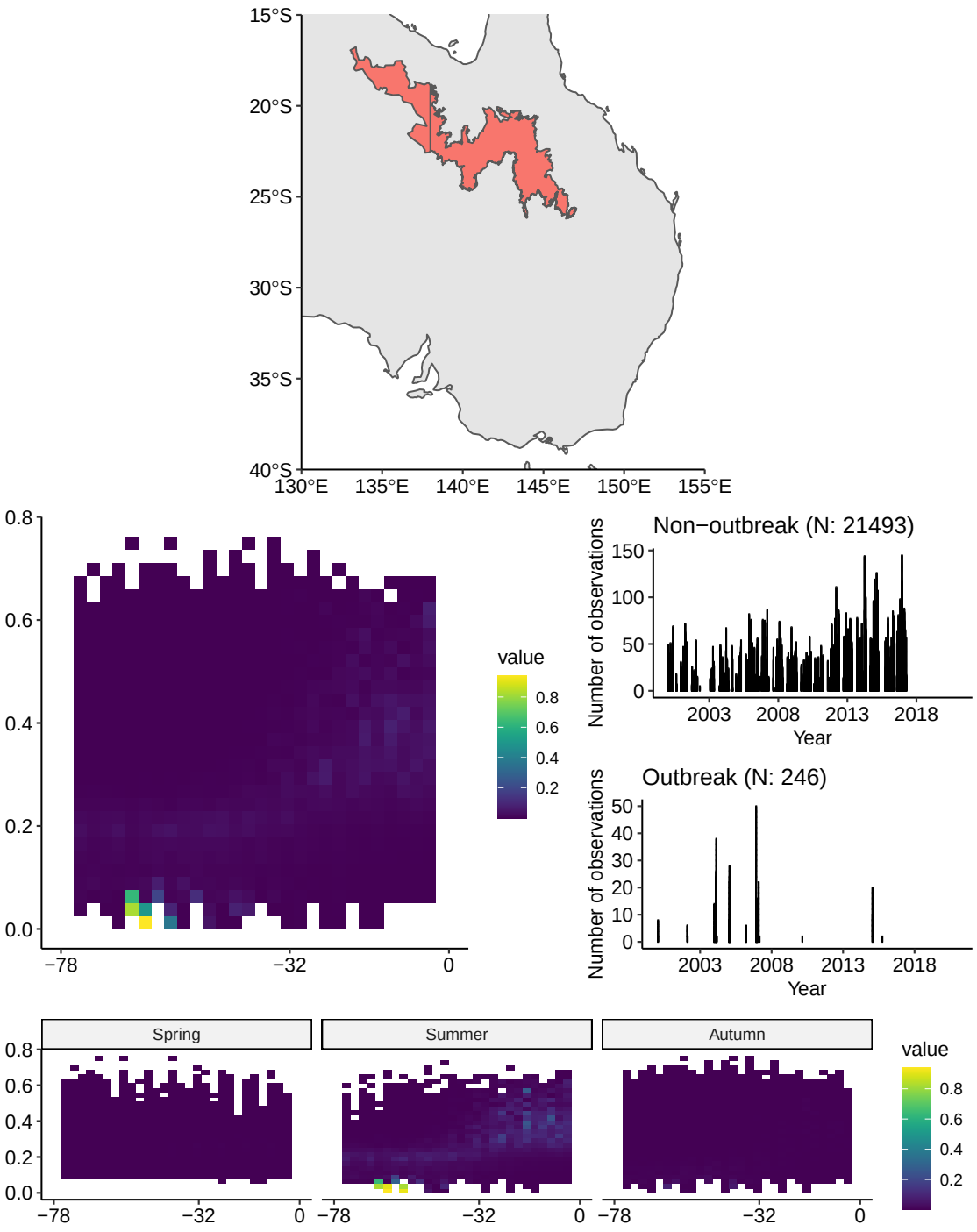
APPENDIX F

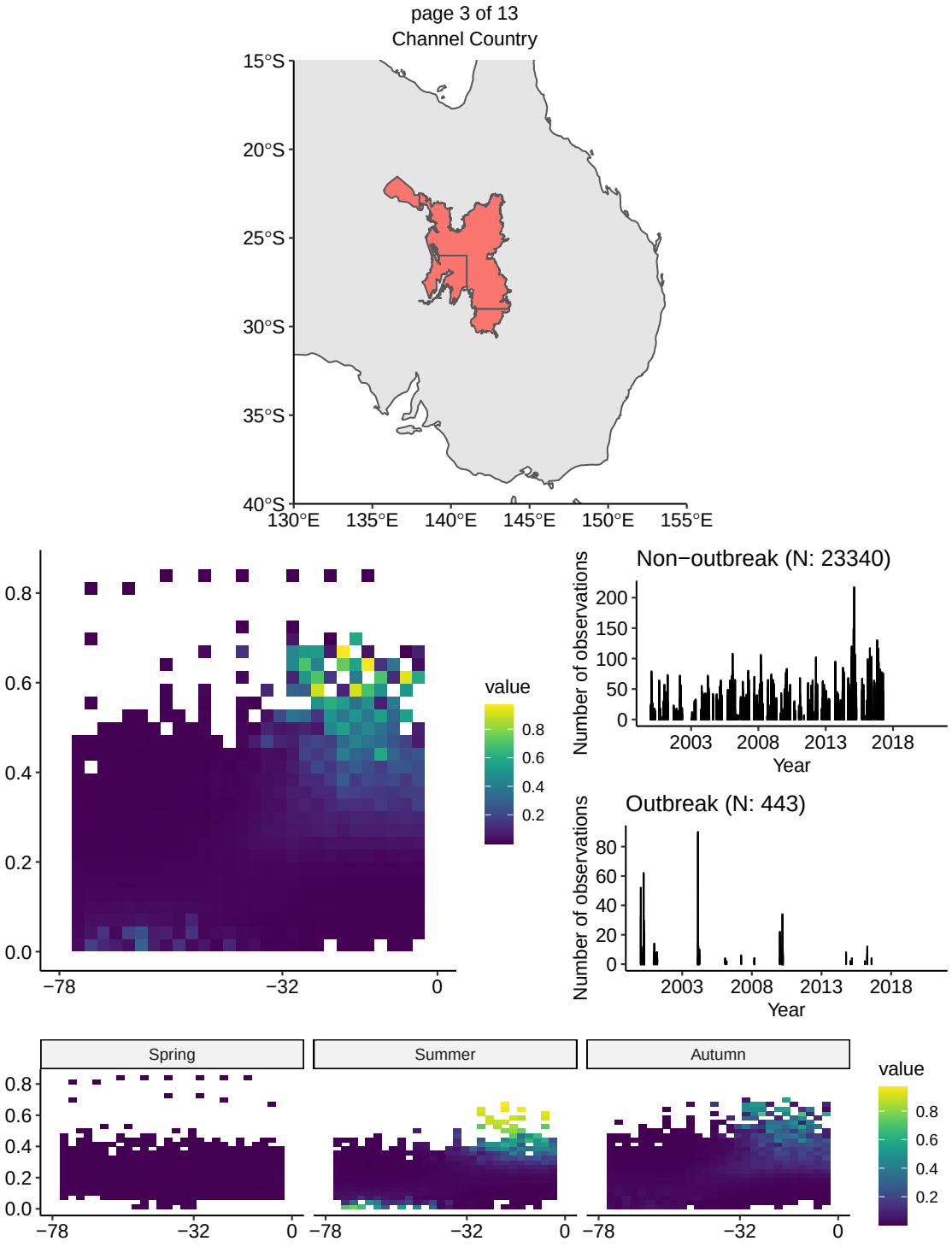
SUPPLEMENTARY FIGURE 11 FOR CHAPTER 5

Mulga Lands

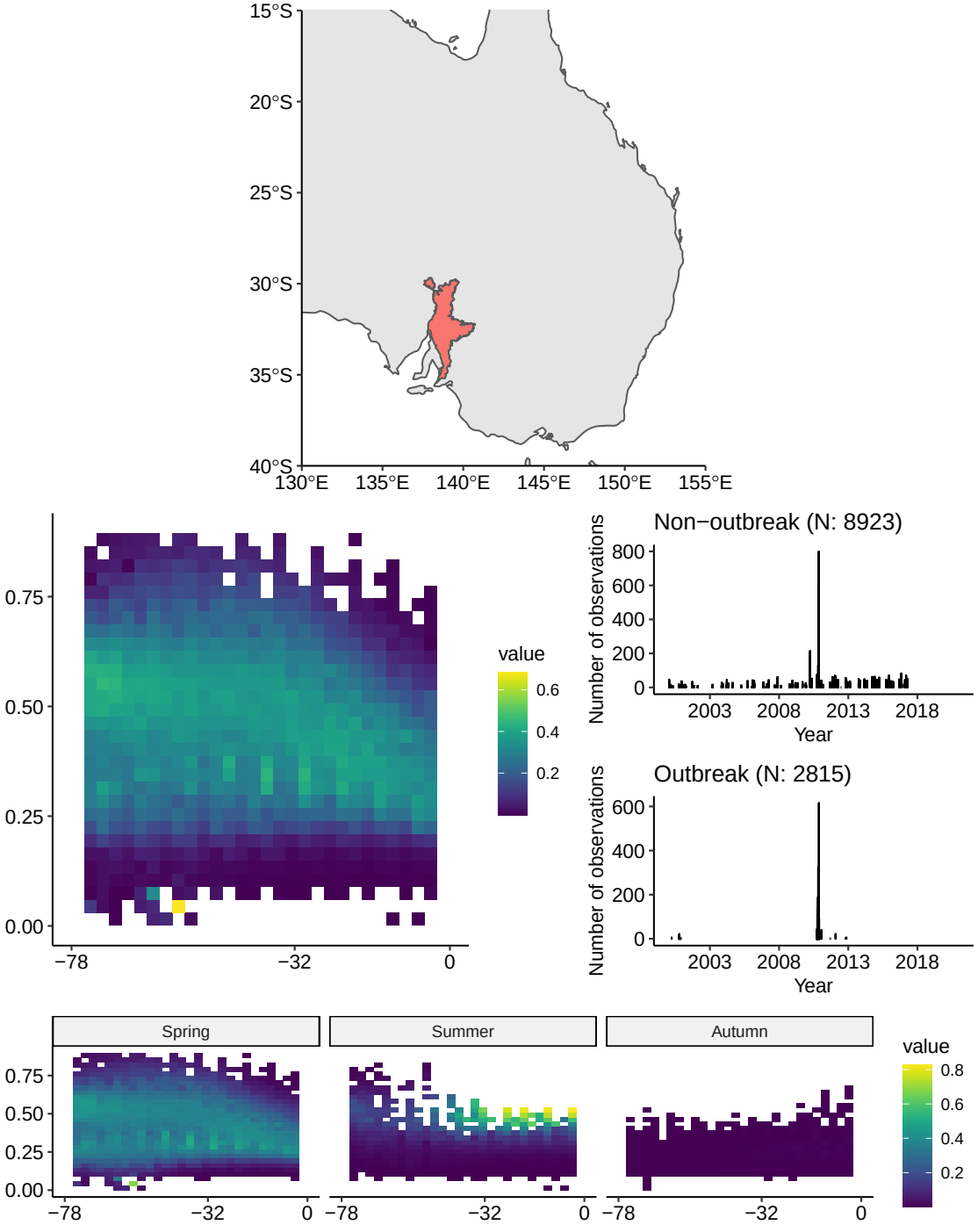

15°S
20°S
25°S
30°S
35°S
40°S
130°E
135°E
140°E
145°E
150°E
155°E
0.6
0.4
0.2
0.0
−78
−32
0
value
0.8
0.6
0.4
0.2
Non−outbreak (N: 21409)
Number of observations
200
150
100
50
0
2003
2008
2013
2018
Year
Outbreak (N: 442)
Number of observations
80
60
40
20
0
2003
2008
2013
2018
Year
Spring
Summer
Autumn
value
0.8
0.6
0.4
0.2

Mitchell Grass Downs

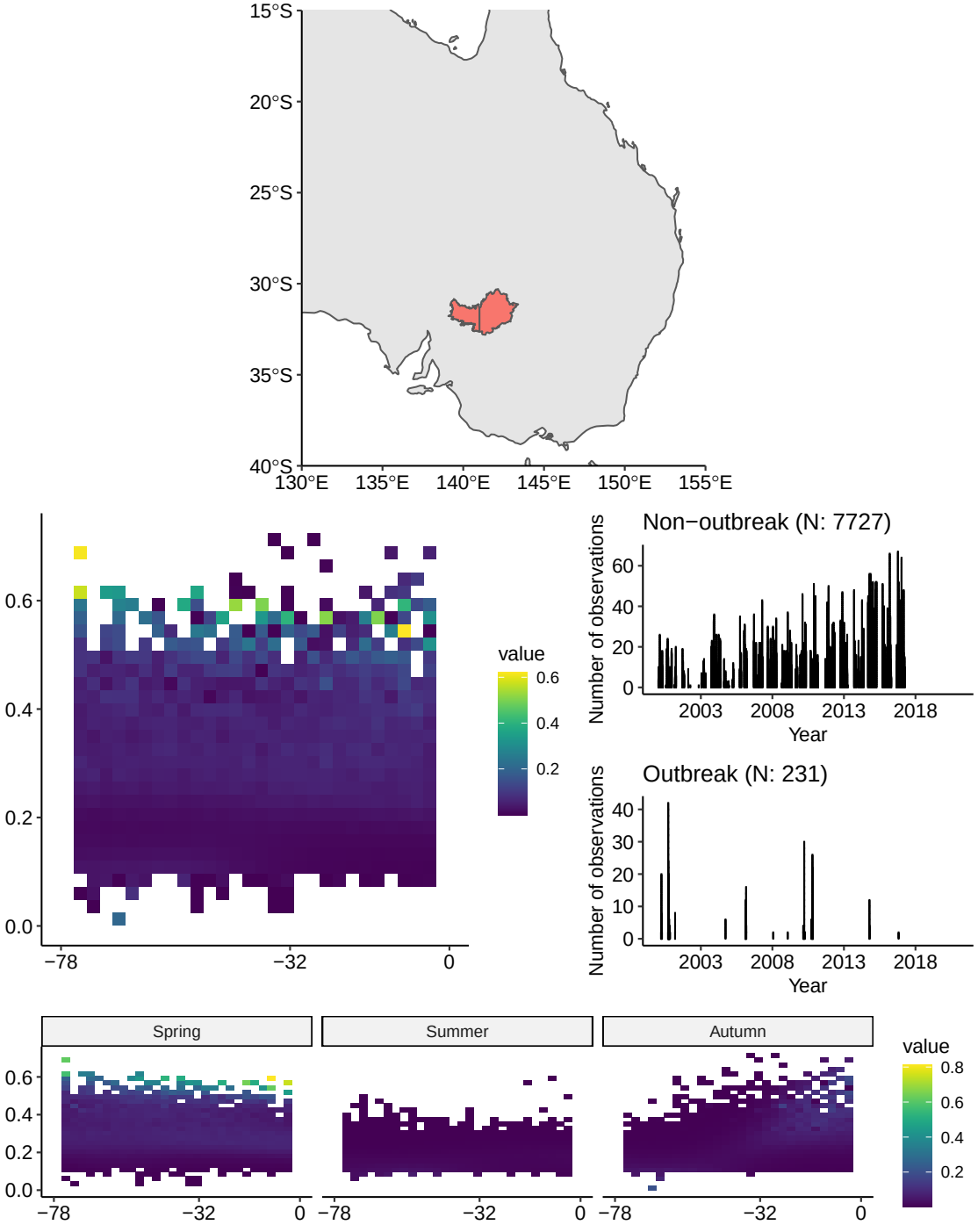



Channel Country
15°S
20°S
25°S
30°S
35°S
40°S
130°E
135°E
140°E
145°E
150°E
155°E
value
0.8
0.6
0.4
0.2
−78
−32
0
Non−outbreak (N: 23340)
Number of observations
200
150
100
50
0
2003
2008
2013
2018
Year
Outbreak (N: 443)
80
60
40
20
Spring
Summer
Autumn

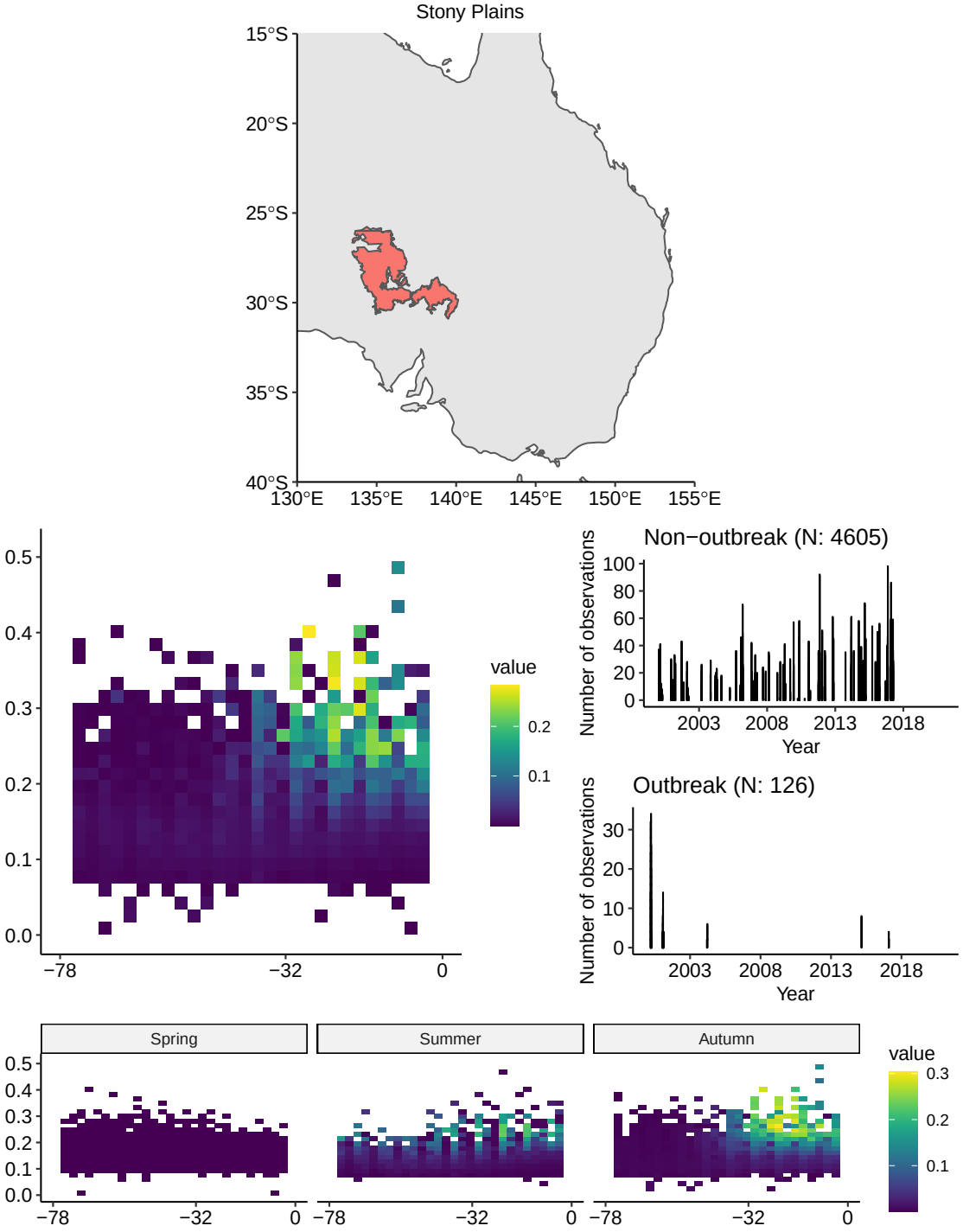
Flinders Lofty Block



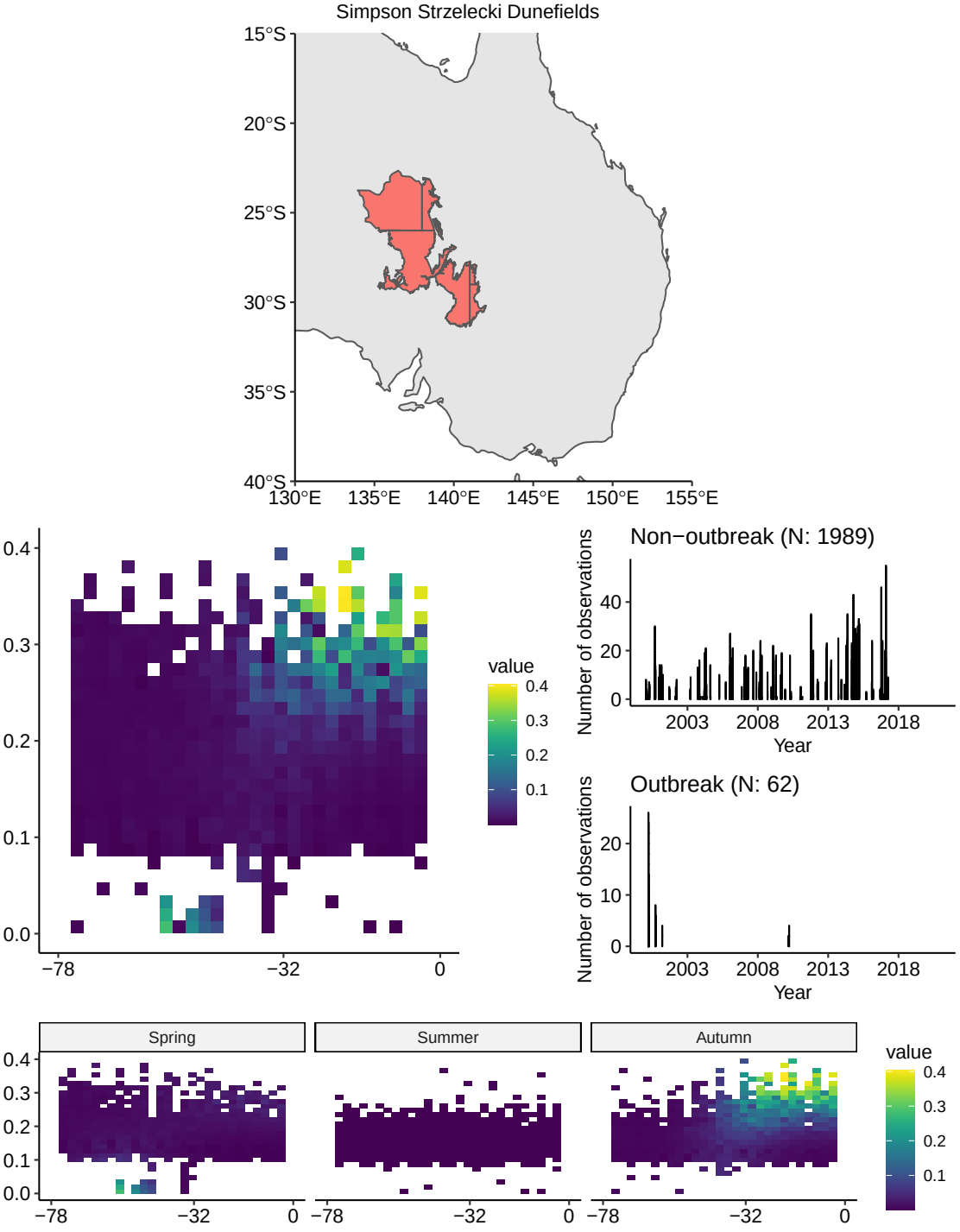
Broken Hill Complex



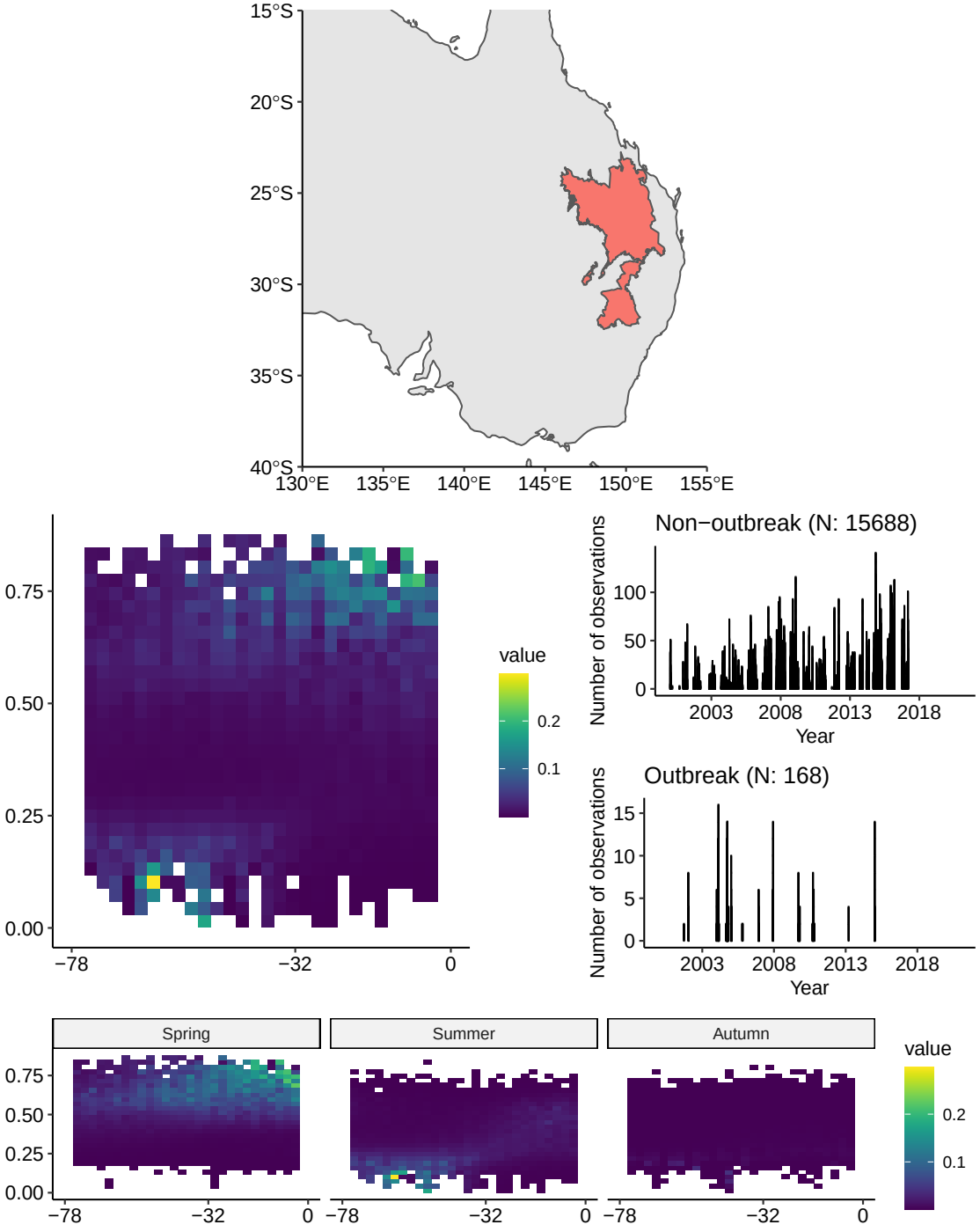
Stony Plains



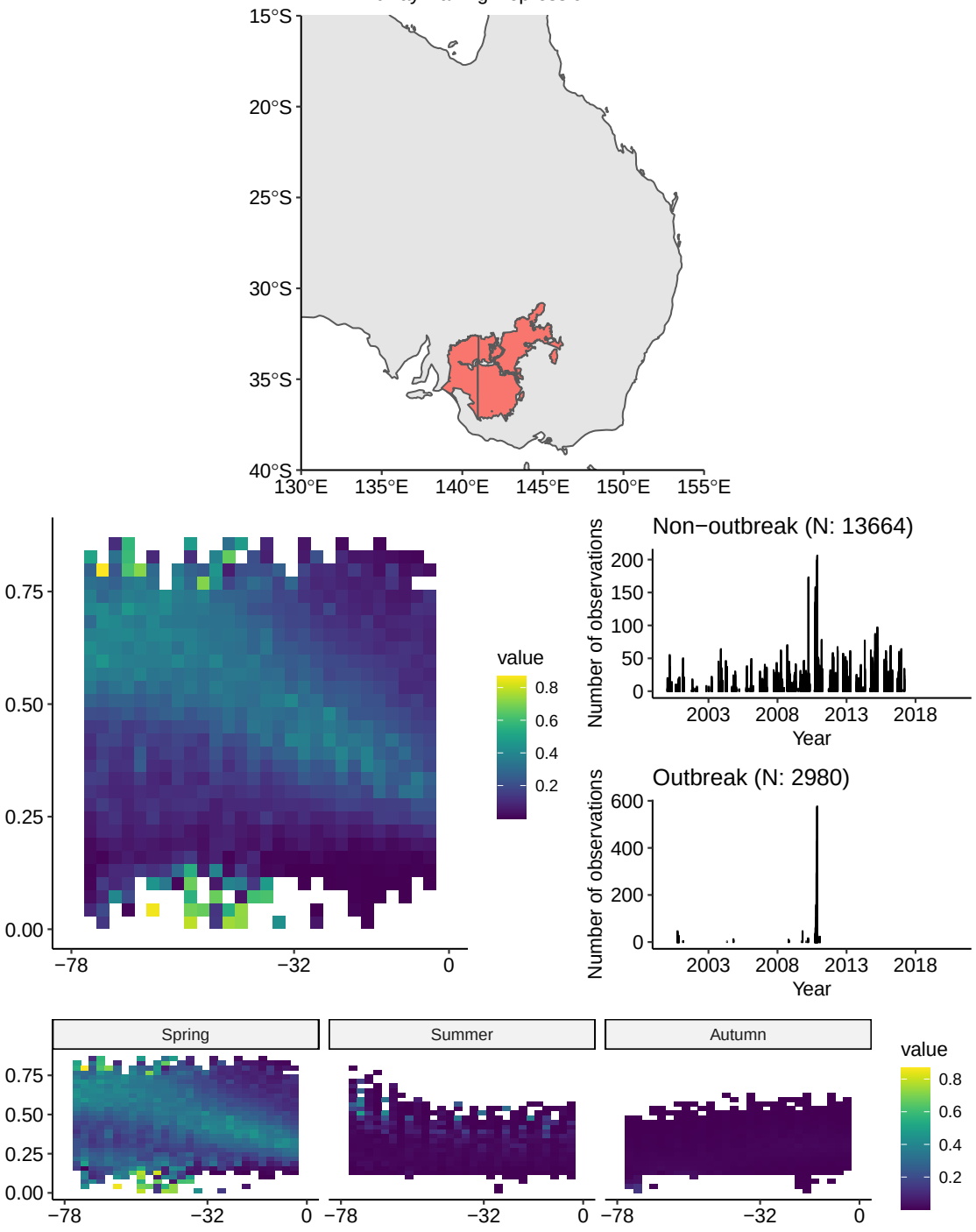
Simpson Strzelecki Dunefields



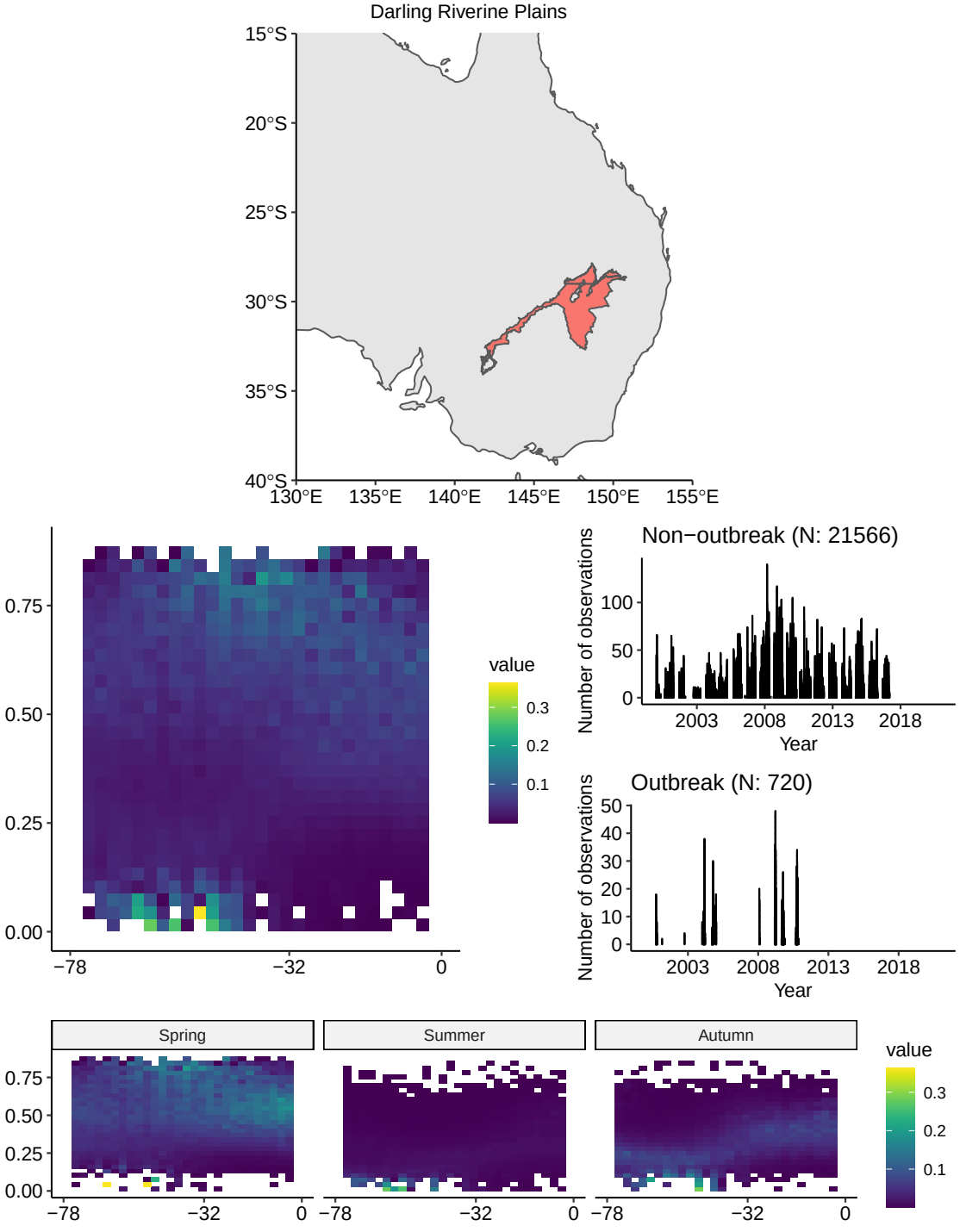
Brigalow Belt South



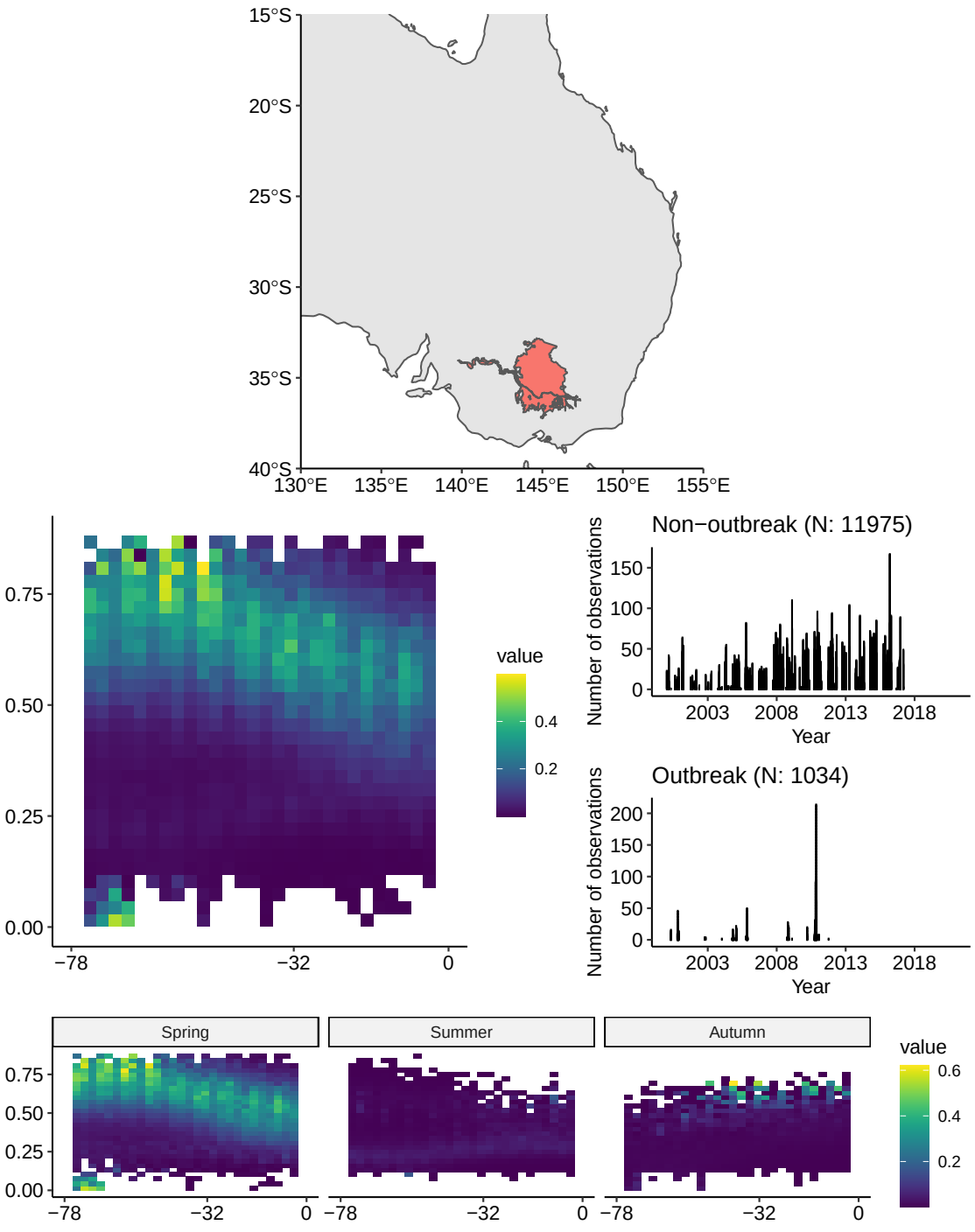
Murray Darling Depression



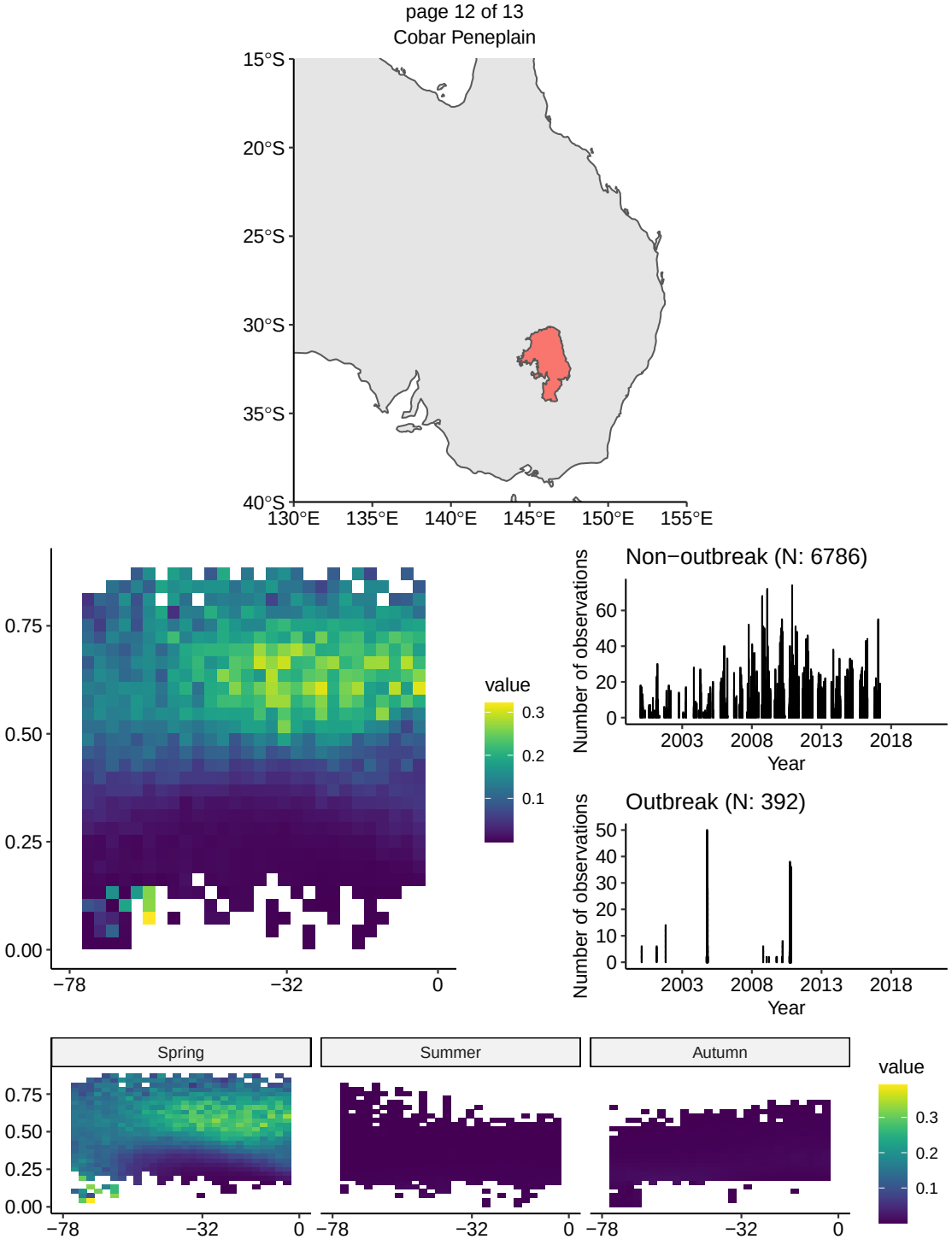
Darling Riverine Plains



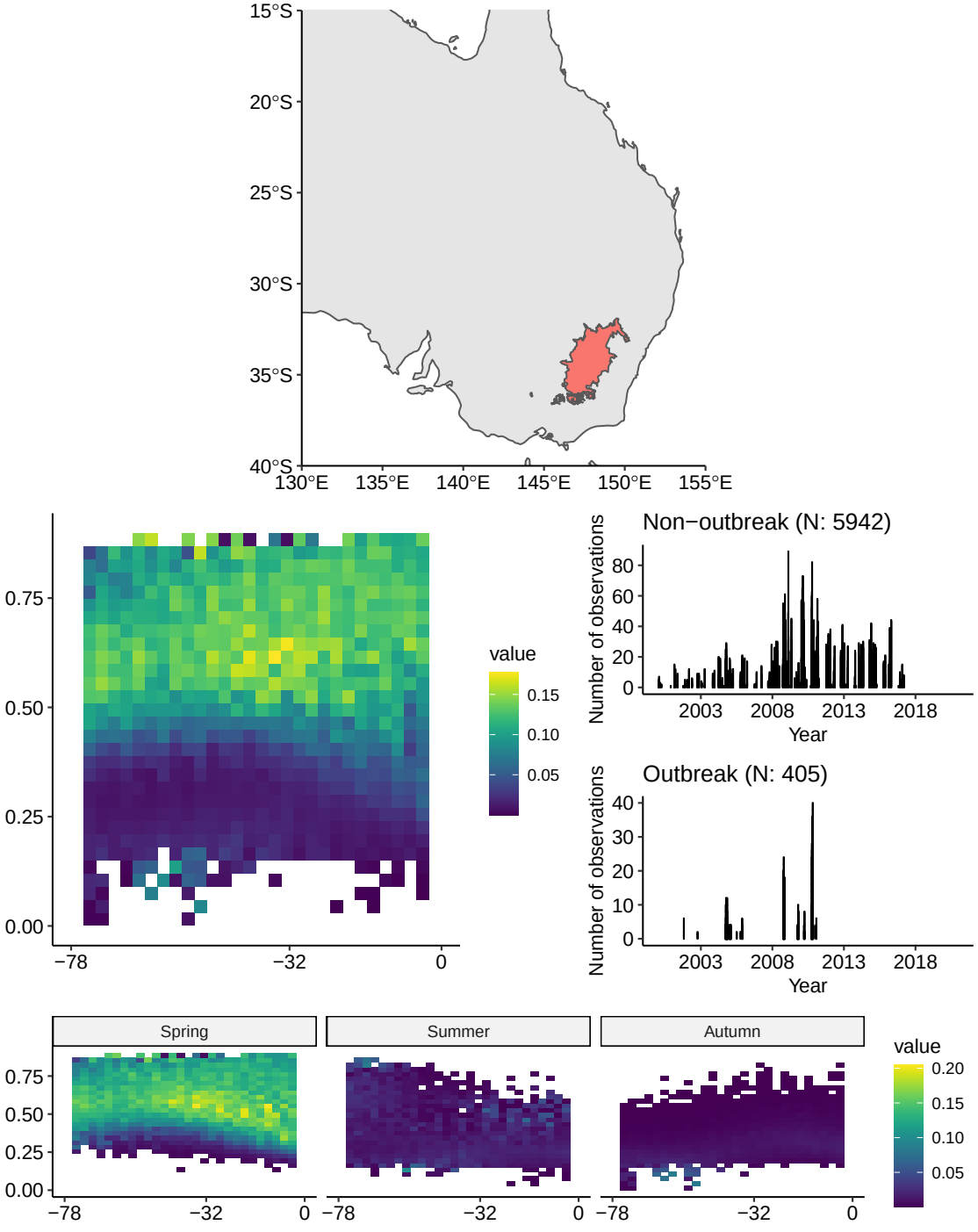
Riverina


15°S
20°S
25°S
30°S
35°S
40°S
130°E
135°E
140°E
145°E
150°E
155°E
0.75
0.50
0.25
0.00
−78
−32
0
value
0.4
0.2
Non−outbreak (N: 11975)
Number of observations
150
100
50
0
2003
2008
2013
2018
Year
Outbreak (N: 1034)
200
150
100
50
0
Spring
Summer
Autumn
0.6
0.4
0.2

Cobar Peneplain



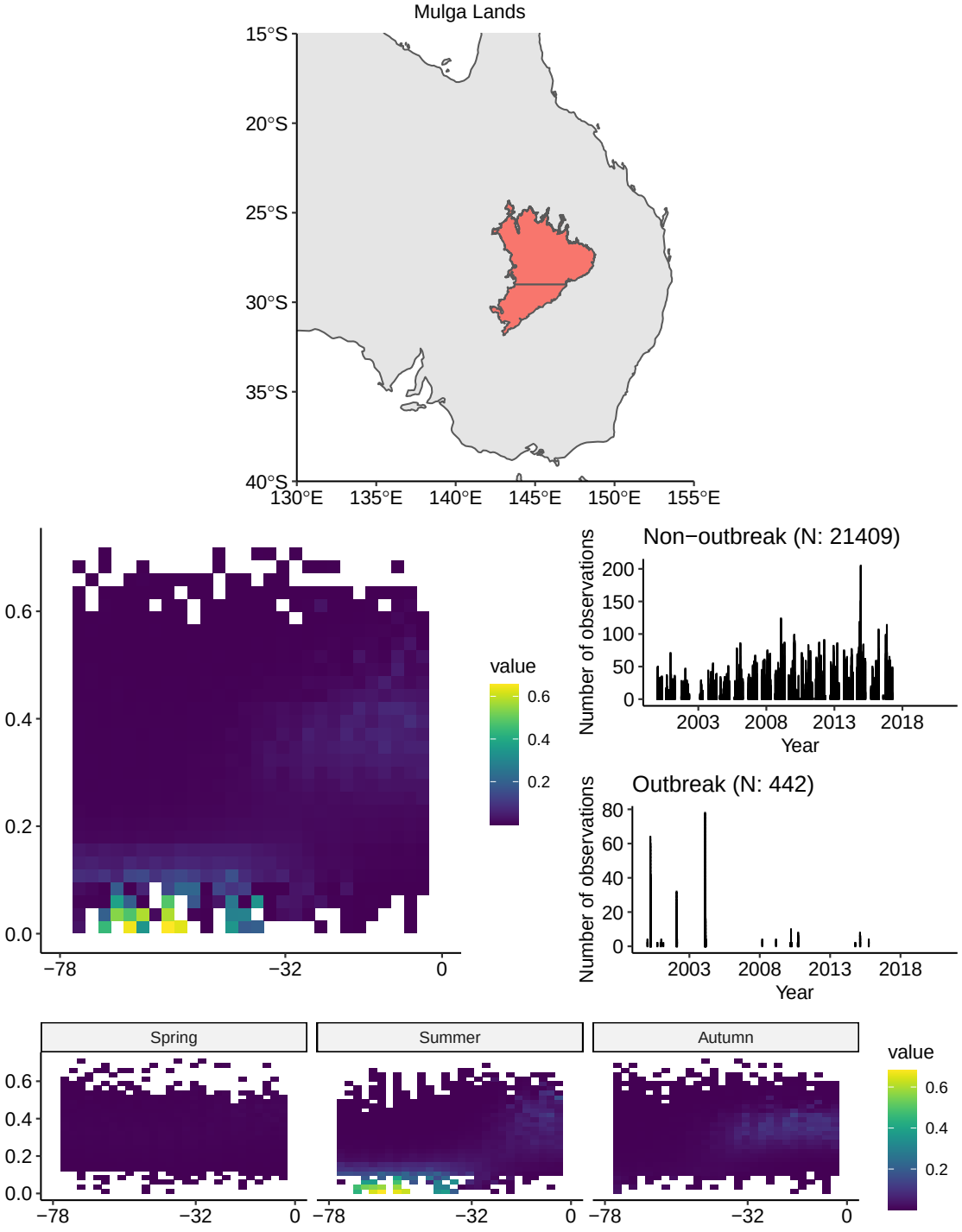
NSW South Western Slopes



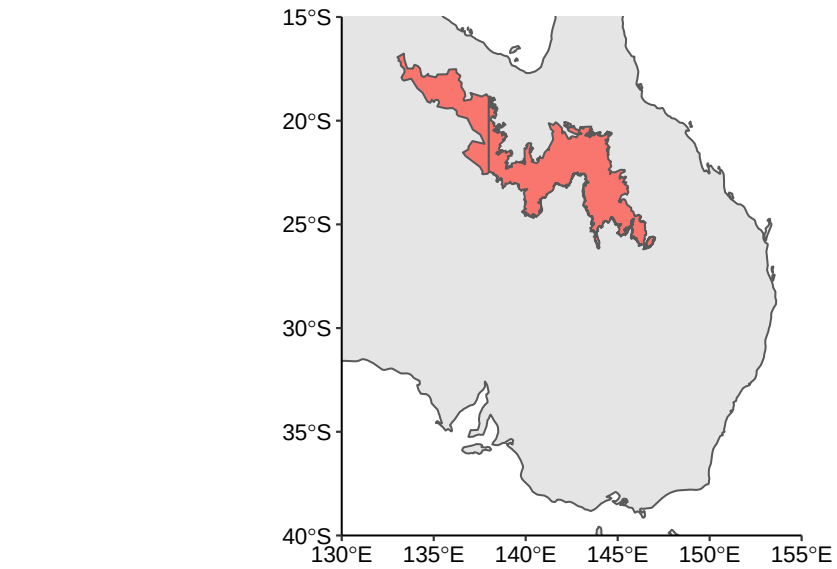
APPENDIX G

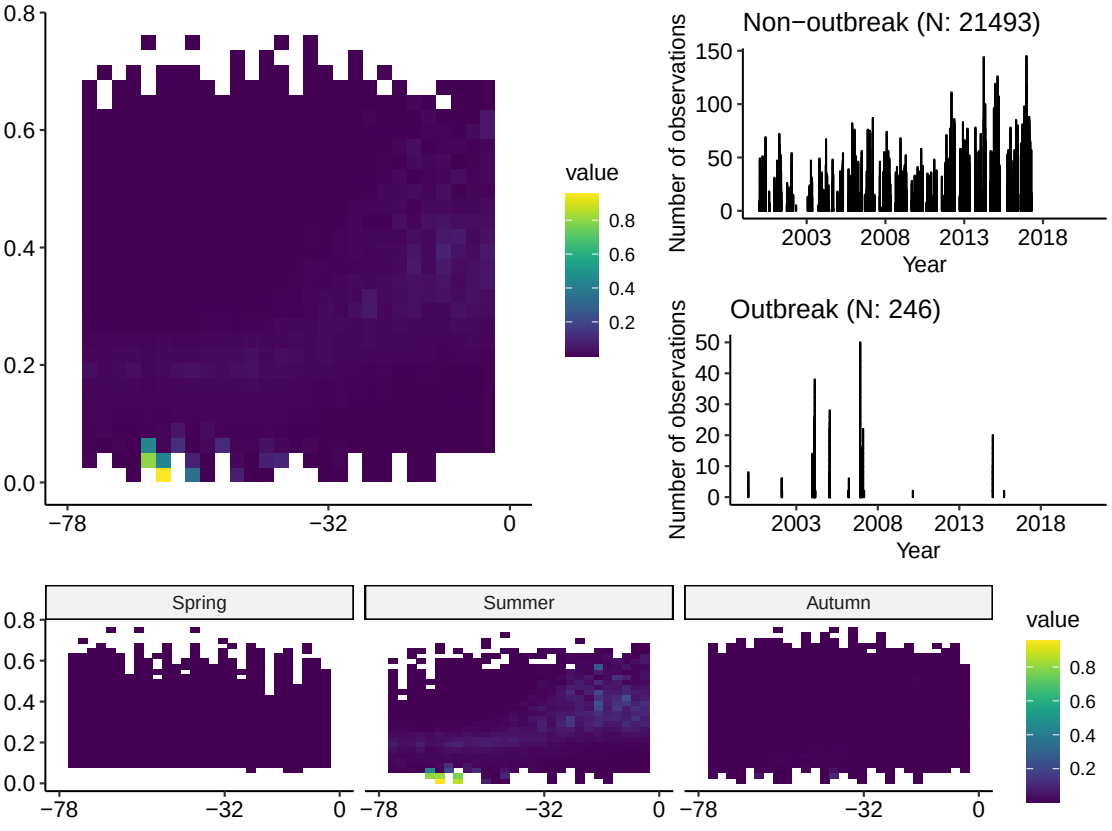
SUPPLEMENTARY FIGURE 12 FOR CHAPTER 5

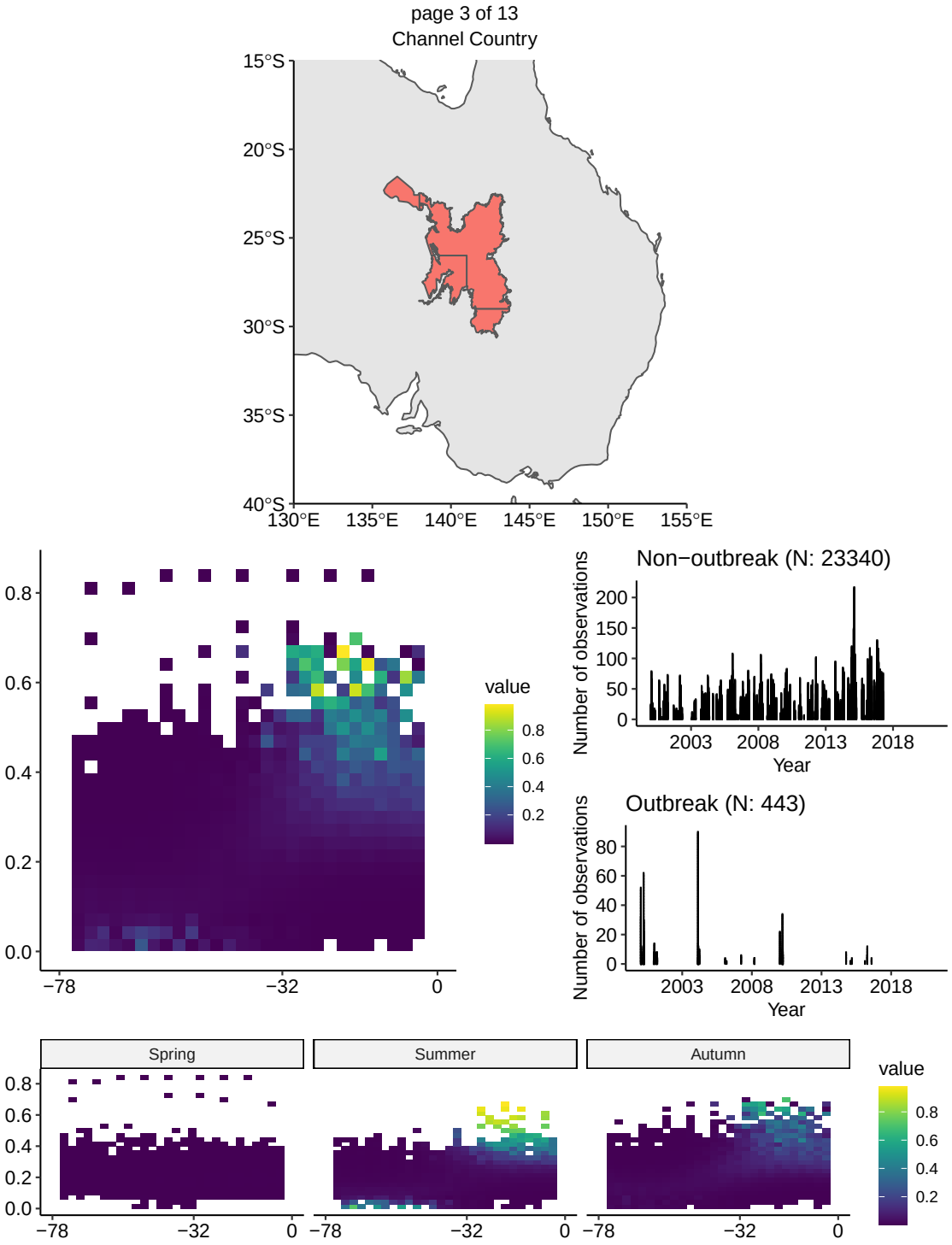
Mulga Lands


15°S
20°S
25°S
30°S
35°S
40°S
130°E
135°E
140°E
145°E
150°E
155°E
0.6
0.4
0.2
0.0
−78
−32
0
value
0.6
0.4
0.2
Non−outbreak (N: 21409)
Number of observations
200
150
100
50
0
2003
2008
2013
2018
Year
Outbreak (N: 442)
Number of observations
80
60
40
20
0
2003
2008
2013
2018
Year
Spring
Summer
Autumn
value
0.6
0.4
0.2

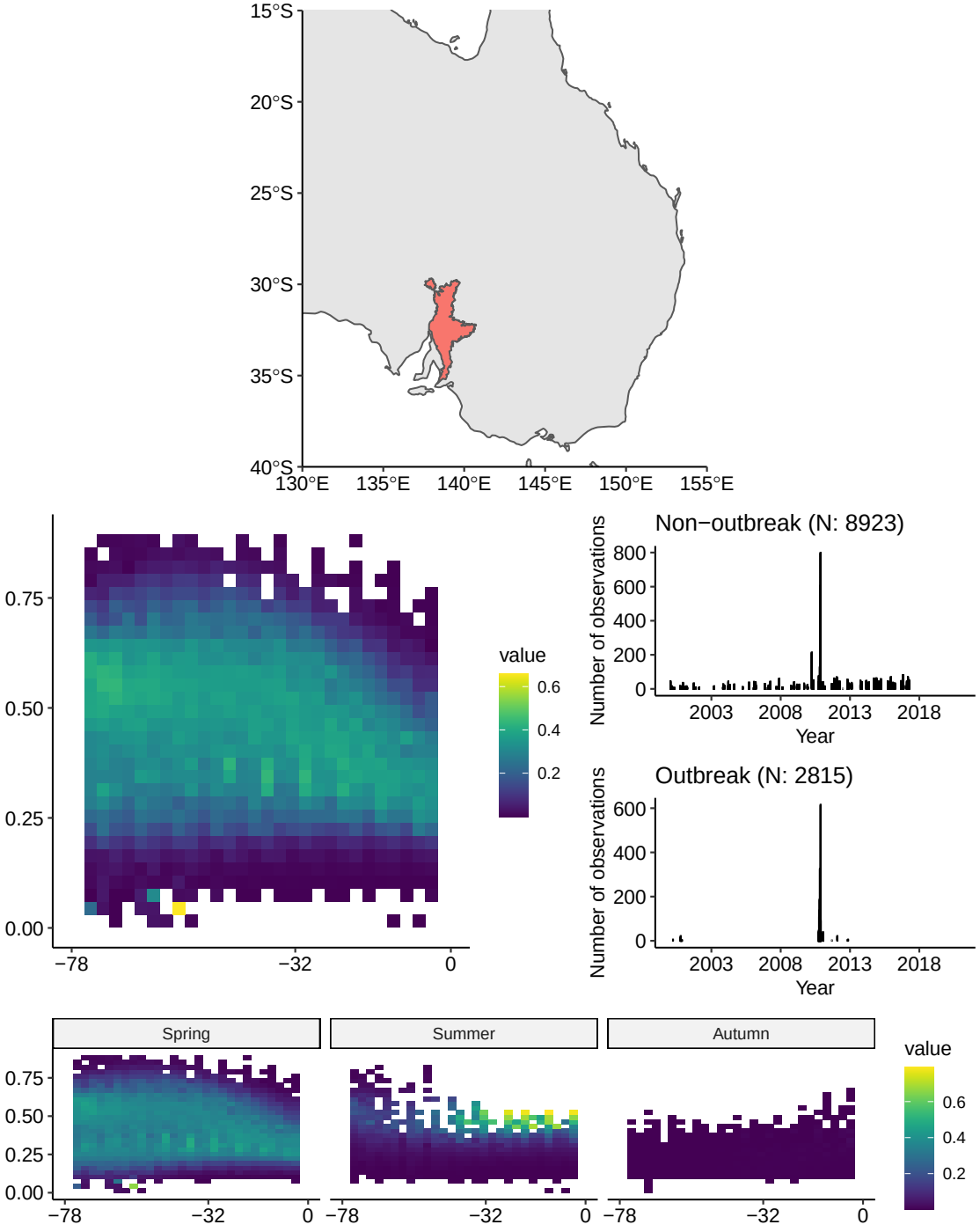
Mitchell Grass Downs



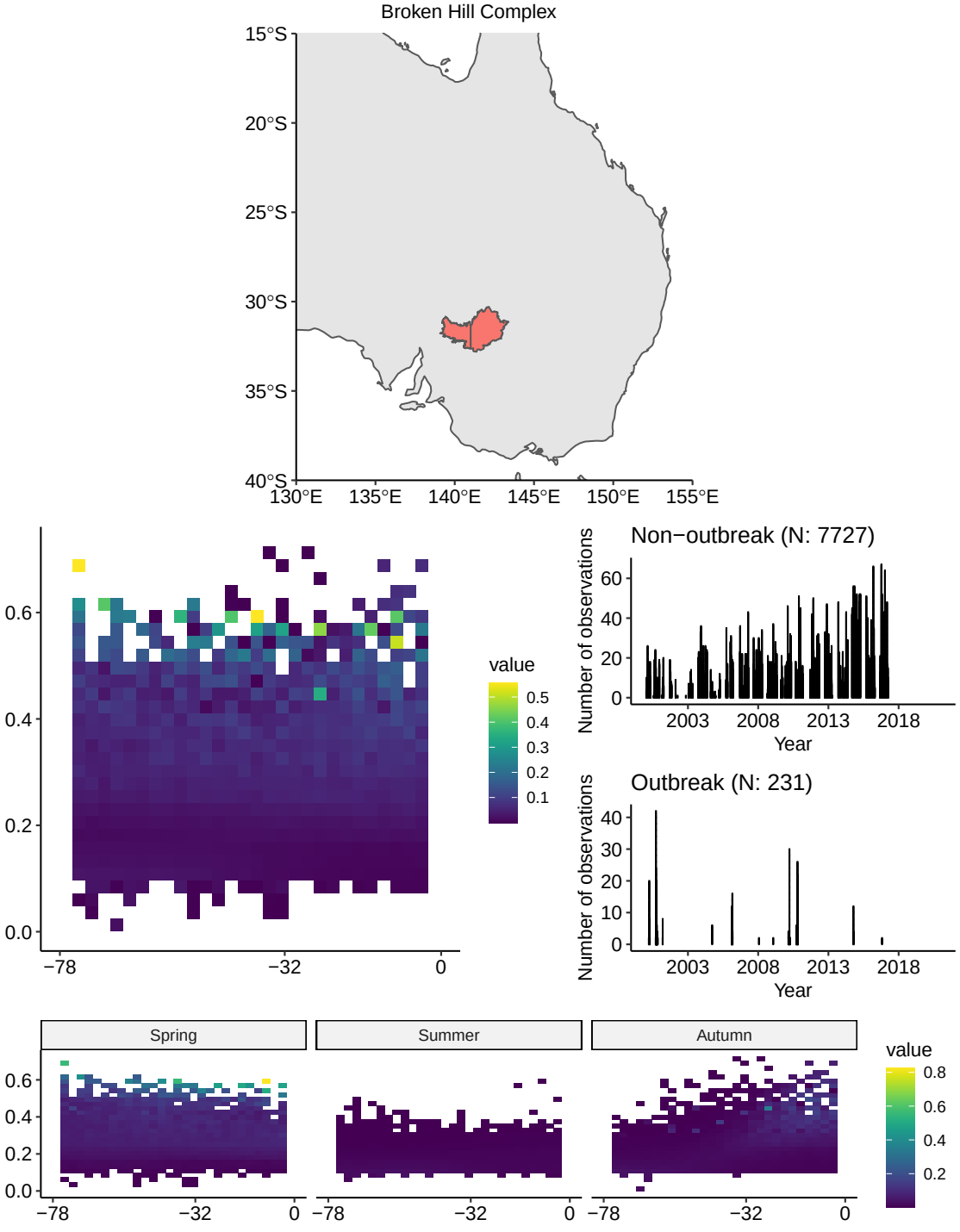



Channel Country
15°S
20°S
25°S
30°S
35°S
40°S
130°E
135°E
140°E
145°E
150°E
155°E
value
0.8
0.6
0.4
0.2
−78
−32
0
Non−outbreak (N: 23340)
Number of observations
200
150
100
50
0
2003
2008
2013
2018
Year
Outbreak (N: 443)
80
60
40
20
Spring
Summer
Autumn

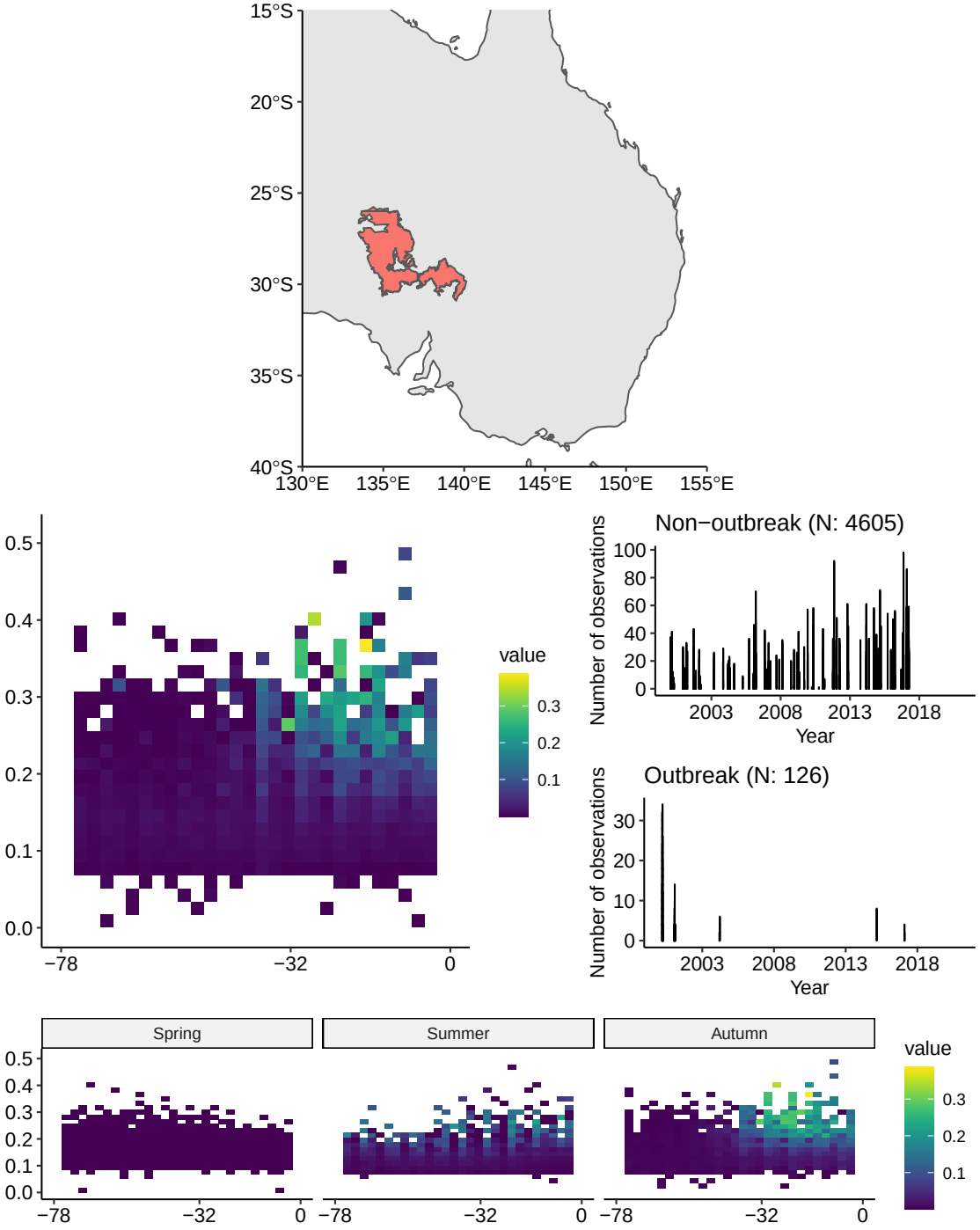
Flinders Lofty Block



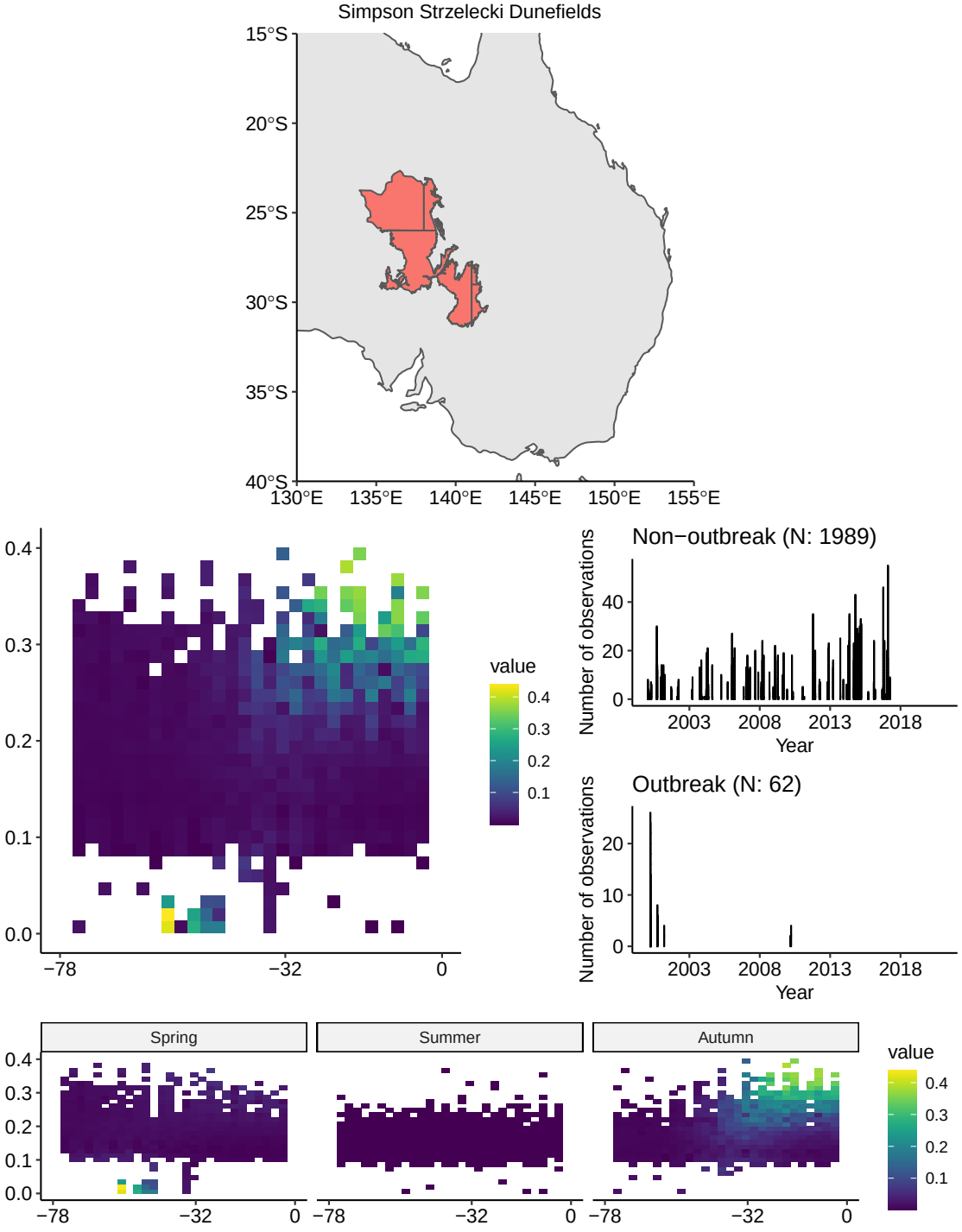
Broken Hill Complex



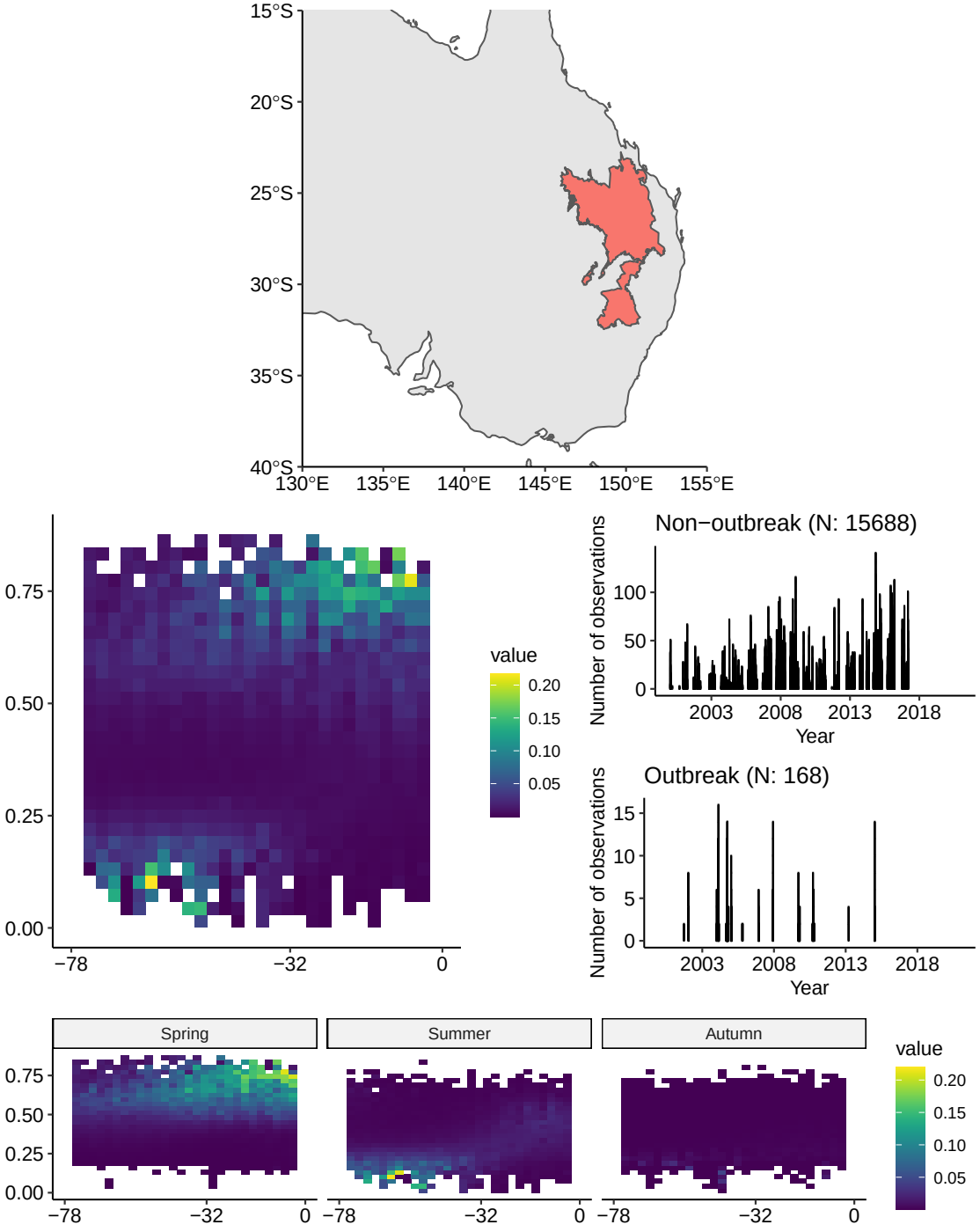
Stony Plains



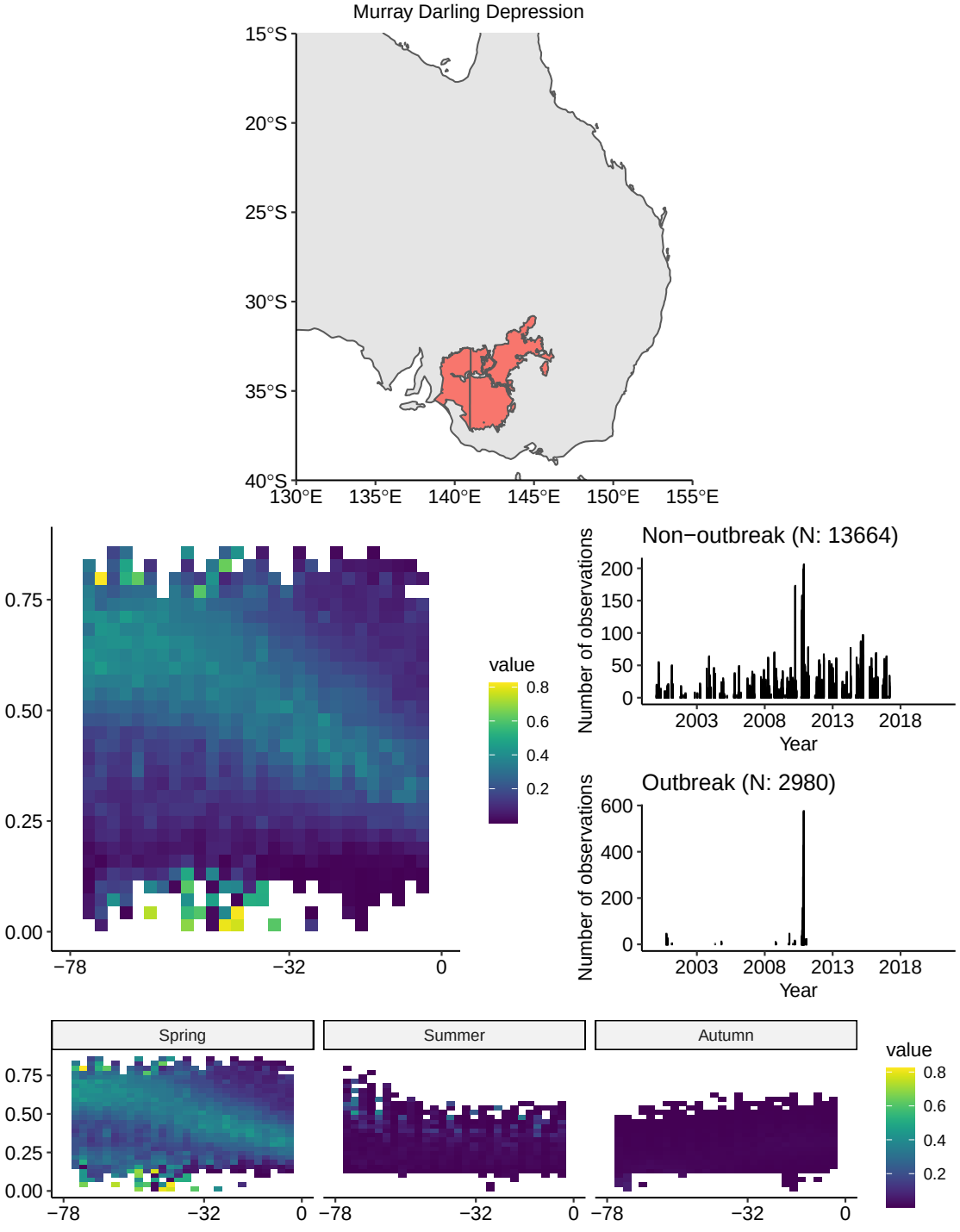
Simpson Strzelecki Dunefields



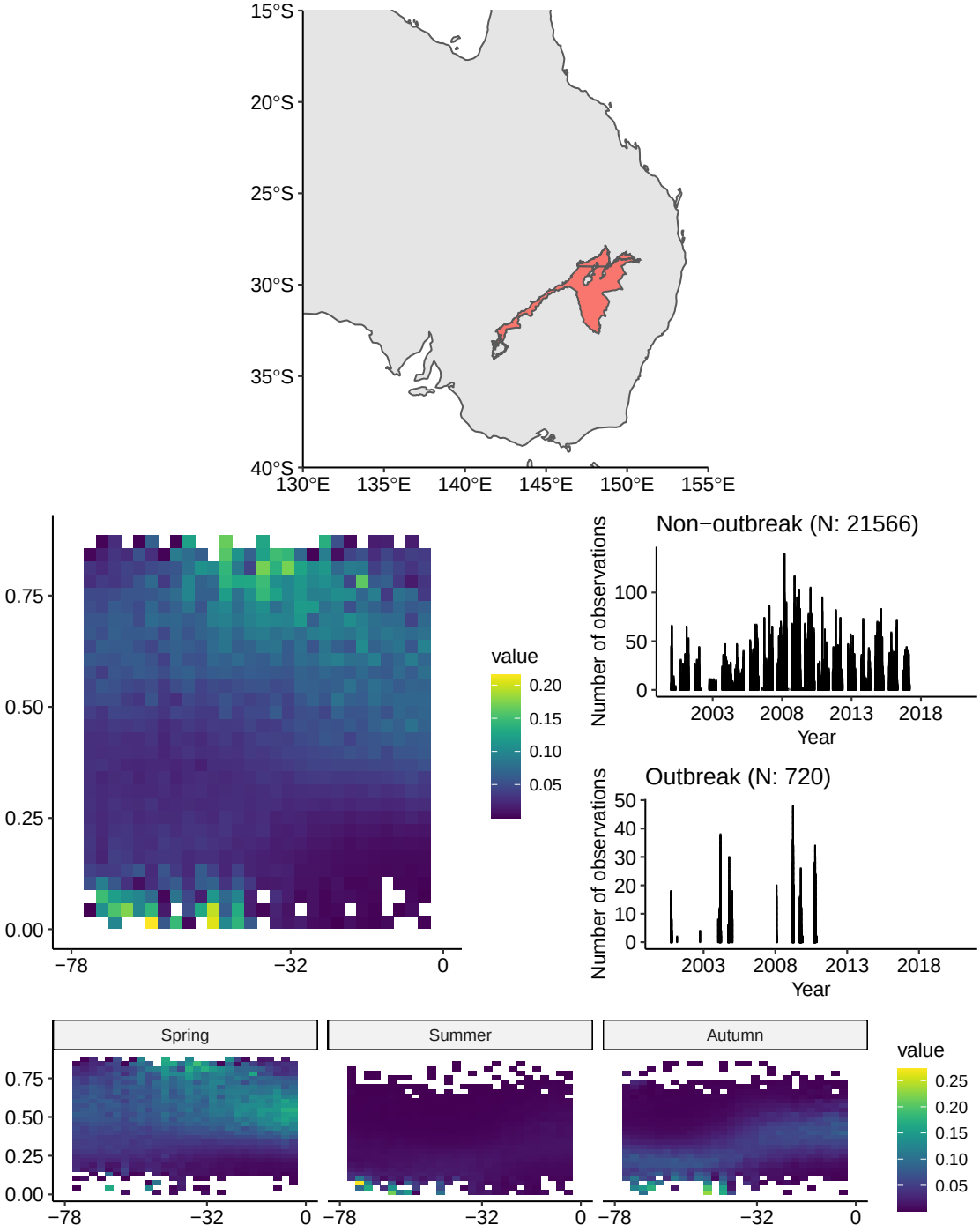
Brigalow Belt South

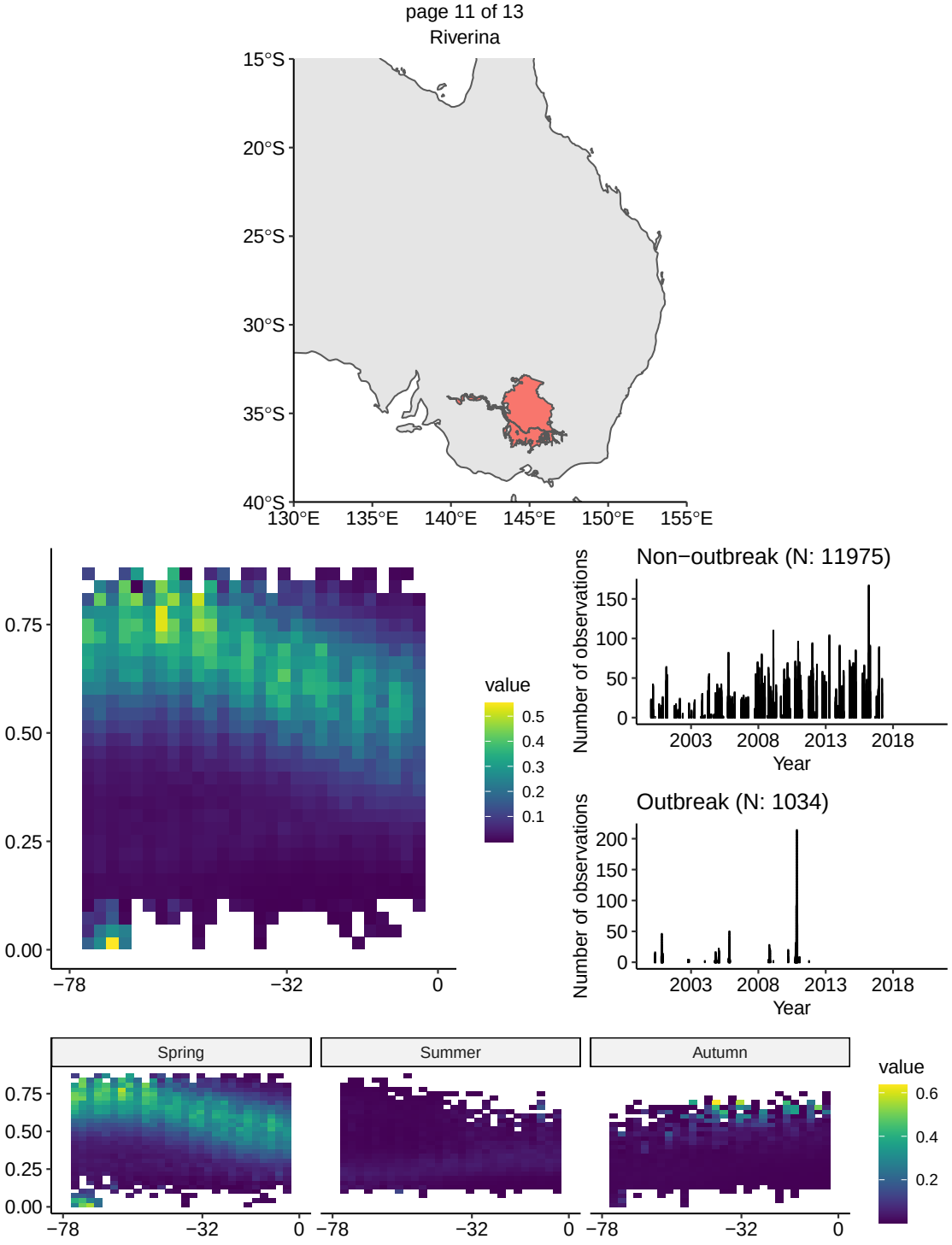


Murray Darling Depression

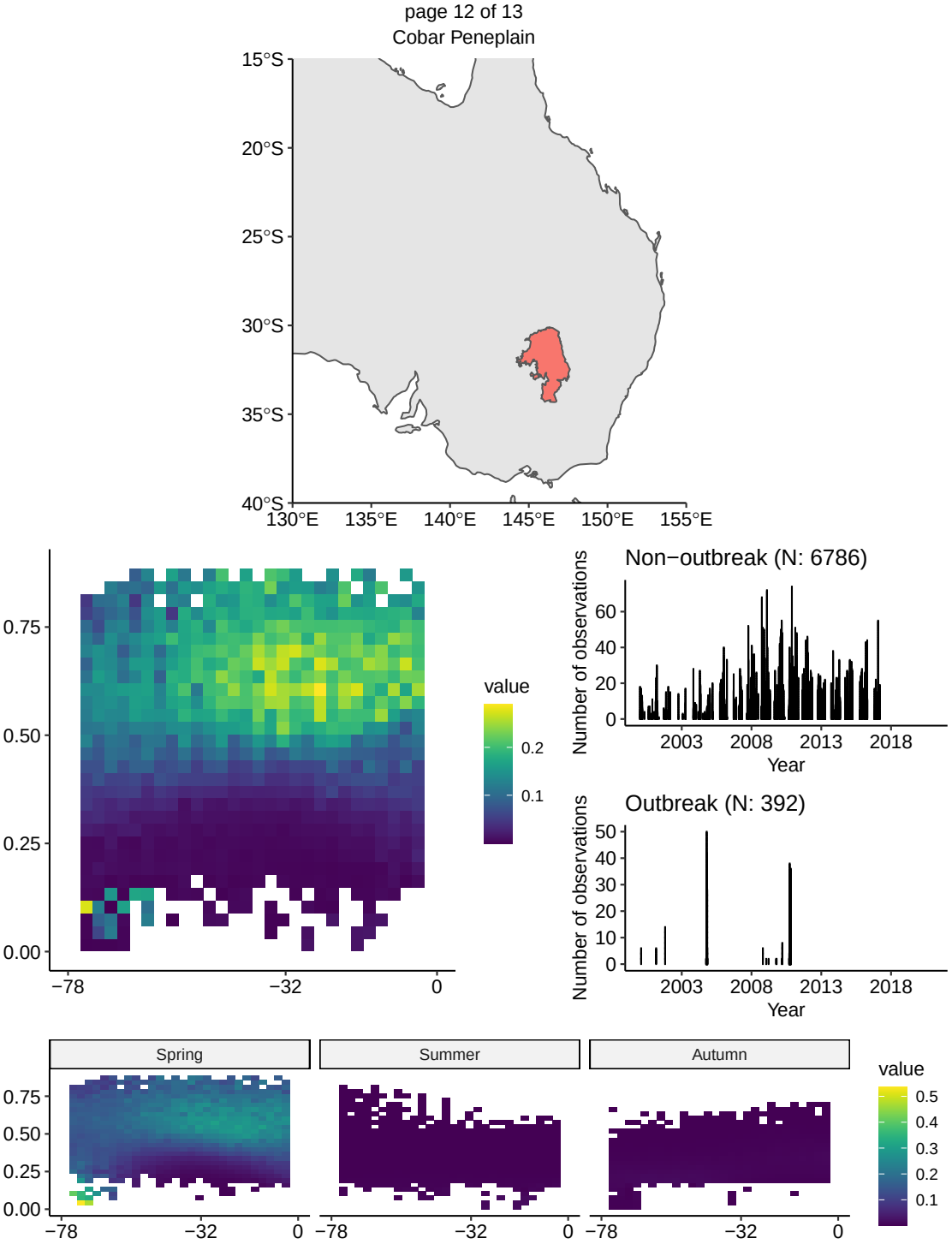


Darling Riverine Plains

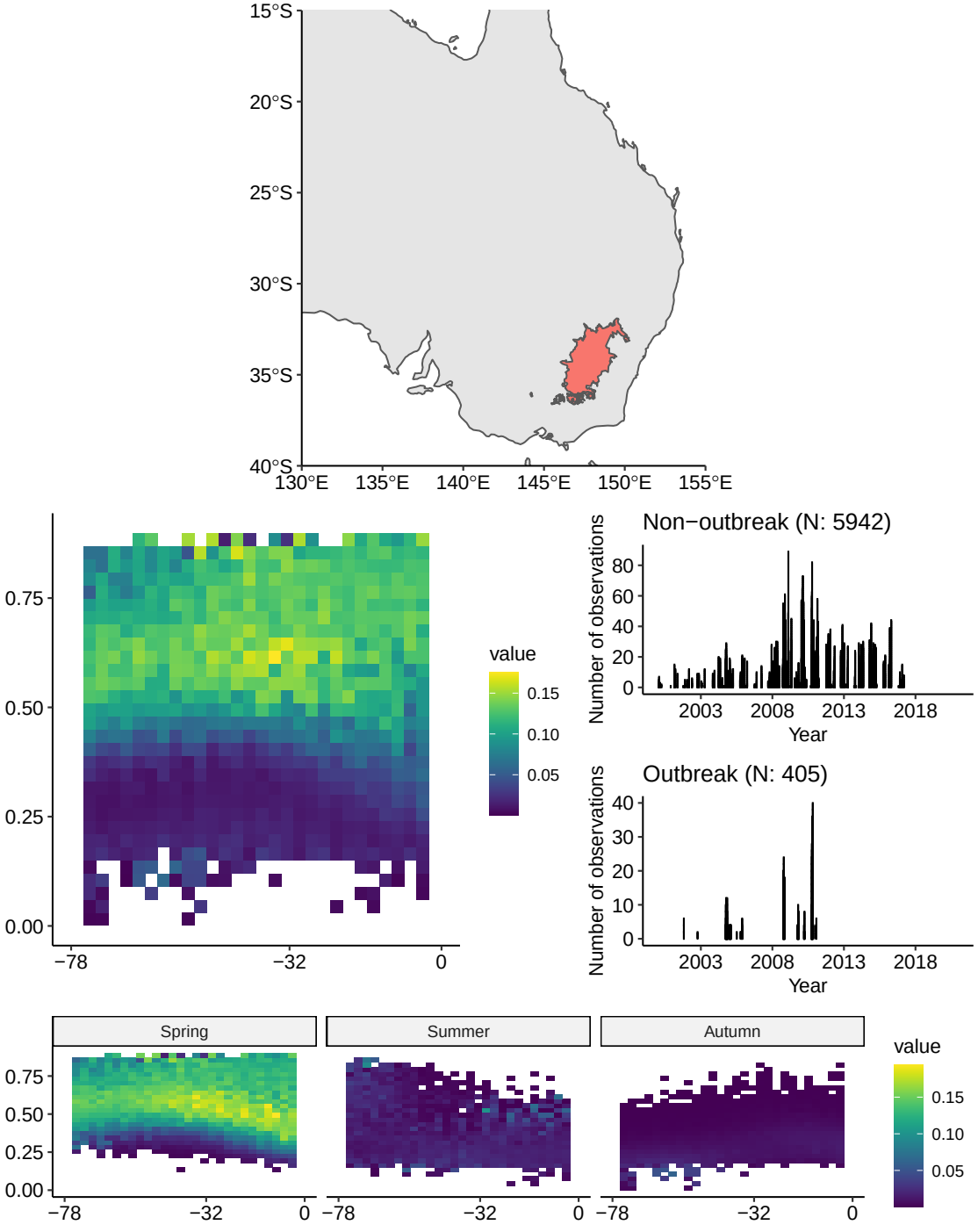



Riverina
15°S
20°S
25°S
30°S
35°S
40°S
130°E
135°E
140°E
145°E
150°E
155°E
0.75
0.50
0.25
0.00
−78
−32
0
value
0.5
0.4
0.3
0.2
0.1
Non−outbreak (N: 11975)
Number of observations
150
100
50
0
2003
2008
2013
2018
Year
Outbreak (N: 1034)
200
150
100
50
0
Spring
Summer
Autumn
value
0.6
0.4
0.2

Cobar Peneplain



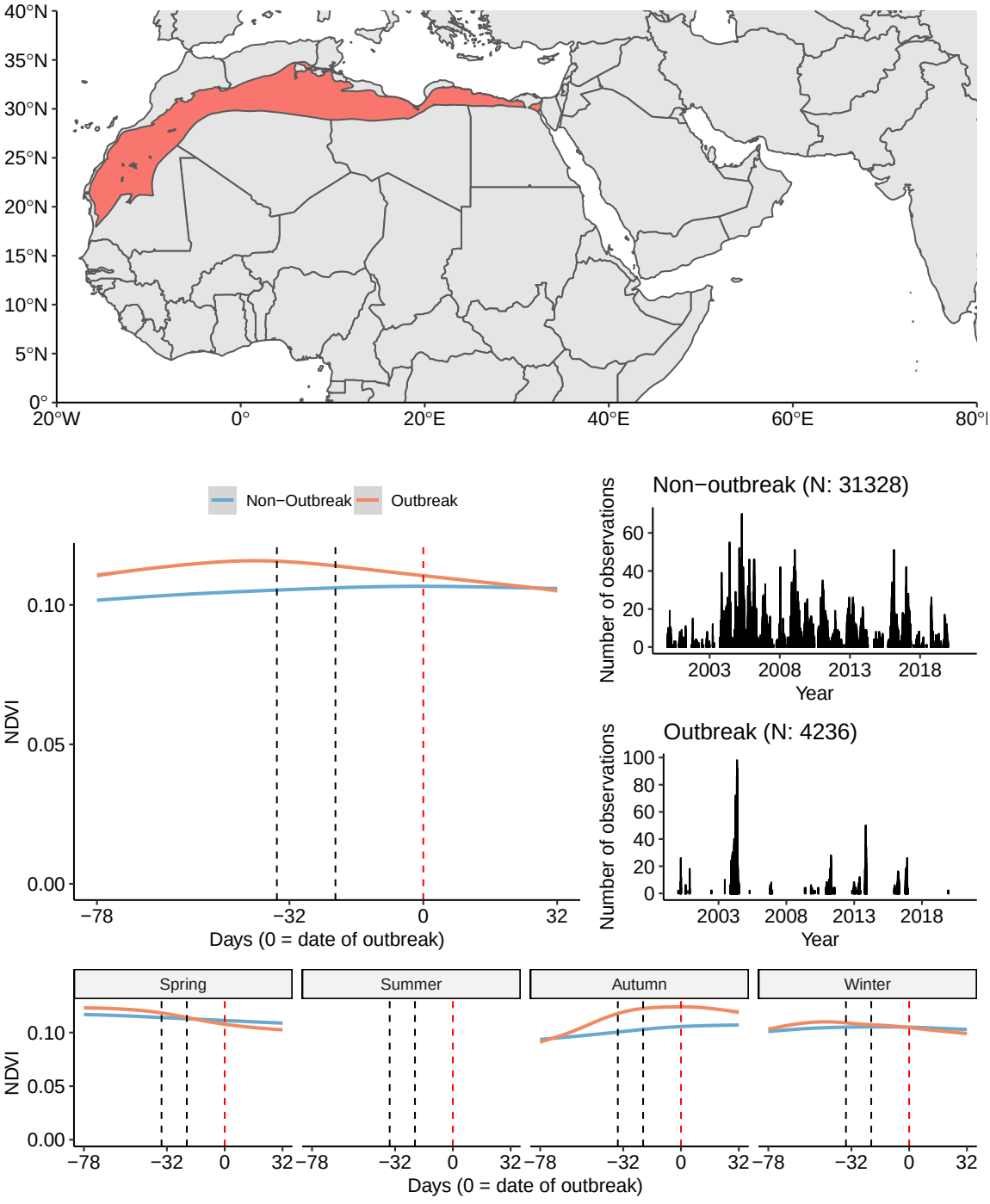
NSW South Western Slopes



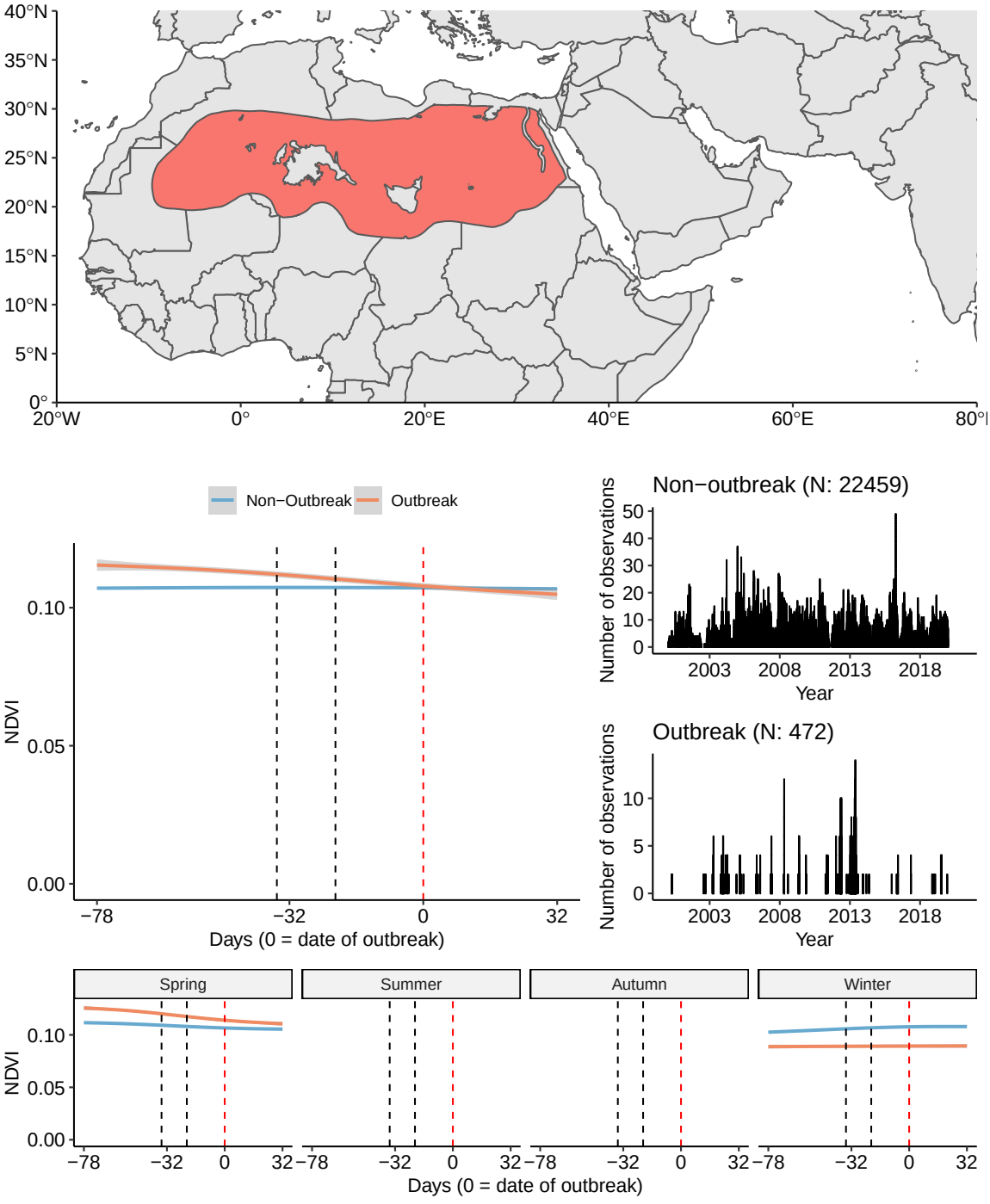
APPENDIX H

SUPPLEMENTARY FIGURE 13 FOR CHAPTER 5

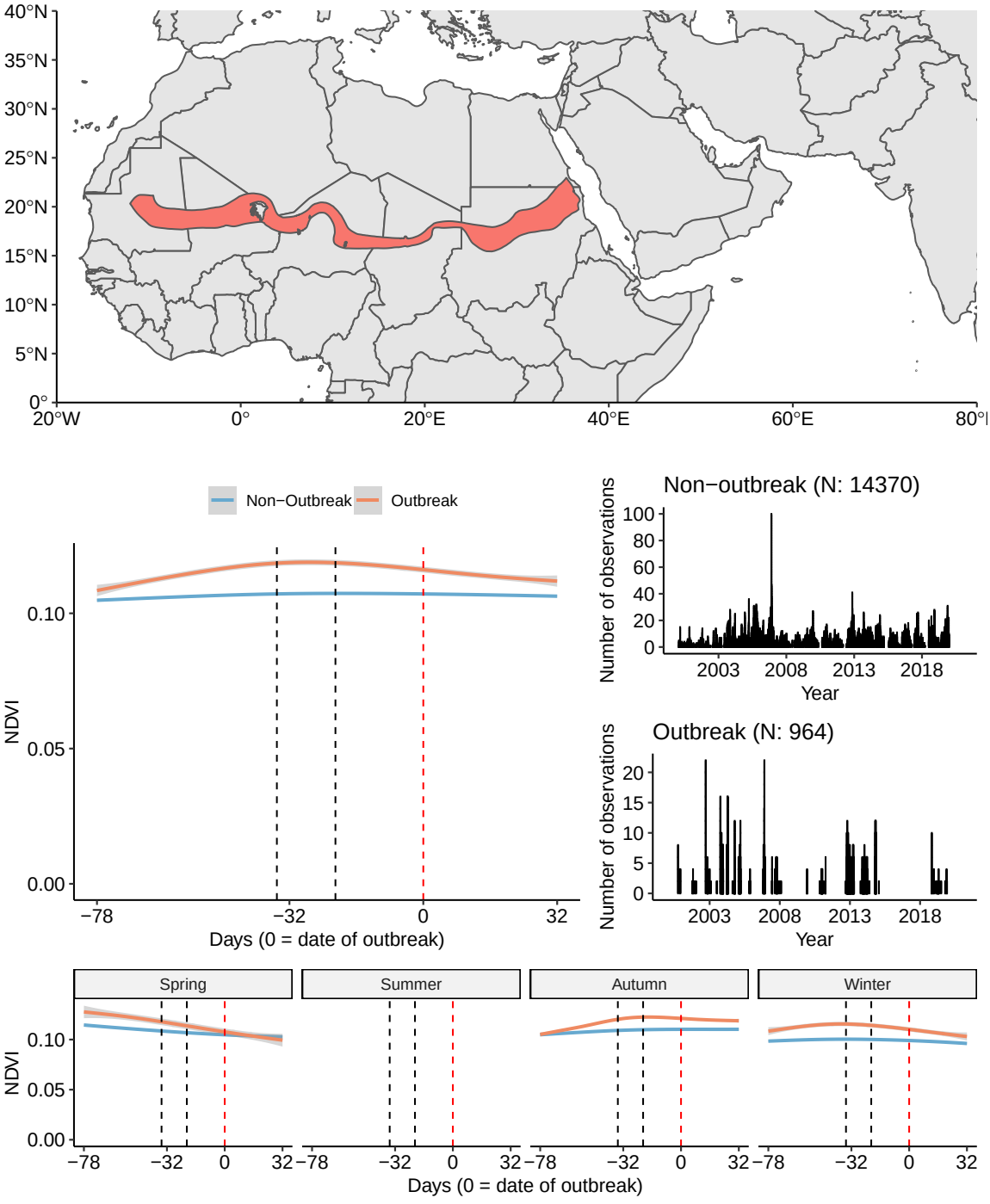
North Saharan steppe and woodlands



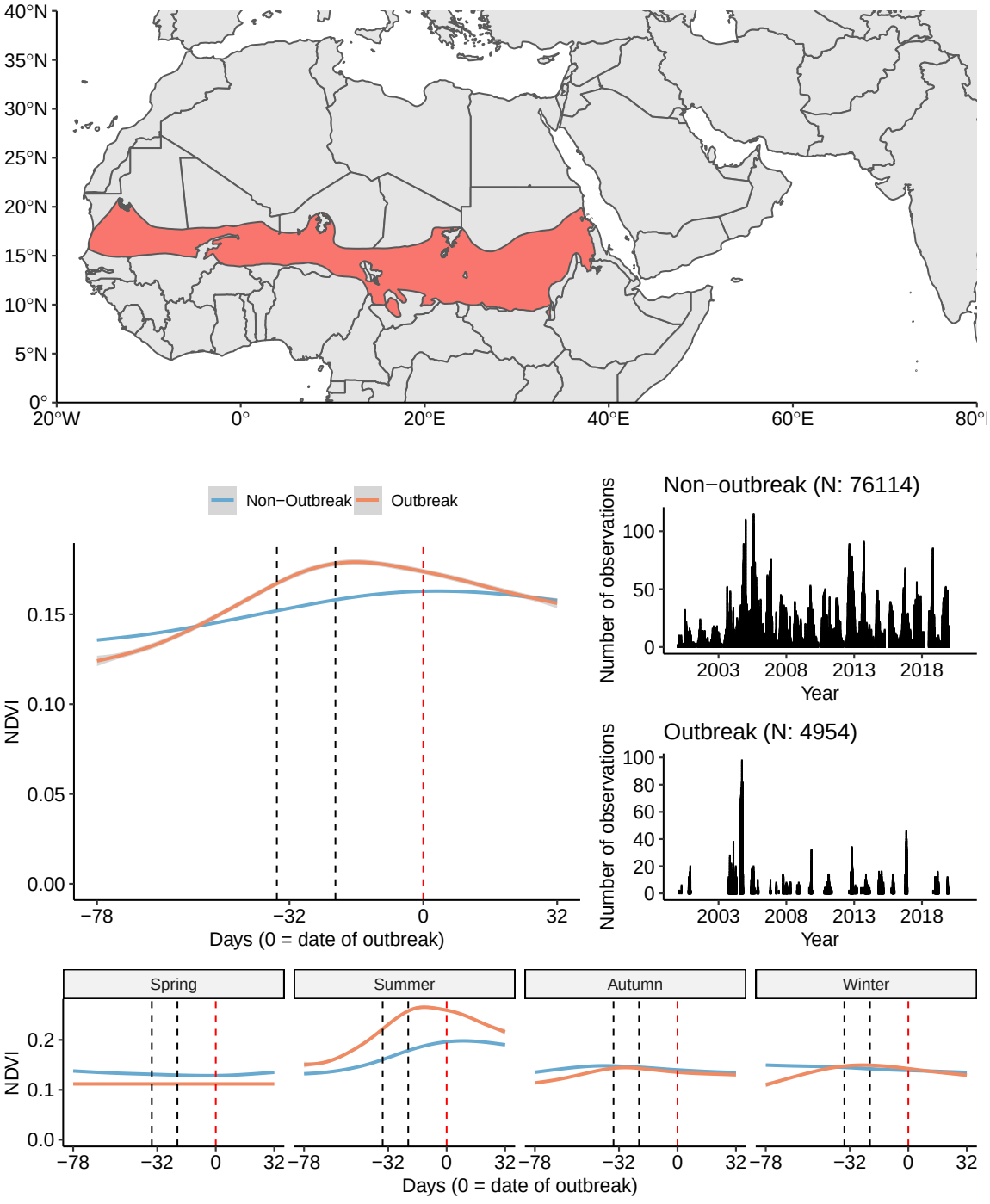
Sahara desert

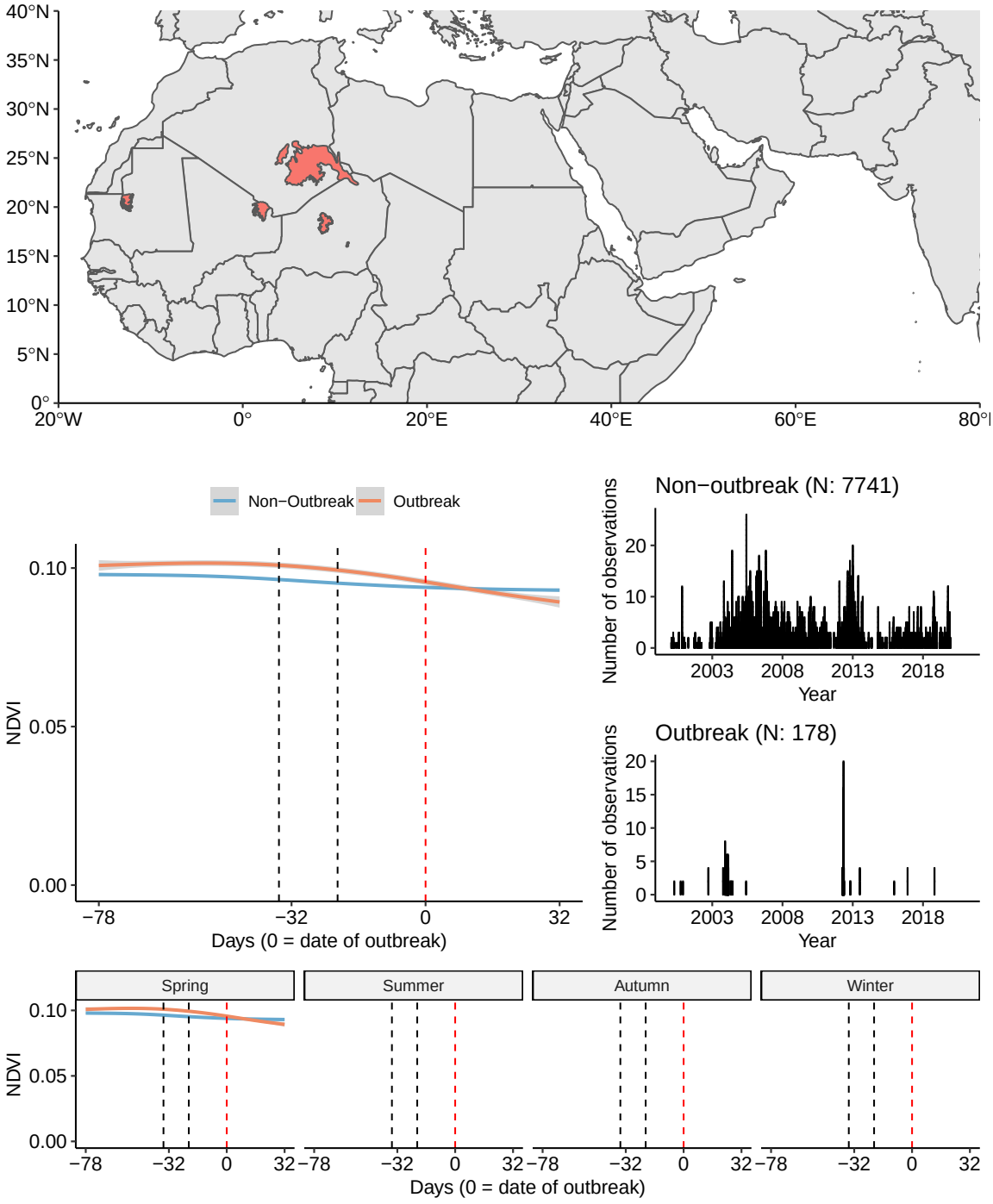


South Saharan steppe and woodlands

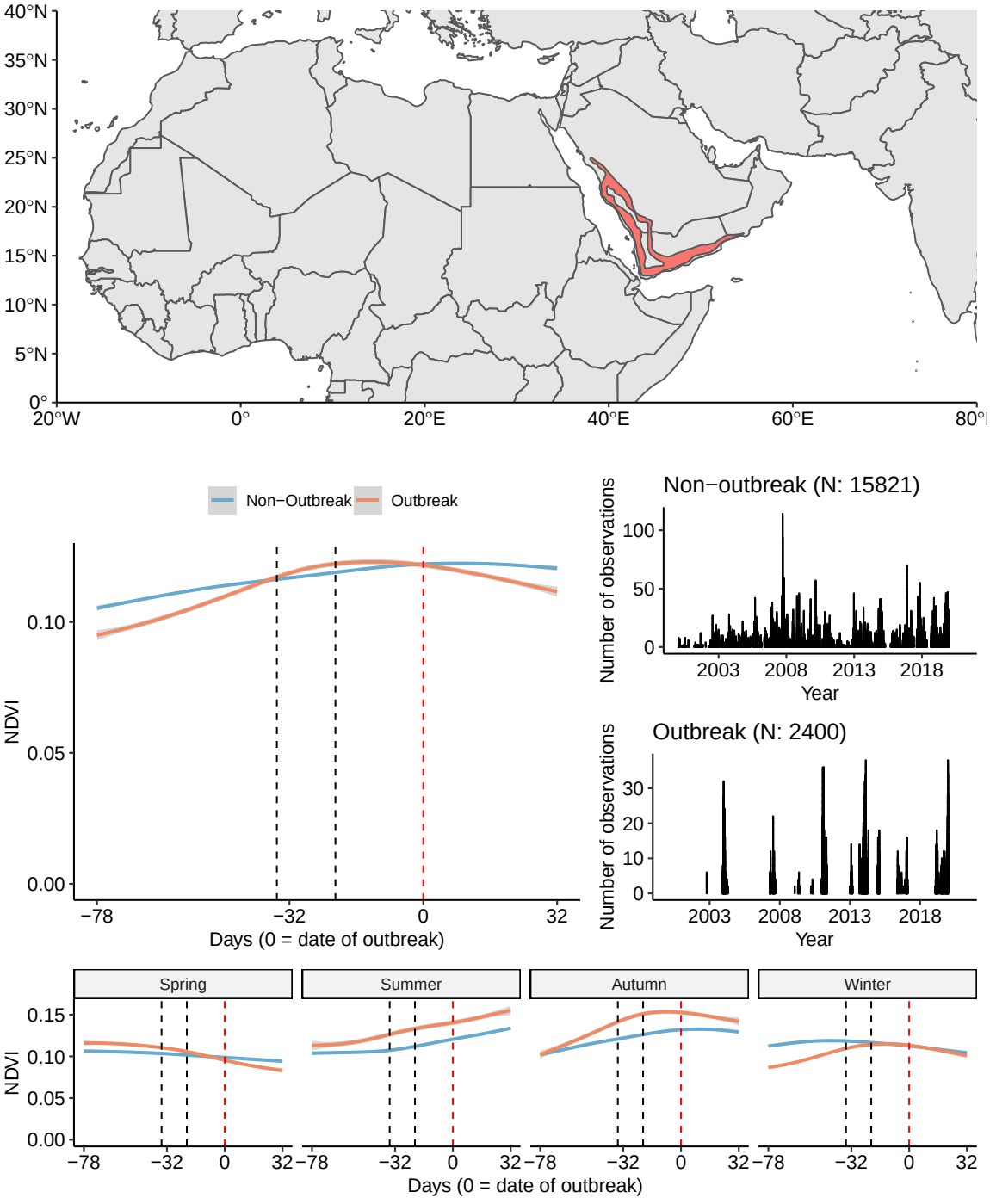


Sahelian Acacia savanna

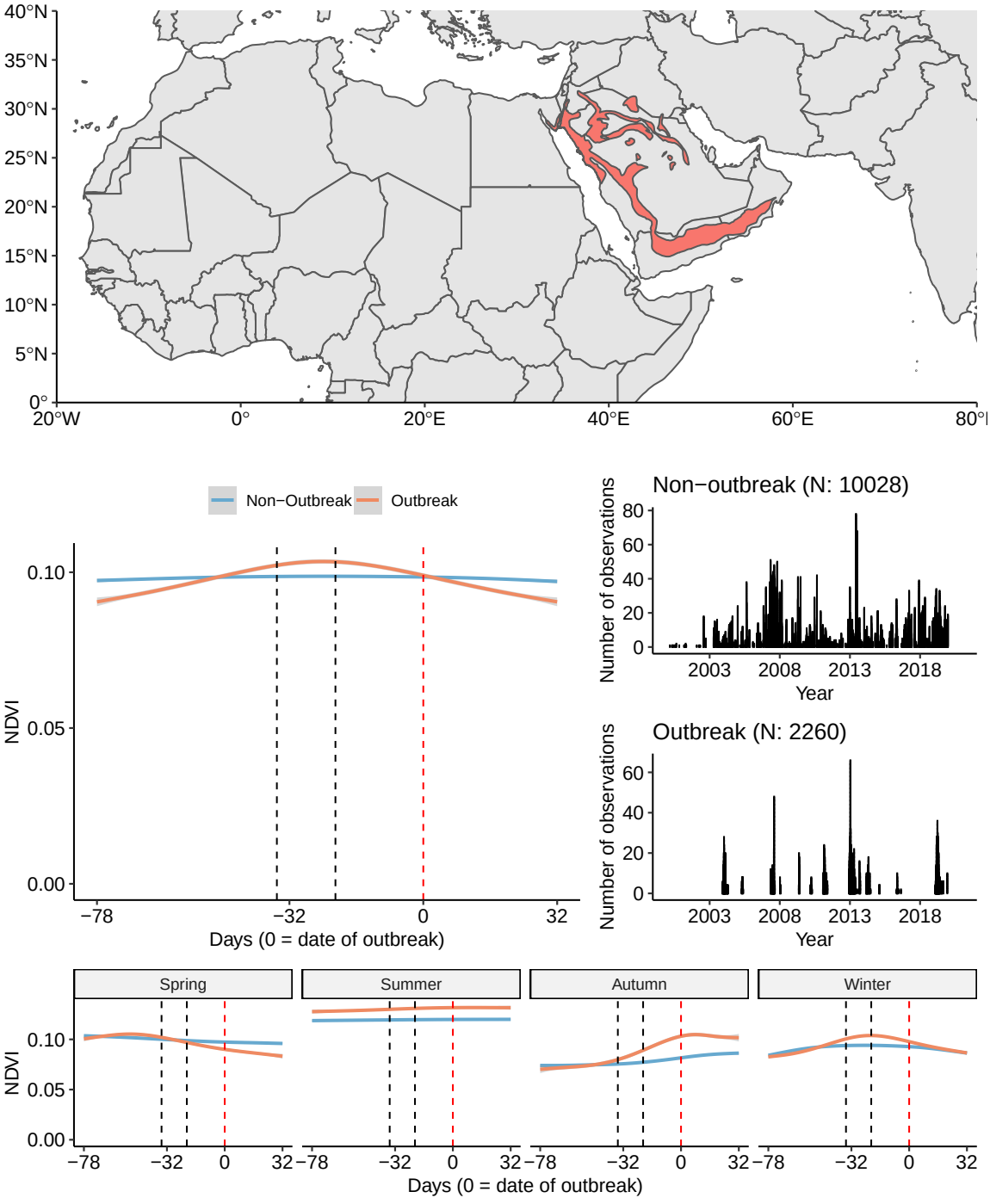


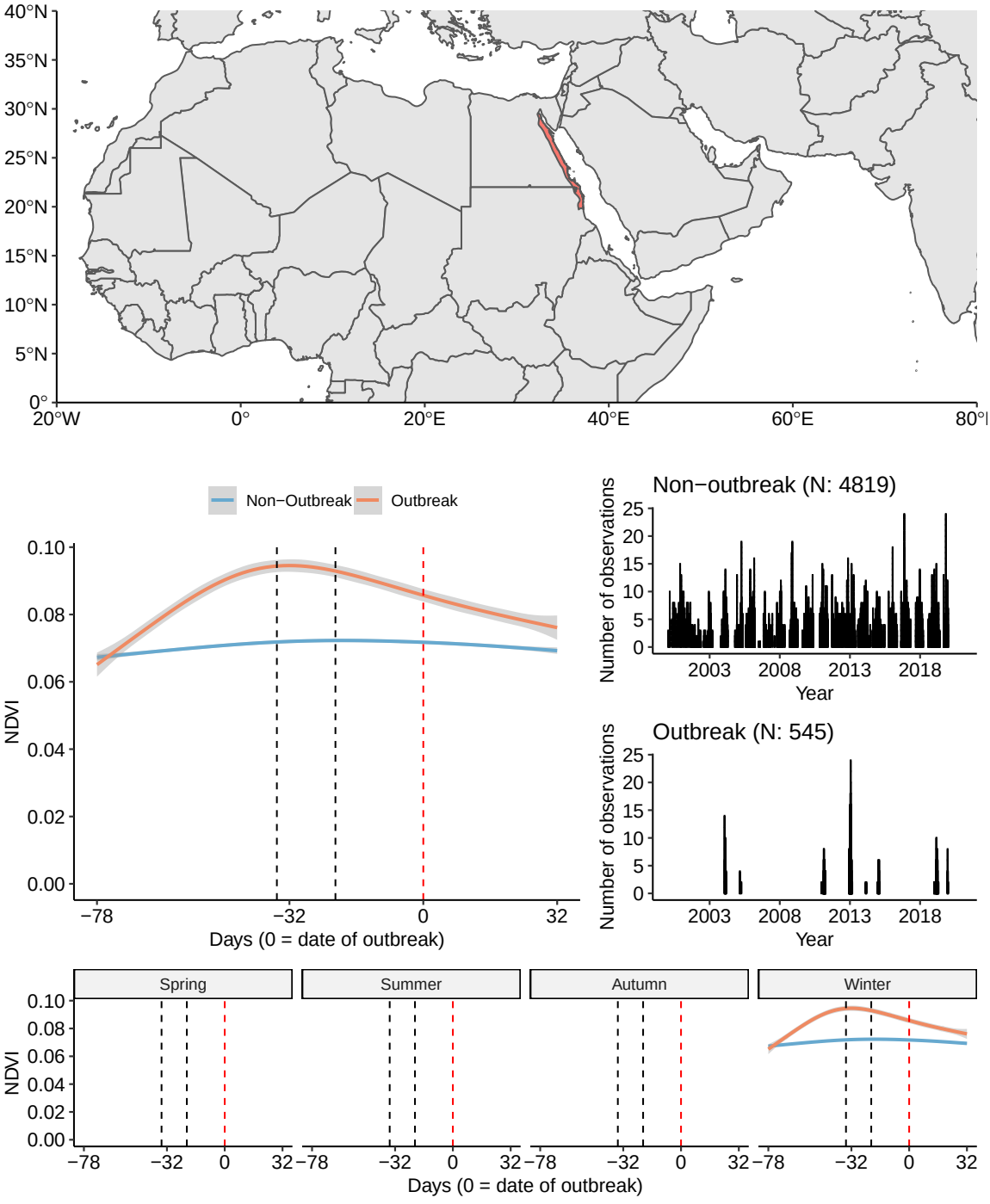

40°N
35°N
30°N
25°N
20°N
15°N
10°N
5°N
0°
20°W
0°
20°E
40°E
60°E
Non−Outbreak
Outbreak
NDVI
0.10
0.05
0.00
−78
−32
0
32
Days (0 = date of outbreak)
Non−outbreak (N: 7741)
Number of observations
20
10
0
2003
2008
2013
2018
Year
Outbreak (N: 178)
15
5
Spring
Summer
Autumn
Winter

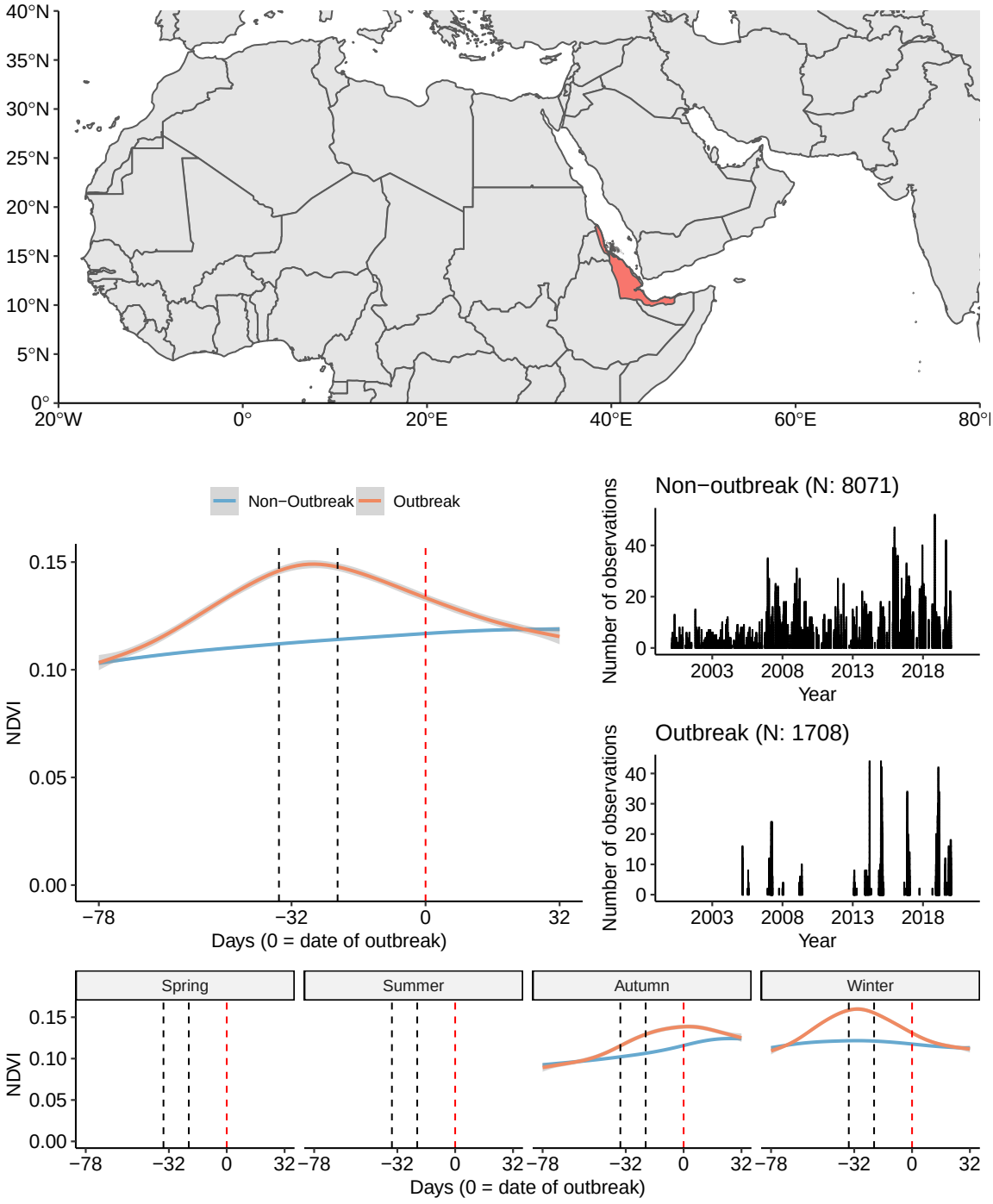
Southwestern Arabian foothills savanna



Red Sea Nubo−Sindian tropical desert and semi−desert




40°N
35°N
30°N
25°N
20°N
15°N
10°N
5°N
0°
20°W
0°
20°E
40°E
60°E
Non−Outbreak
Outbreak
NDVI
0.10
0.08
0.06
0.04
0.02
0.00
−78
−32
0
32
Days (0 = date of outbreak)
Non−outbreak (N: 4819)
Number of observations
25
20
15
10
5
0
2003
2008
2013
2018
Year
Outbreak (N: 545)
Spring
Summer
Autumn
Winter


40°N
35°N
30°N
25°N
20°N
15°N
10°N
5°N
0°
20°W
0°
20°E
40°E
60°E
80°
Non−Outbreak
Outbreak
NDVI
0.15
0.10
0.05
0.00
−78
−32
0
32
Days (0 = date of outbreak)
Non−outbreak (N: 8071)
Number of observations
40
20
0
2003
2008
2013
2018
Year
Outbreak (N: 1708)
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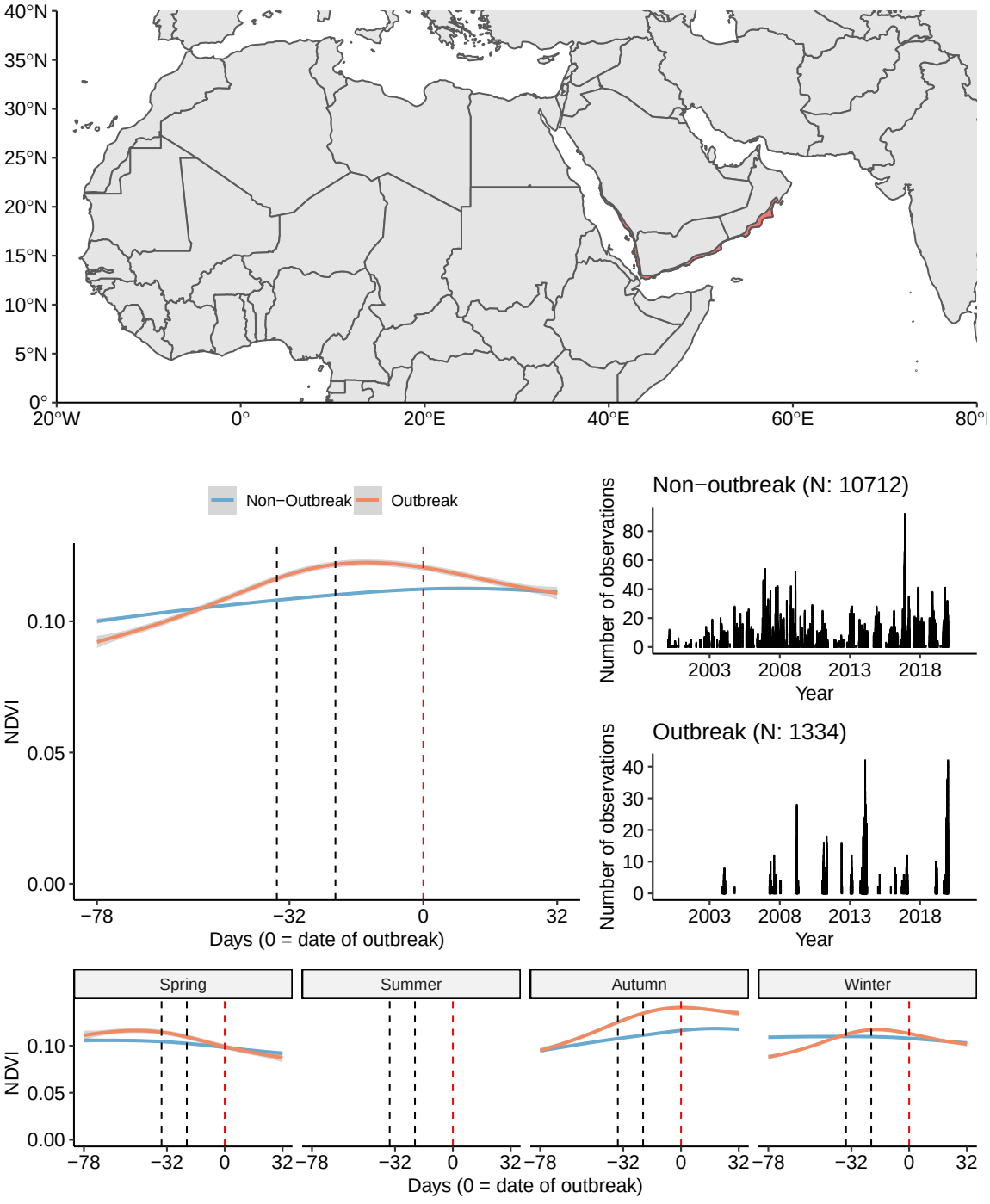
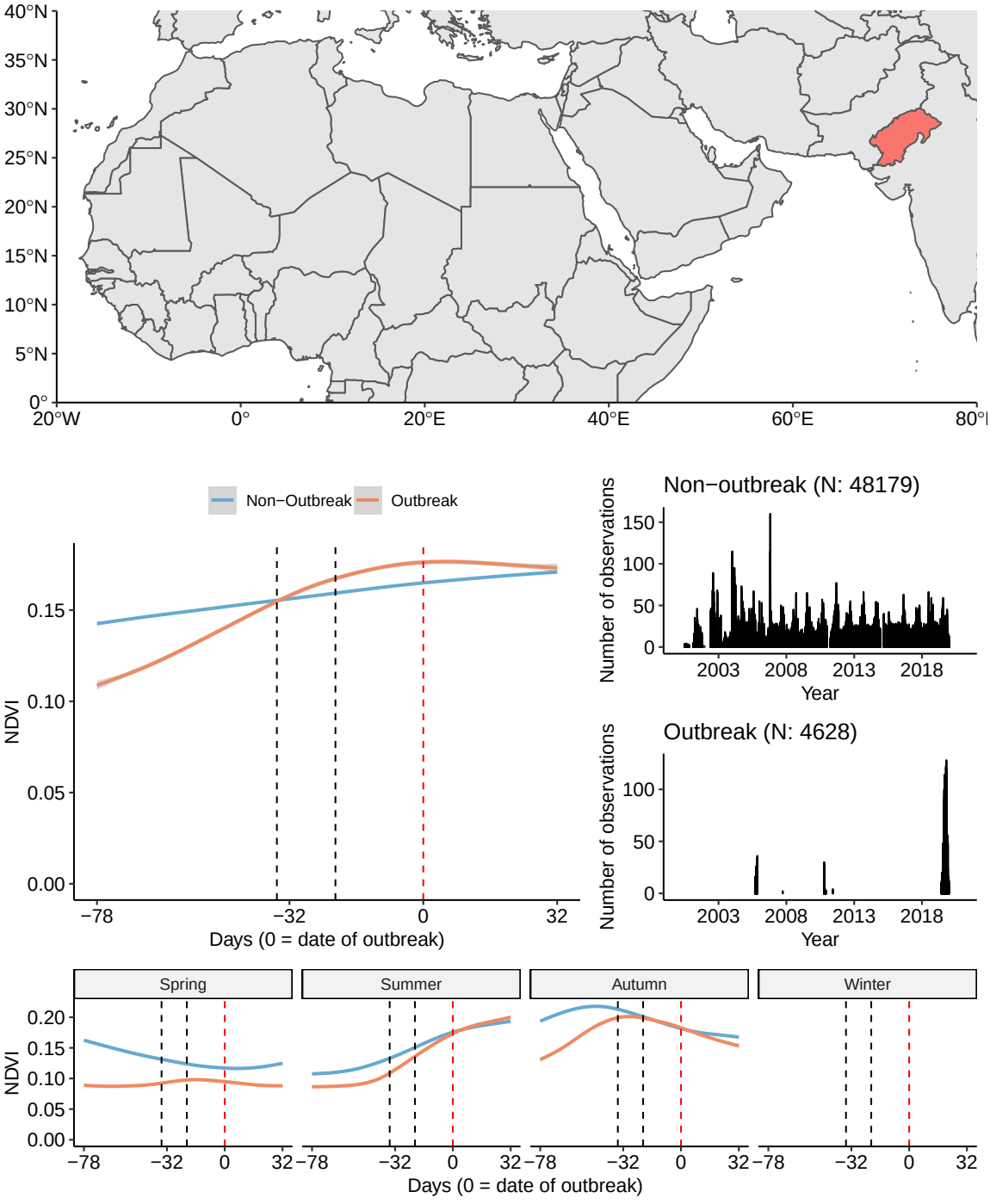
30
20
10
0
Spring
Summer
Autumn
Winter


40°N
35°N
30°N
25°N
20°N
15°N
10°N
5°N
0°
20°W
0°
20°E
40°E
60°E
80°
Non−Outbreak
Outbreak
NDVI
0.10
0.05
0.00
−78
−32
0
32
Days (0 = date of outbreak)
Non−outbreak (N: 10712)
Number of observations
80
60
40
20
0
2003
2008
2013
2018
Year
Outbreak (N: 1334)
40
30
20
10
0
Spring
Summer
Autumn
Winter

Thar desert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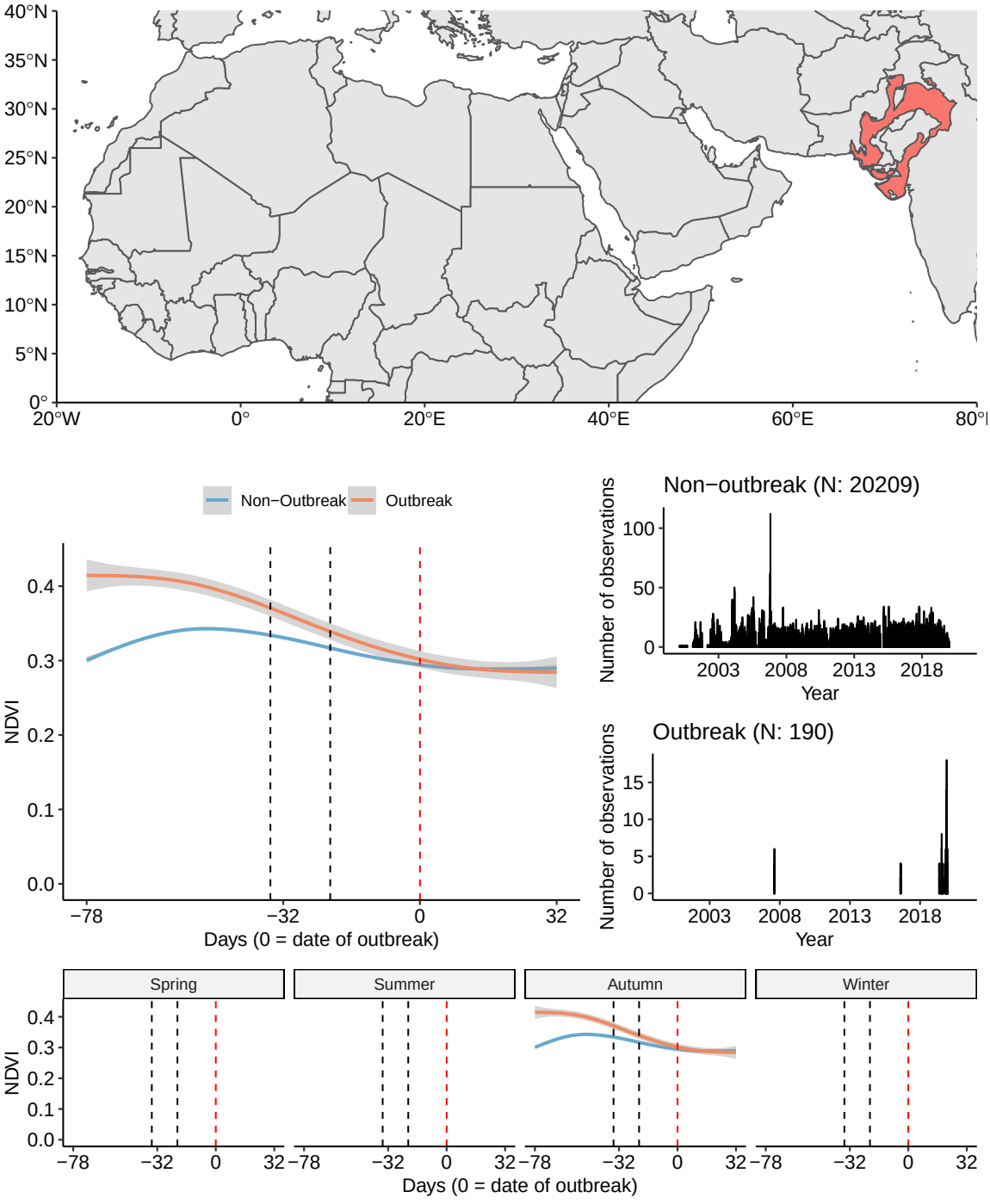
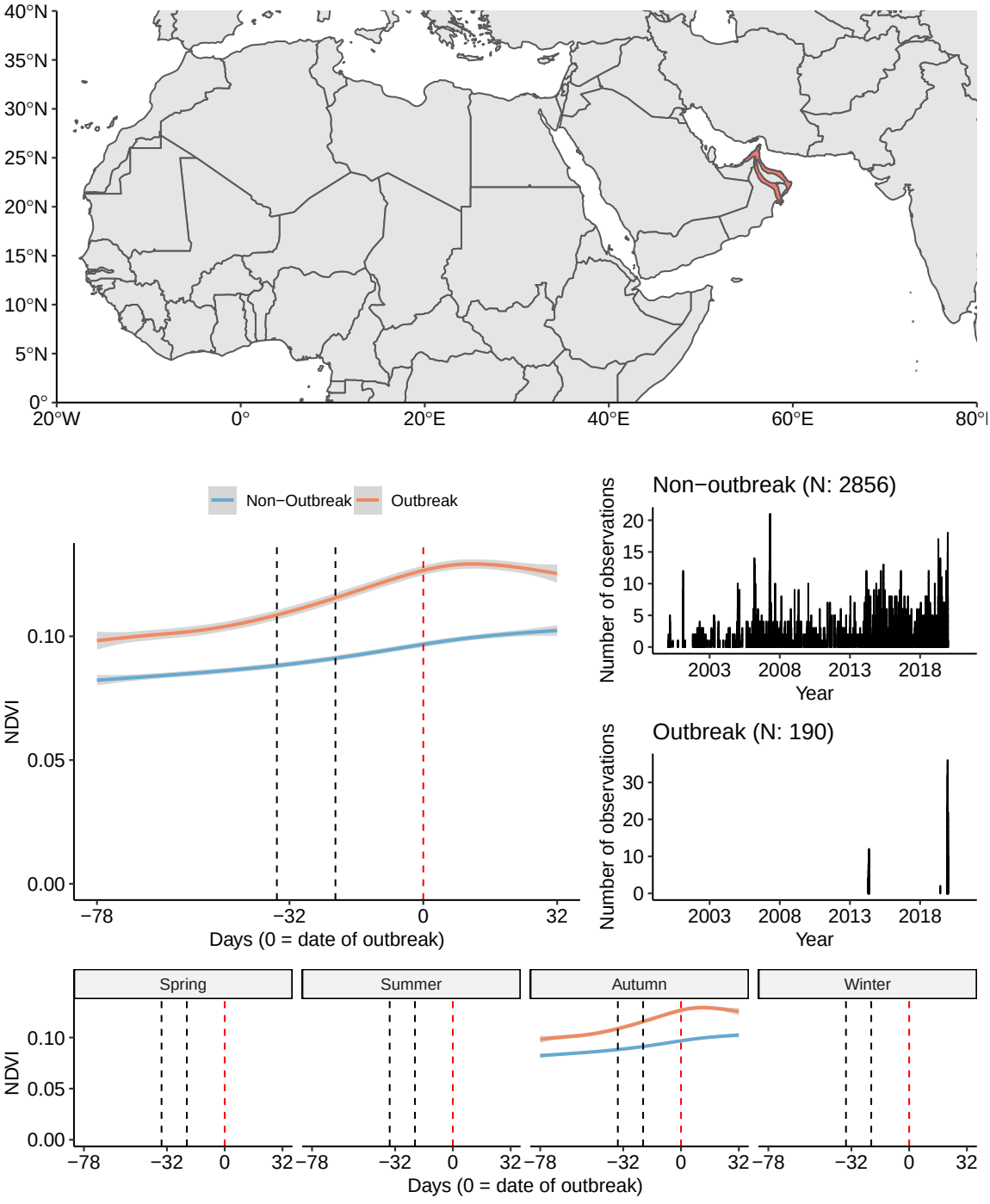
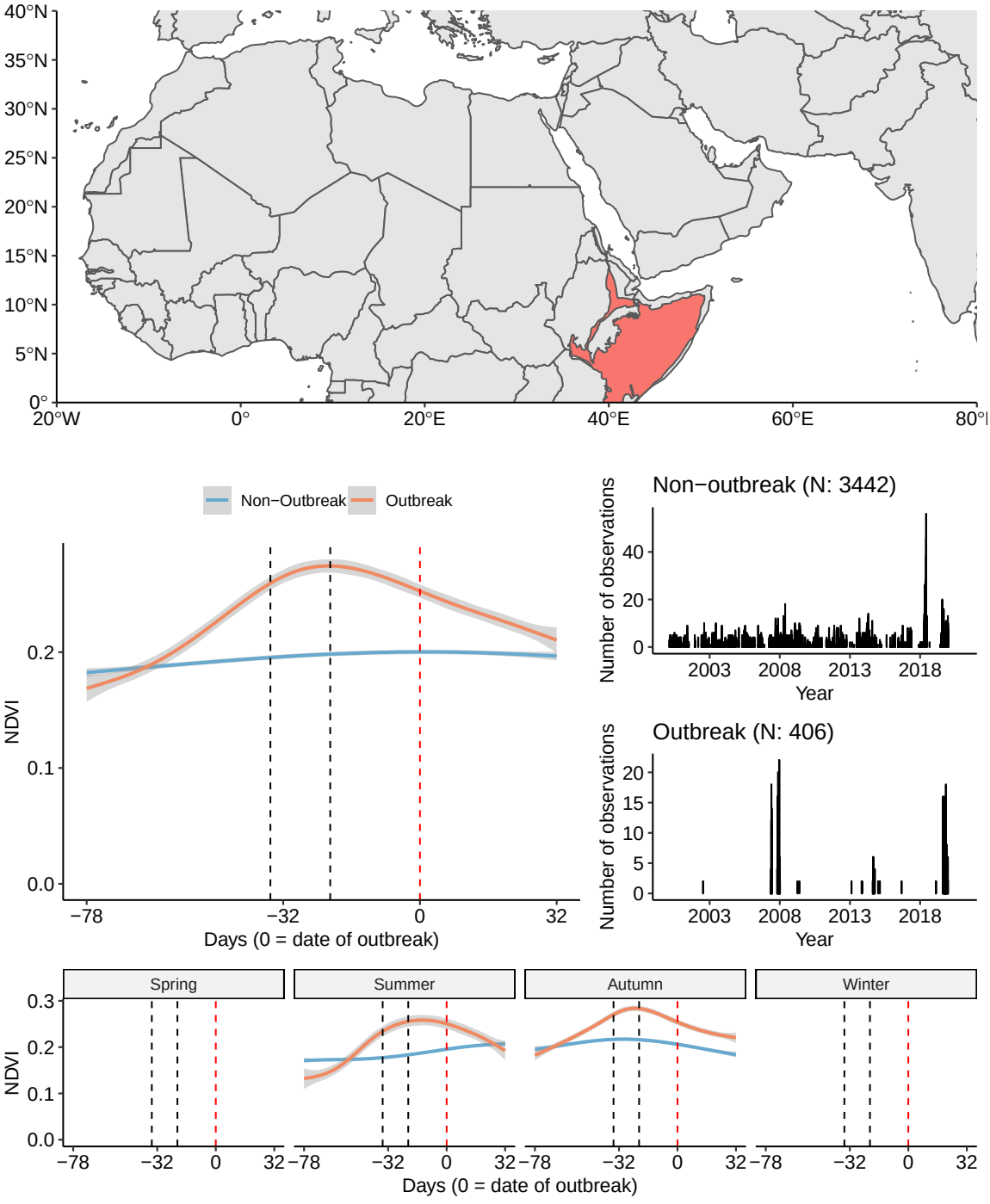
30°N
25°N
20°N
15°N
10°N
5°N
0°
20°W
0°
20°E
40°E
60°E
80°
Non−Outbreak
Outbreak
NDVI
0.15
0.10
0.05
0.00
−78
−32
0
32
Days (0 = date of outbreak)
Non−outbreak (N: 48179)
Number of observations
150
100
50
0
2003
2008
2013
2018
Year
Outbreak (N: 4628)
Number of observations
100
50
0
2003
2008
2013
2018
Year
Spring
Summer
Autumn
Winter
NDVI
0.20
0.15
0.10
0.05
0.00
−78
−32
0
32
Days (0 = date of outbreak)

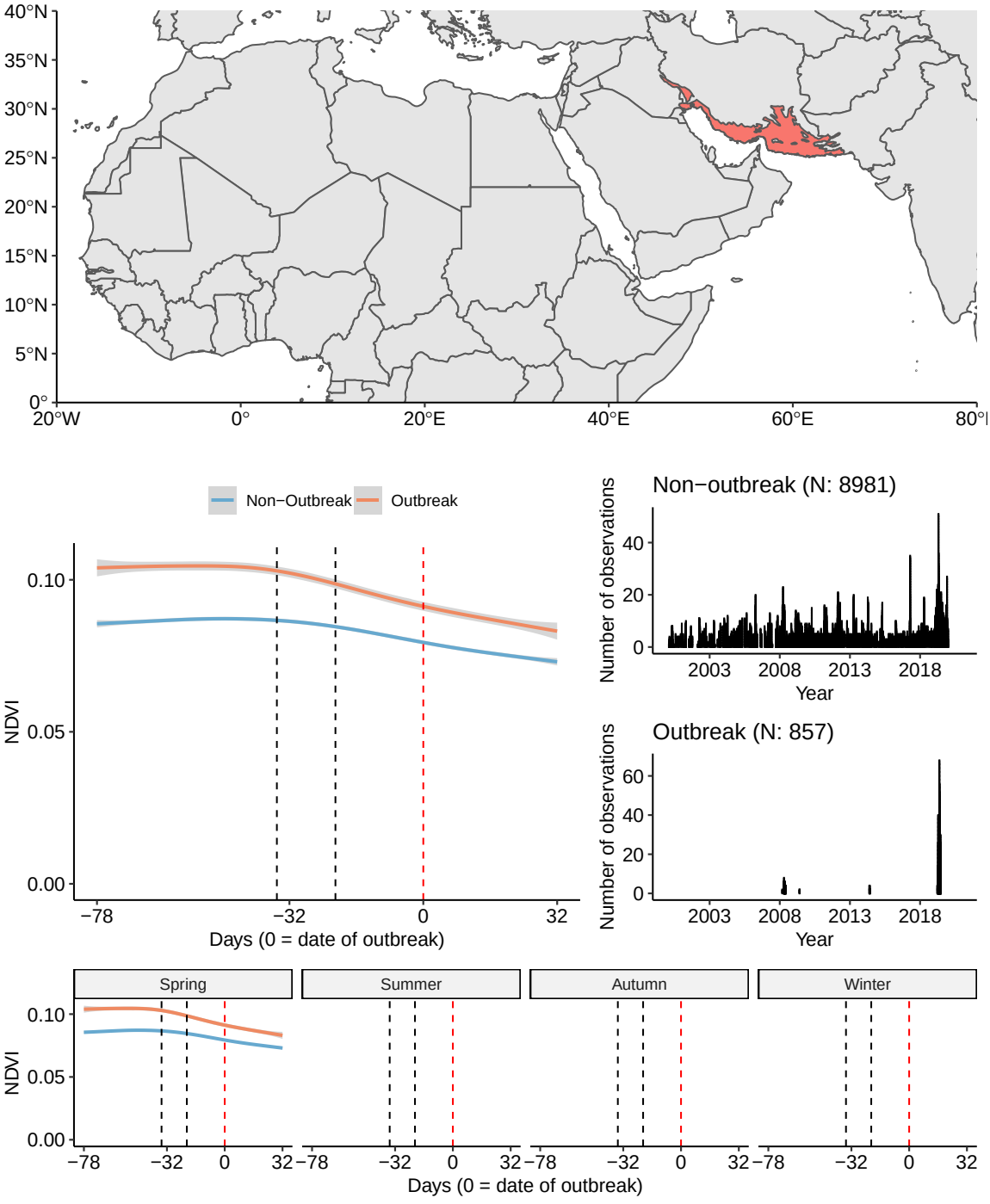

40°N
35°N
30°N
25°N
20°N
15°N
10°N
5°N
0°
20°W
0°
20°E
40°E
60°E
80°
Non−Outbreak
Outbreak
NDVI
Days (0 = date of outbreak)
Non−outbreak (N: 20209)
Number of observations
Year
Outbreak (N: 190)
Spring
Summer
Autumn
Winter

Gulf of Oman desert and semi−desert

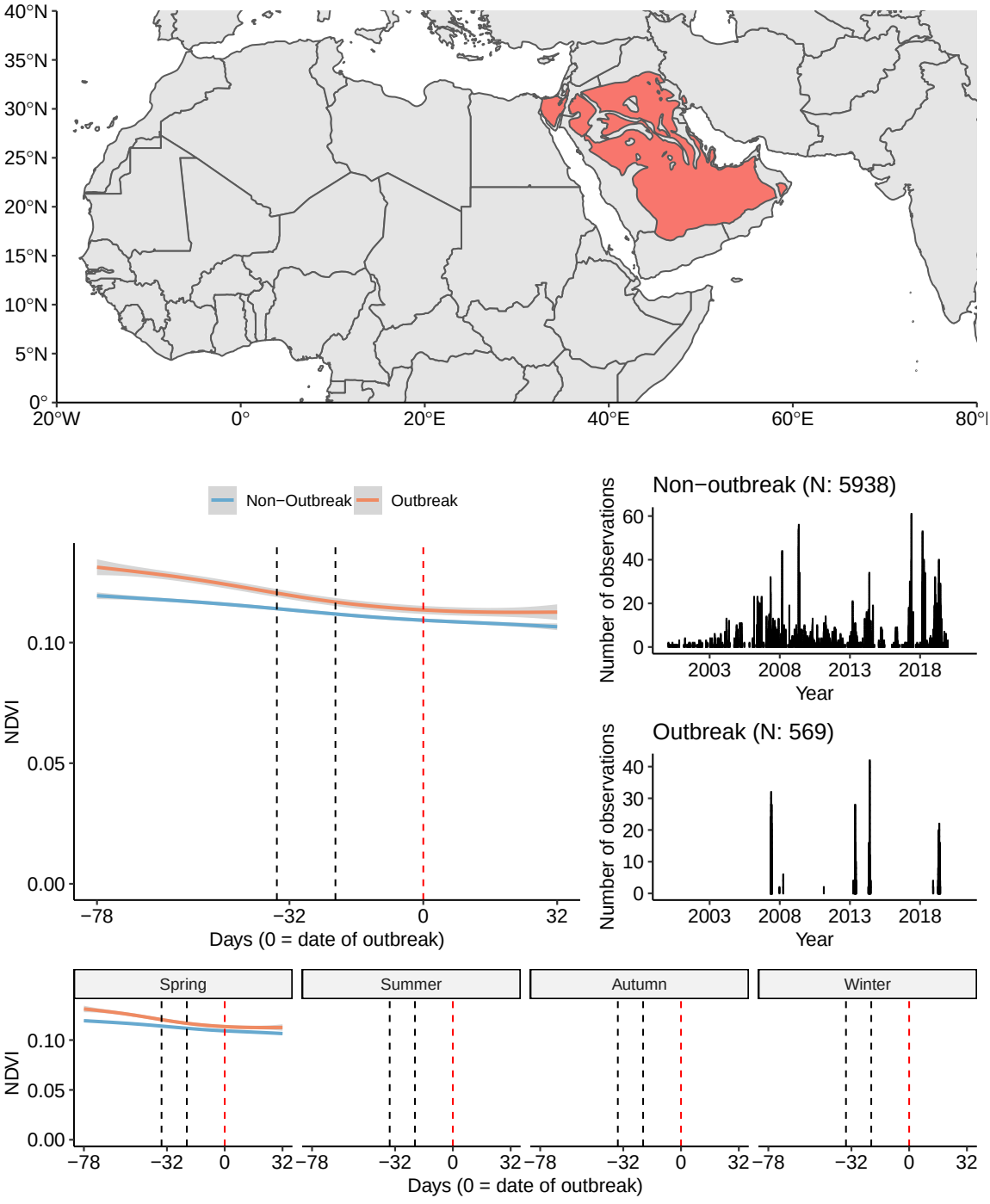



40°N
35°N
30°N
25°N
20°N
15°N
10°N
5°N
0°
20°W
0°
20°E
40°E
60°E
80°
Non−Outbreak
Outbreak
NDVI
0.2
0.1
0.0
−78
−32
0
32
Days (0 = date of outbreak)
Non−outbreak (N: 3442)
Number of observations
40
20
0
2003
2008
2013
2018
Year
Outbreak (N: 406)
20
15
10
5
0
Spring
Summer
Autumn
Winter
0.3

South Iran Nubo−Sindian desert and semi−desert



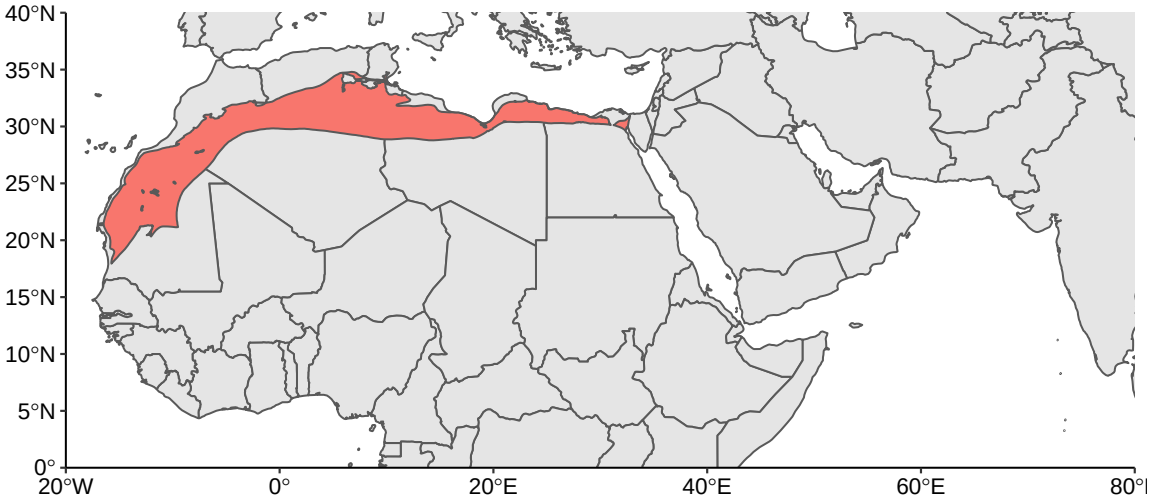
Arabian Desert and East Sahero−Arabian xeric shrublands

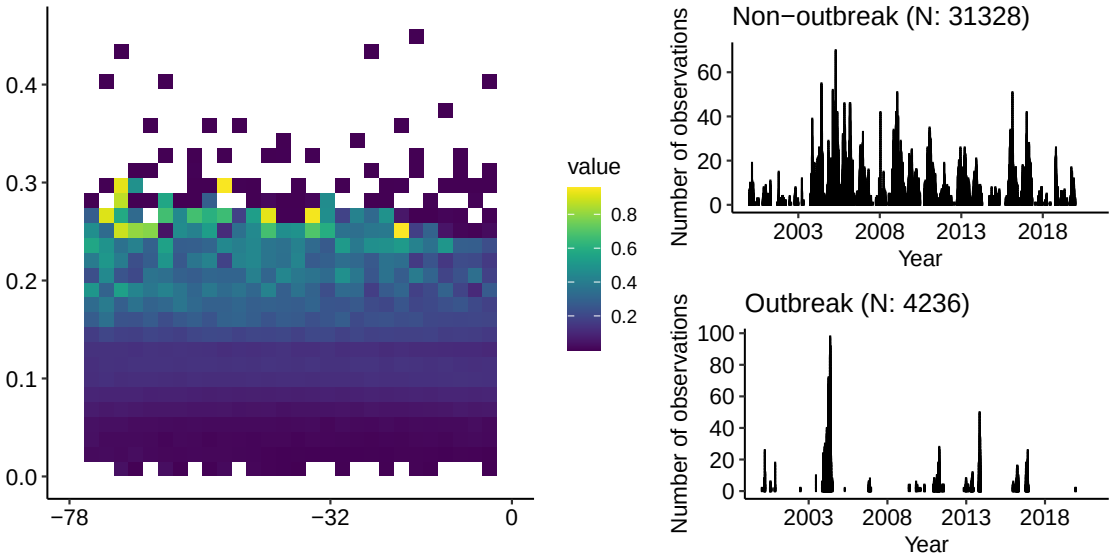


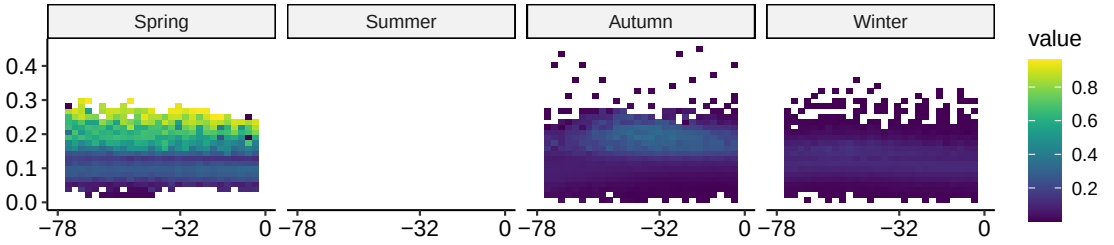
APPENDIX I

SUPPLEMENTARY FIGURE 14 FOR CHAPTER 5

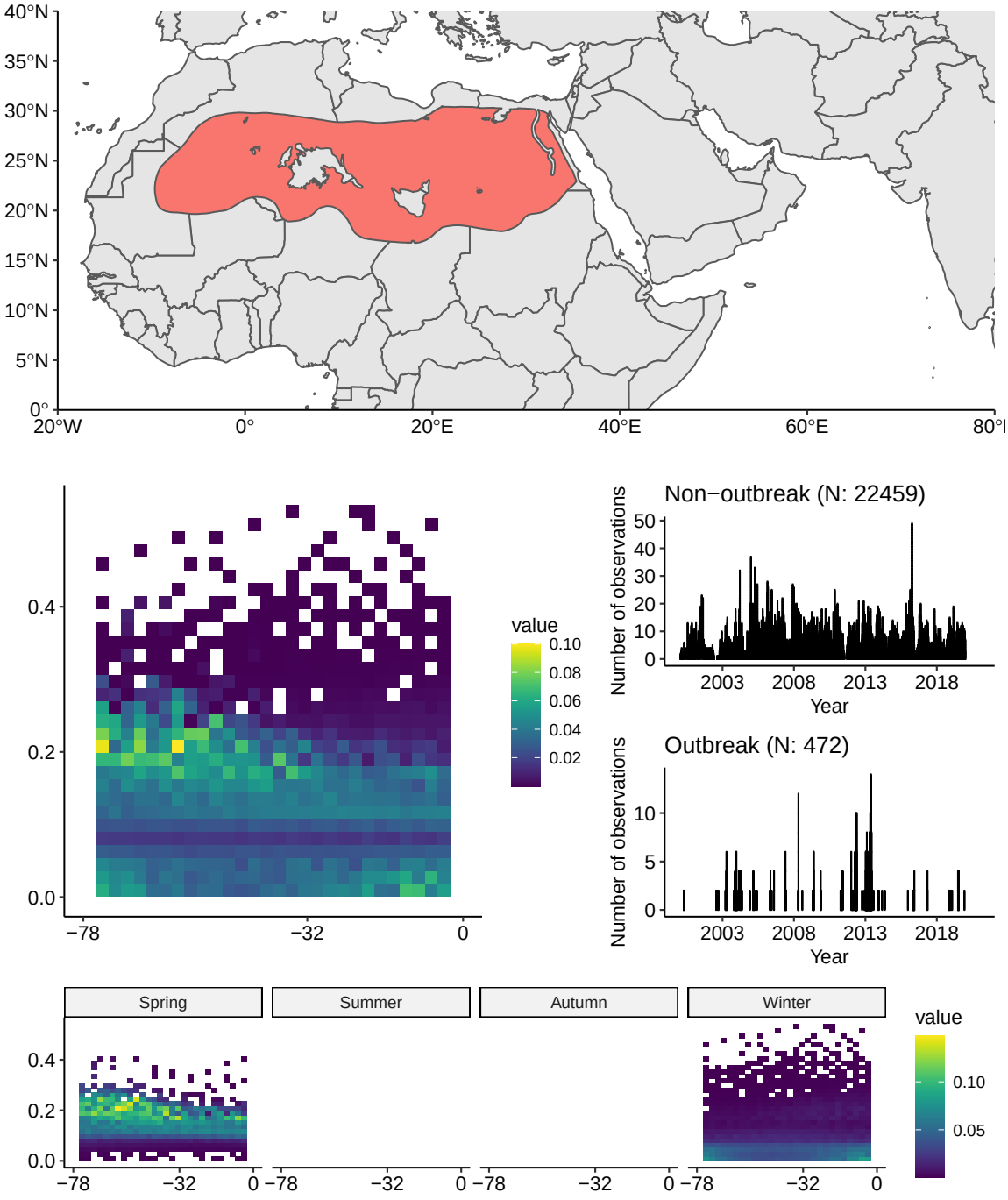
North Saharan steppe and woodlands



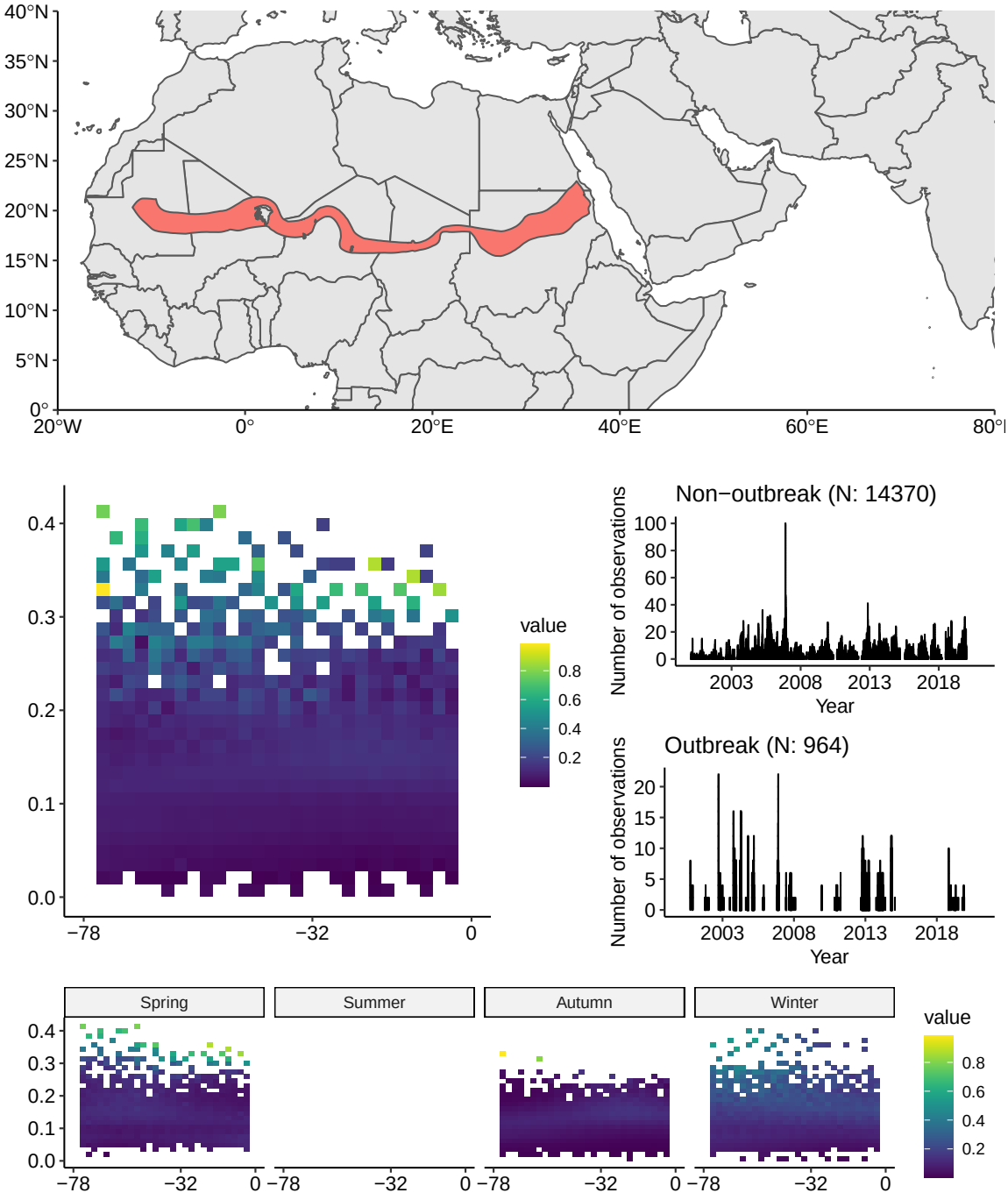




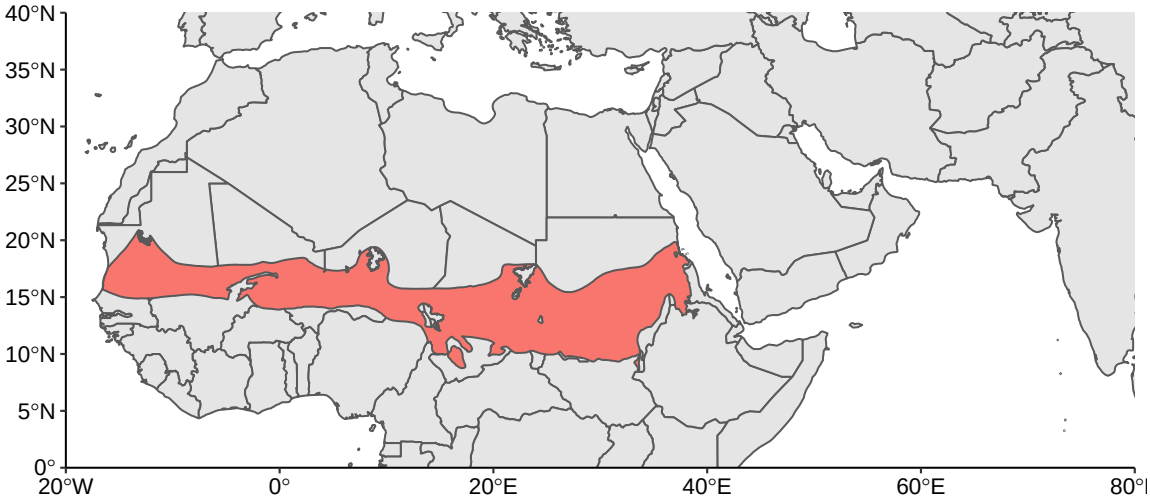
Sahara desert

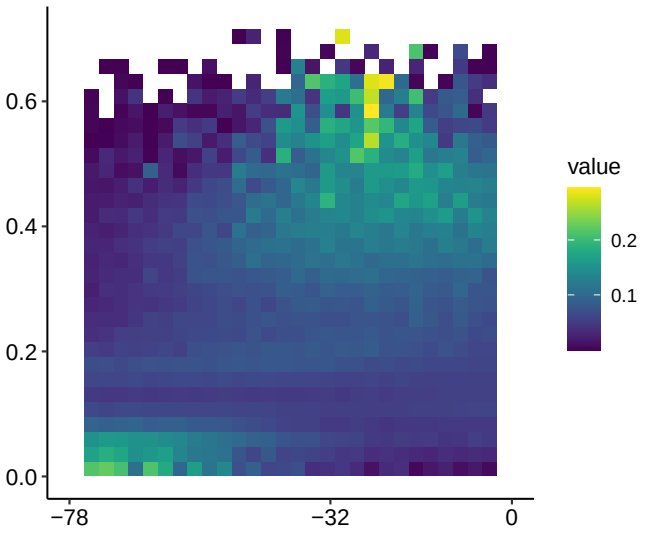


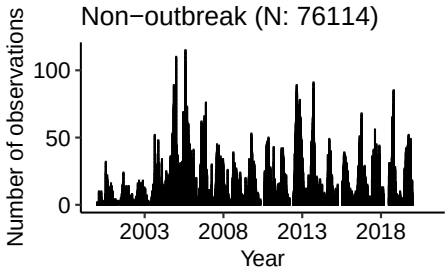
South Saharan steppe and woodlands

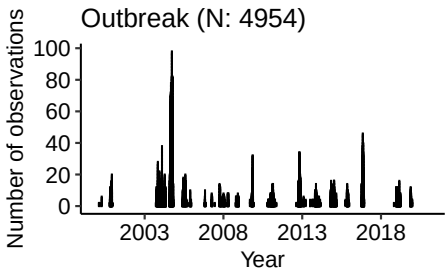


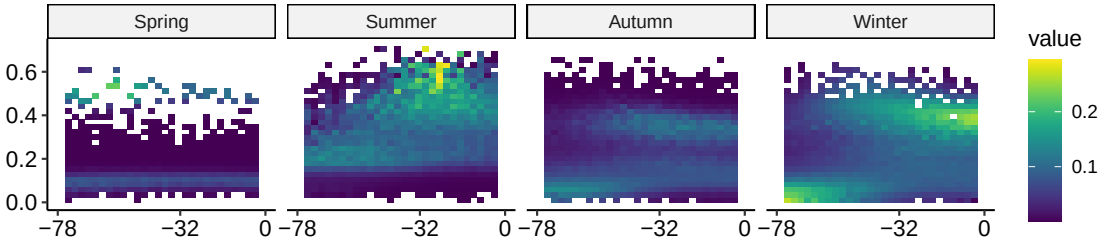
Sahelian Acacia savanna

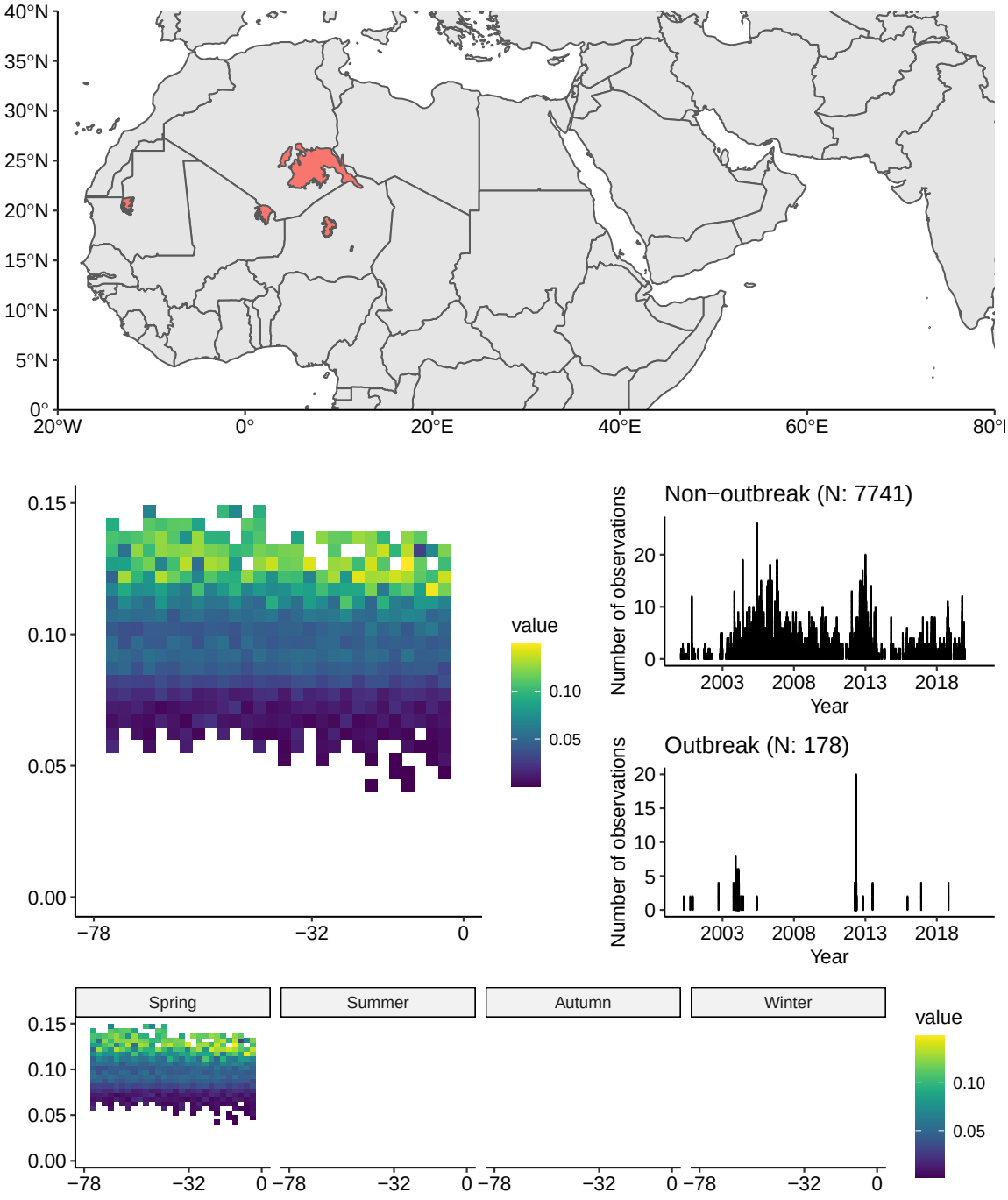




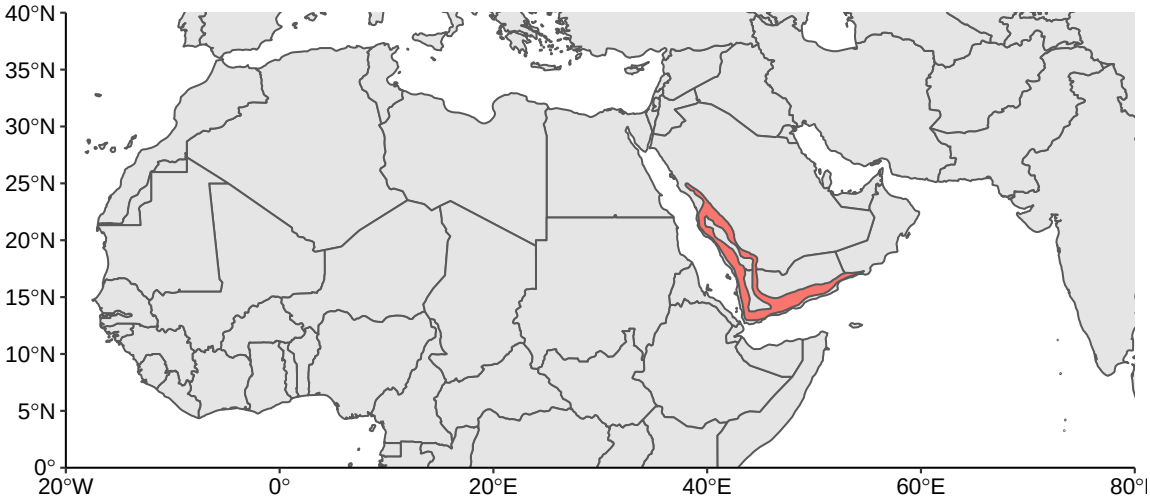


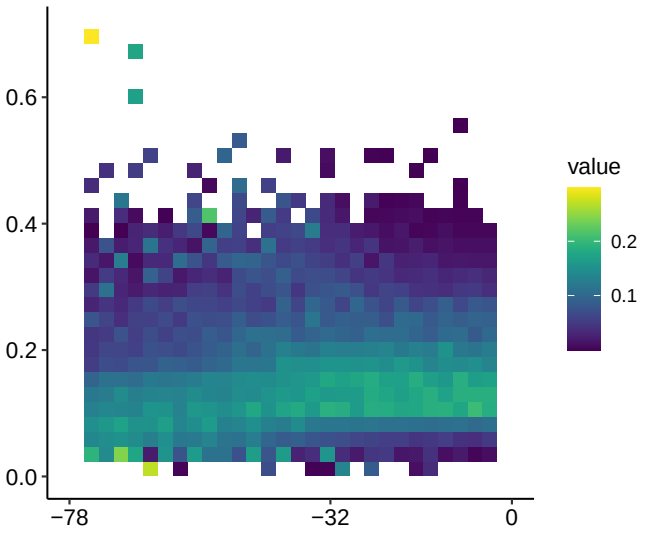


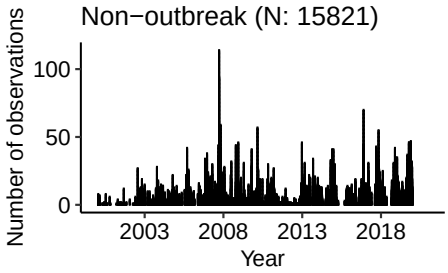


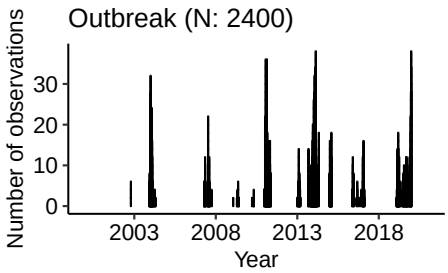

40°N
35°N
30°N
25°N
20°N
15°N
10°N
5°N
0°
20°W
0°
20°E
40°E
60°E
80°
0.15
0.10
0.05
0.00
−78
−32
0
value
0.10
0.05
Non−outbreak (N: 7741)
Number of observations
20
10
0
2003
2008
2013
2018
Year
Outbreak (N: 178)
Number of observations
20
15
10
5
0
2003
2008
2013
2018
Year
Spring
Summer
Autumn
Winter
value
0.10
0.05

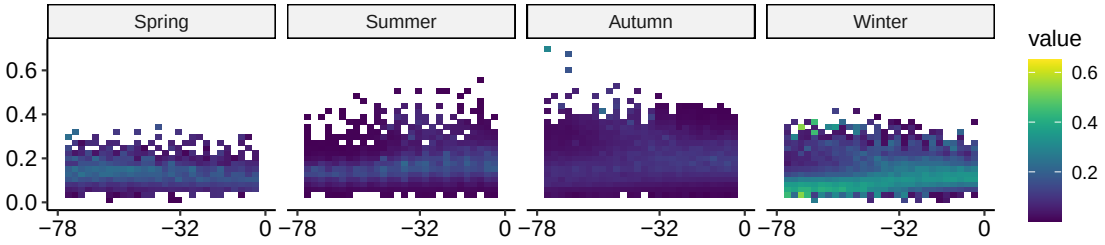
Southwestern Arabian foothills savanna



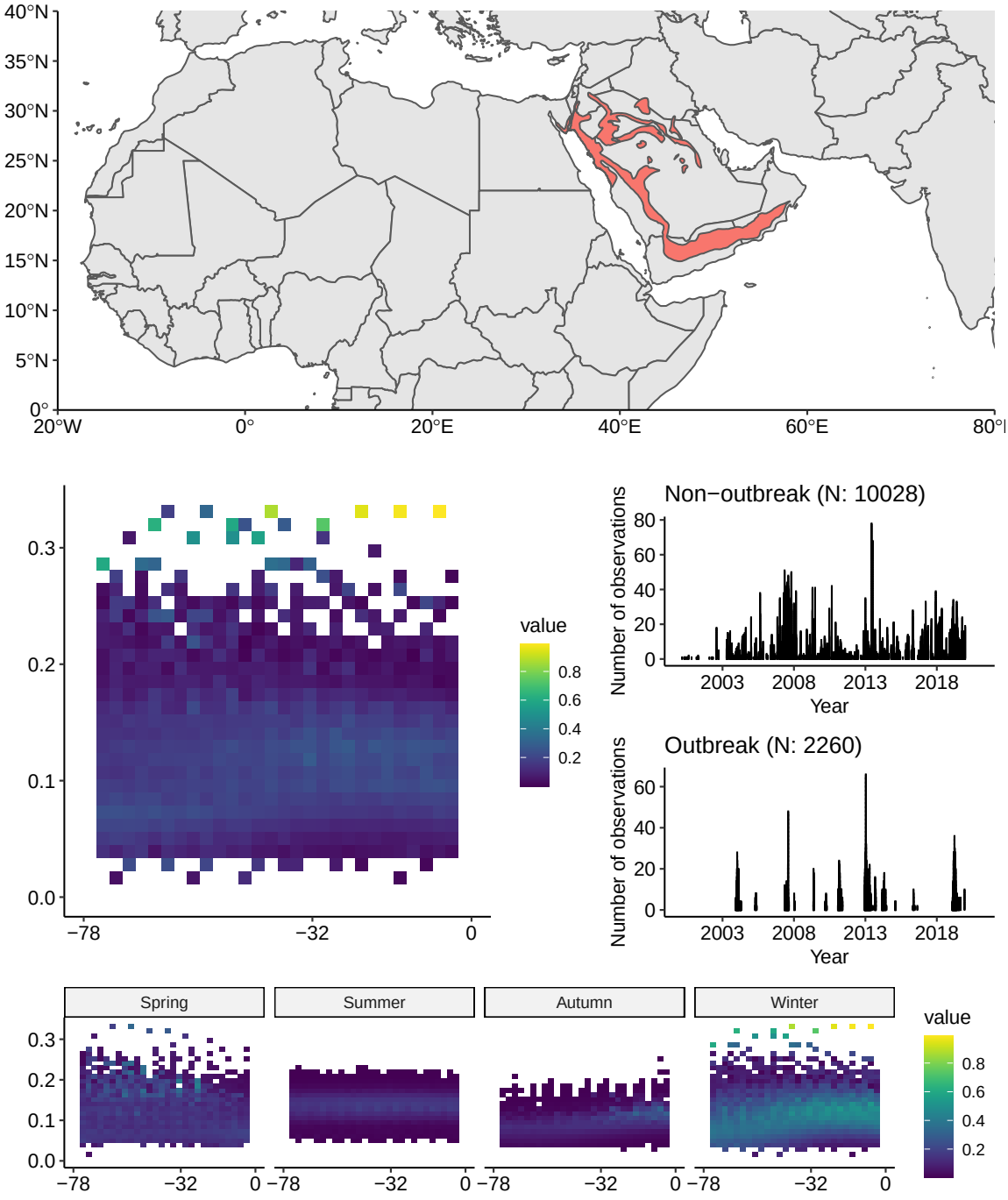




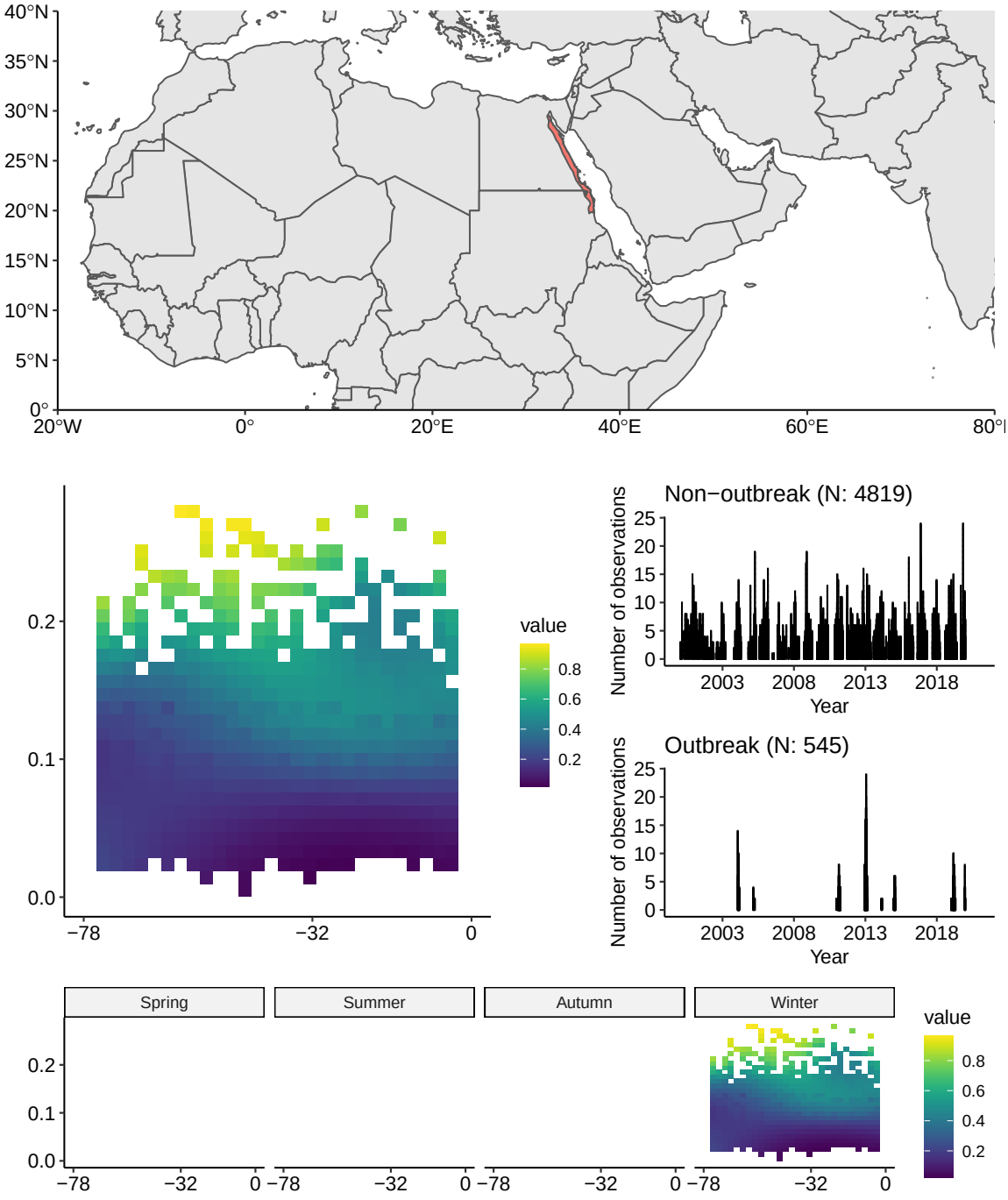


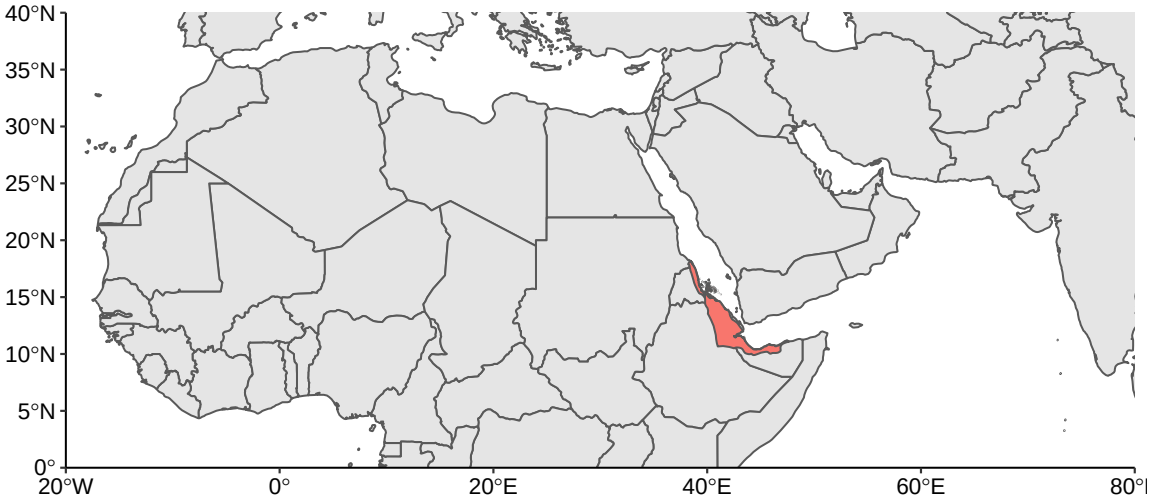


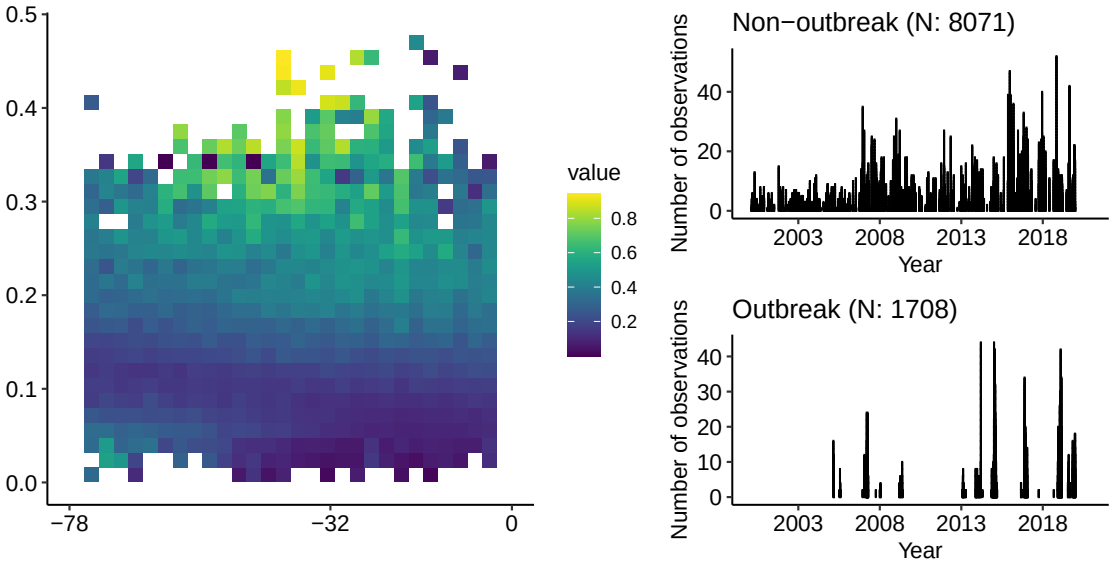
Red Sea Nubo−Sindian tropical desert and semi−desert

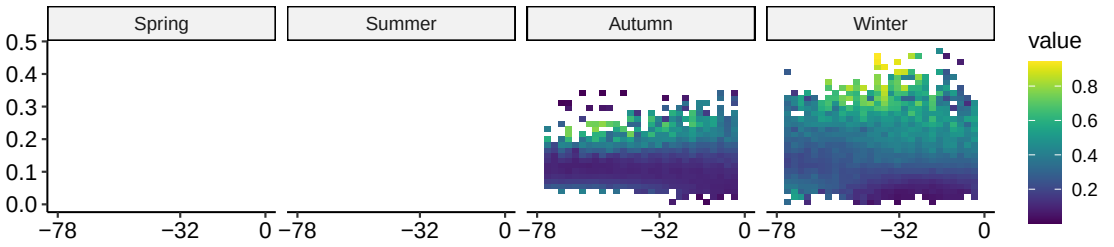


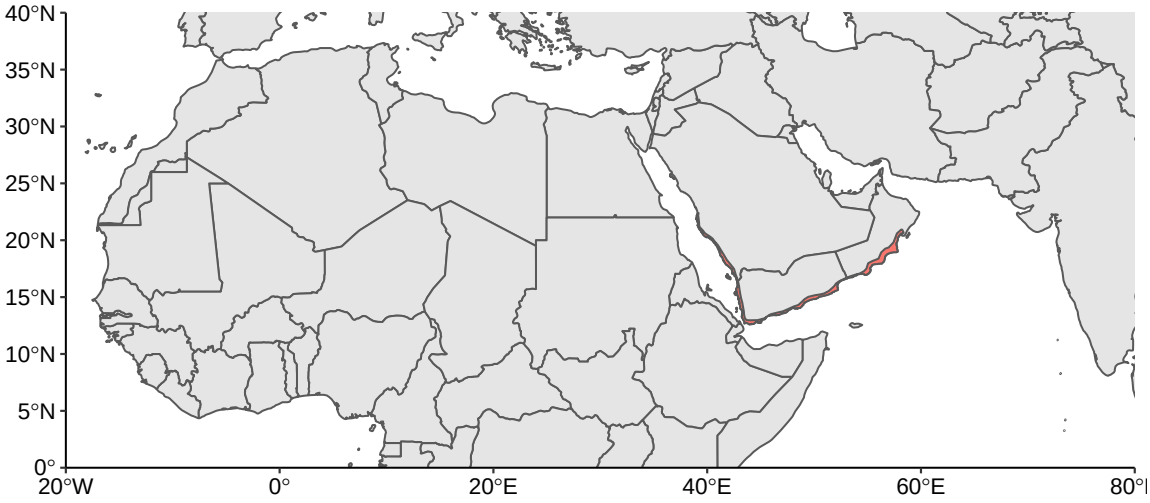
Red Sea coastal desert

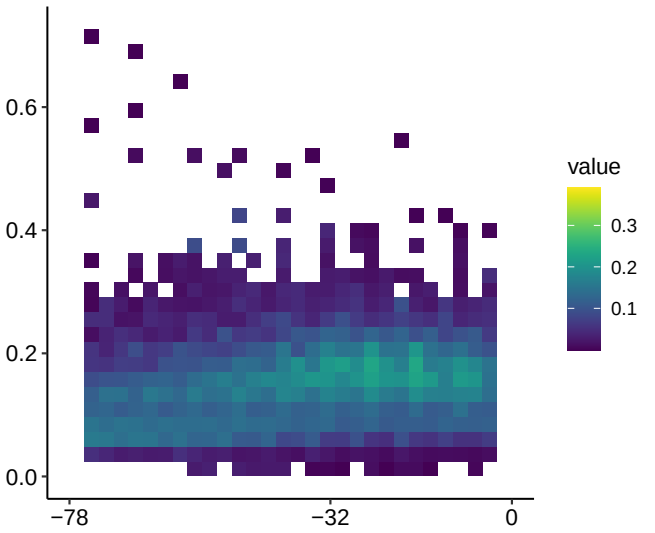


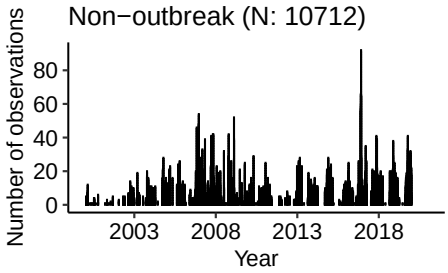

40°N
35°N
30°N
25°N
20°N
15°N
10°N
5°N
0°
20°W
0°
20°E
40°E
60°E
80°


0.5
0.4
0.3
0.2
0.1
0.0
−78
−32
0
value
0.8
0.6
0.4
0.2
Non−outbreak (N: 8071)
Number of observations
40
20
0
2003
2008
2013
2018
Year
Outbreak (N: 1708)
Number of observations
40
30
20
10
0
2003
2008
2013
2018
Year


Spring
Summer
Autumn
Winter
0.5
0.4
0.3
0.2
0.1
0.0
−78
−32
0
value
0.8
0.6
0.4
0.2


40°N
35°N
30°N
25°N
20°N
15°N
10°N
5°N
0°
20°W
0°
20°E
40°E
60°E
80°


0.6
0.4
0.2
0.0
−78
−32
0
value
0.3
0.2
0.1


Non−outbreak (N: 10712)
Number of observations
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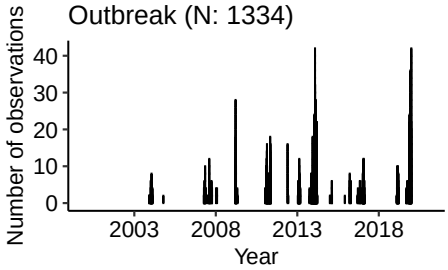
60
40
20
0
2003
2008
2013
2018
Year


Outbreak (N: 1334)
Number of observations
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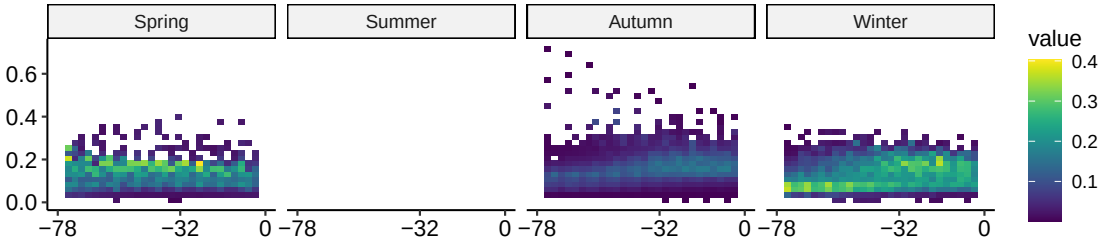
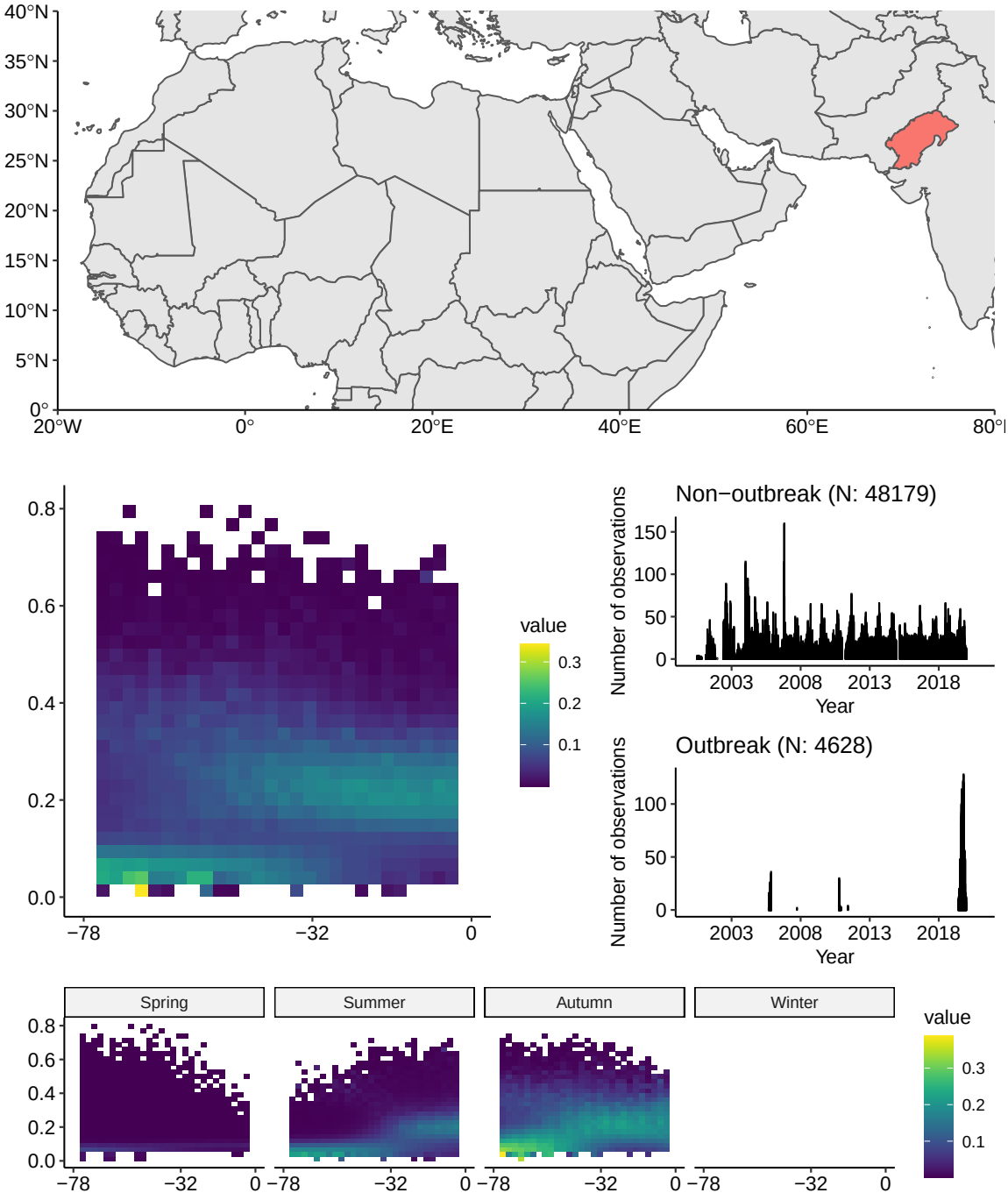
30
20
10
0
2003
2008
2013
2018
Year


Spring
Summer
Autumn
Winter
0.6
0.4
0.2
0.0
−78
−32
0
value
0.4
0.3
0.2
0.1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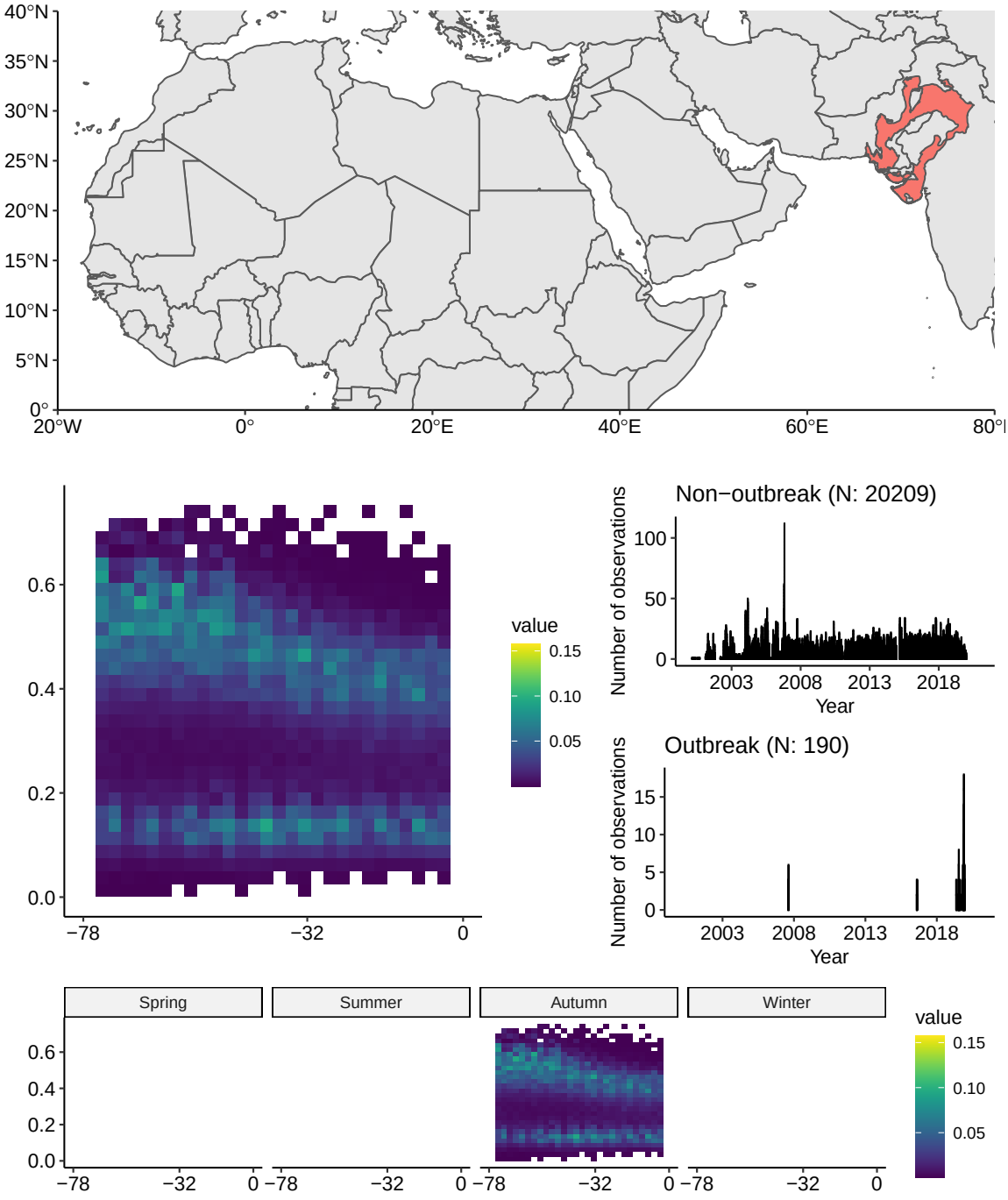
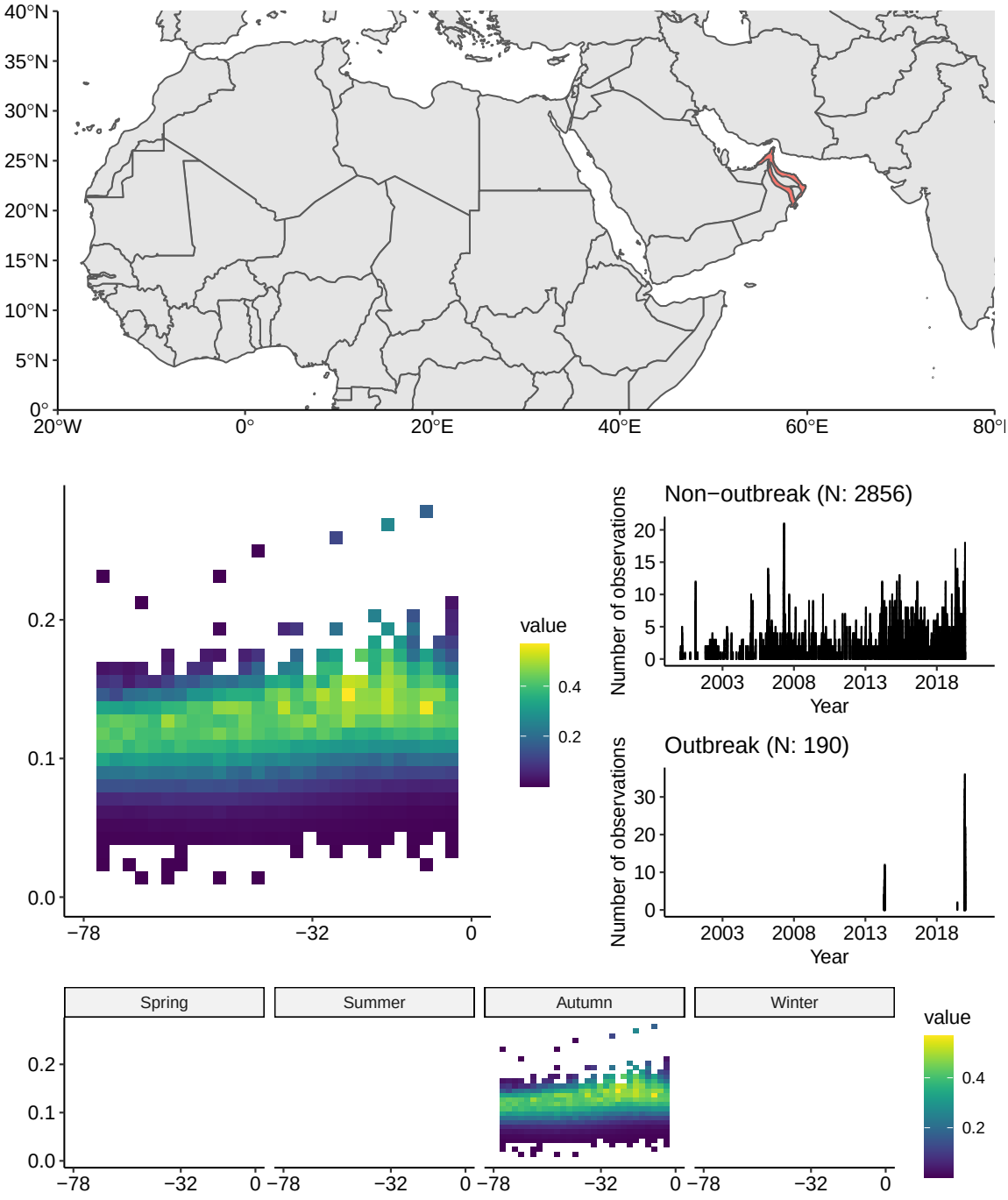
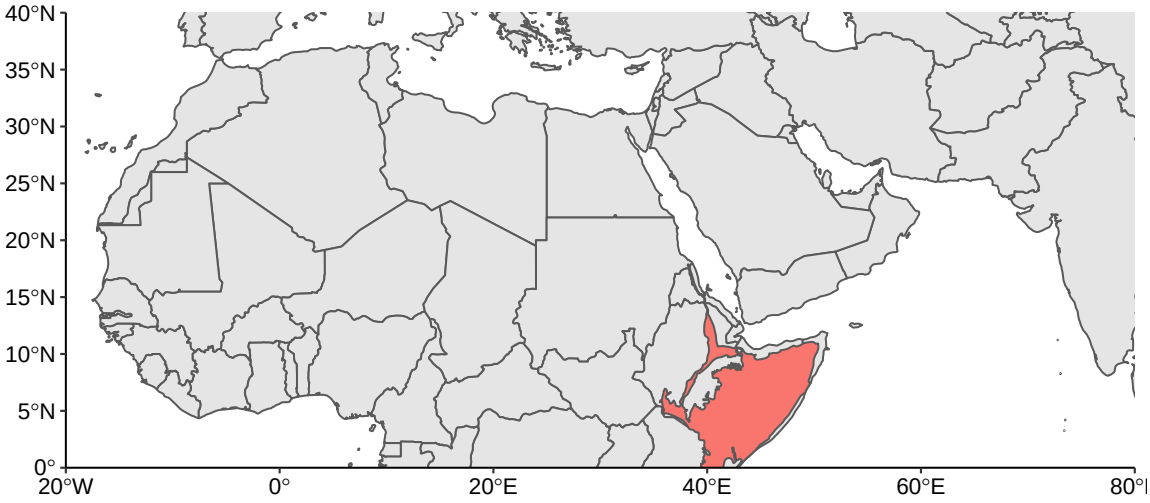
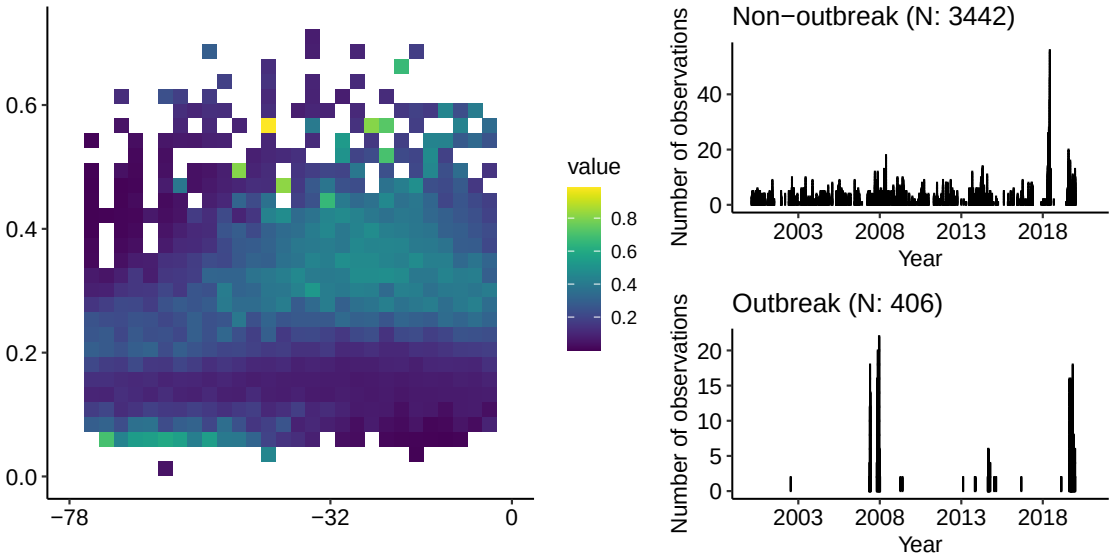
35°N
30°N
25°N
20°N
15°N
10°N
5°N
0°
20°W
0°
20°E
40°E
60°E
80°
0.8
0.6
0.4
0.2
0.0
−78
−32
0
value
0.3
0.2
0.1
Non−outbreak (N: 48179)
Number of observations
150
100
50
0
2003
2008
2013
2018
Year
Outbreak (N: 4628)
Number of observations
100
50
0
2003
2008
2013
2018
Year
Spring
Summer
Autumn
Winter
value
0.3
0.2
0.1

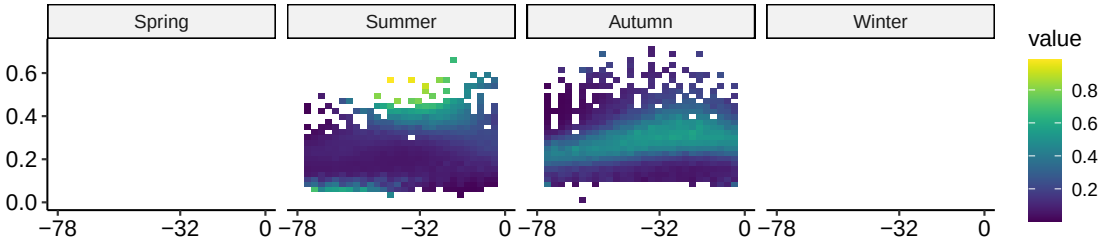

40°N
35°N
30°N
25°N
20°N
15°N
10°N
5°N
0°
20°W
0°
20°E
40°E
60°E
80°
value
0.15
0.10
0.05
Non−outbreak (N: 20209)
Number of observations
100
50
0
2003
2008
2013
2018
Year
Outbreak (N: 190)
15
10
5
0
−78
−32
0
Spring
Summer
Autumn
Winter

Gulf of Oman desert and semi−desert

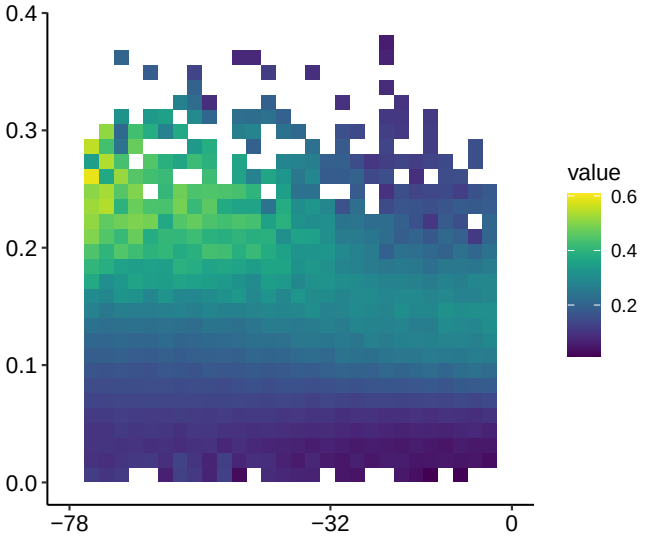


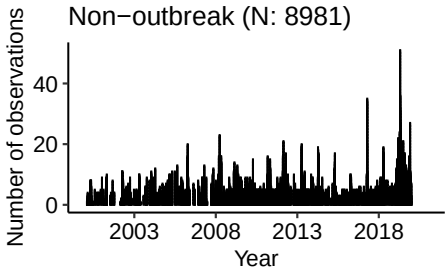

40°N
35°N
30°N
25°N
20°N
15°N
10°N
5°N
0°
20°W
0°
20°E
40°E
60°E
80°

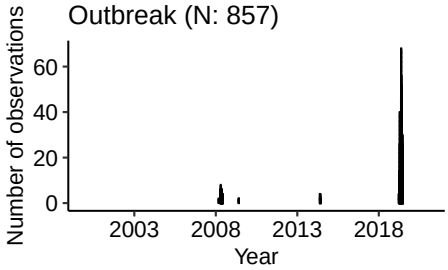

0.6
0.4
0.2
0.0
−78
−32
0
value
0.8
0.6
0.4
0.2
Non−outbreak (N: 3442)
Number of observations
40
20
0
2003
2008
2013
2018
Year
Outbreak (N: 406)
Number of observations
20
15
10
5
0
2003
2008
2013
2018
Year

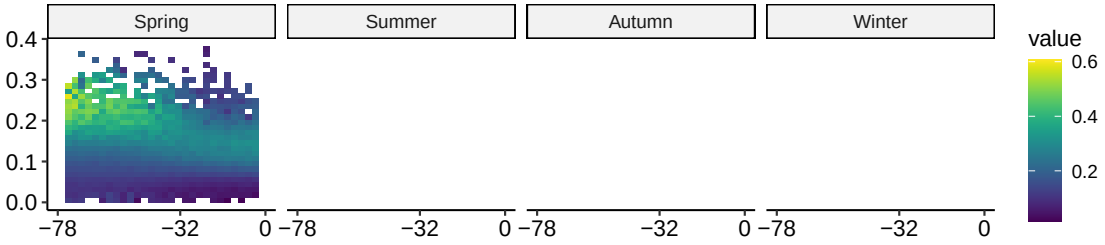

Spring
Summer
Autumn
Winter
0.6
0.4
0.2
0.0
−78
−32
0
value
0.8
0.6
0.4
0.2

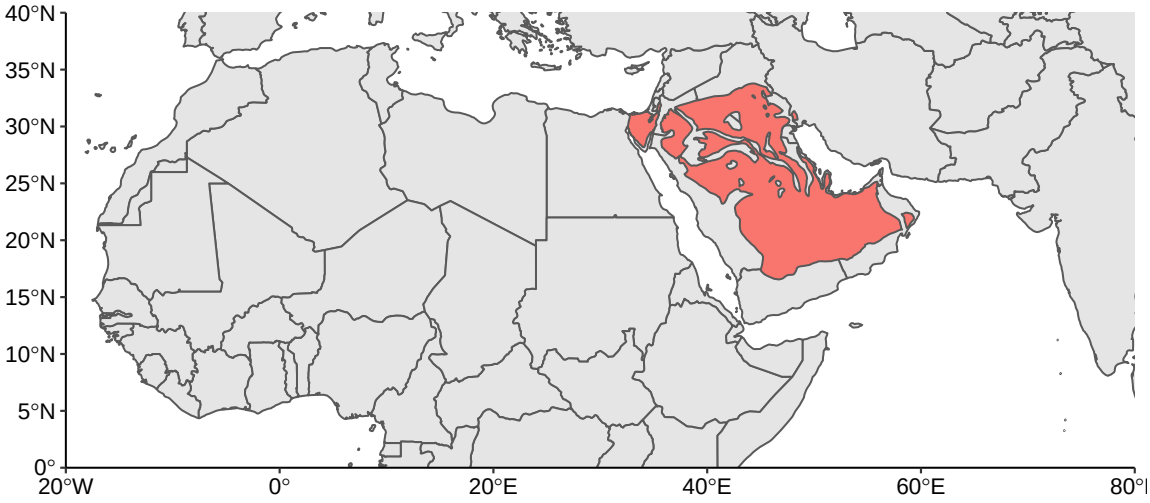
South Iran Nubo−Sindian desert and semi−desert







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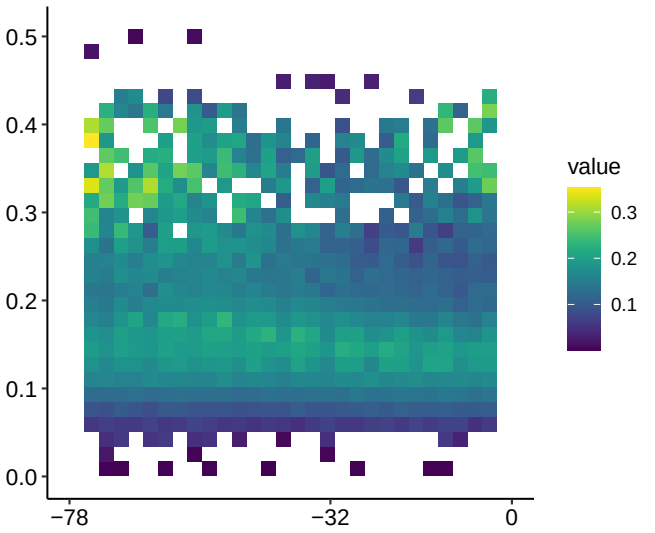
35°N
30°N
25°N
20°N
15°N
10°N
5°N
0°
20°W
0°
20°E
40°E
60°E
80°


0.5
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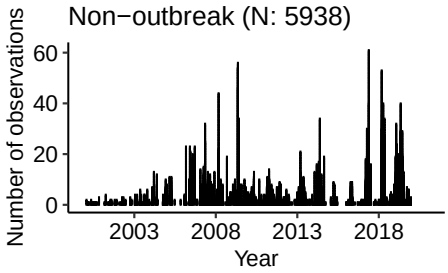
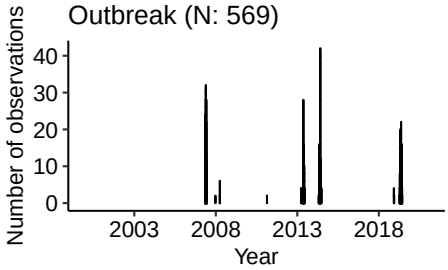
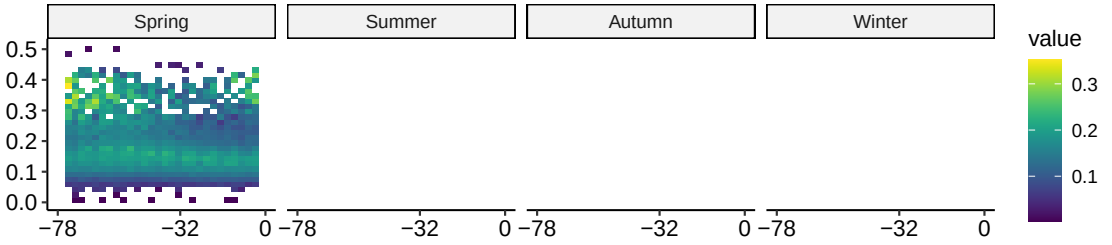
0.3
0.2
0.1
0.0
−78
−32
0
value
0.3
0.2
0.1


Non−outbreak (N: 5938)
Number of observations
60
40
20
0
2003
2008
2013
2018
Year

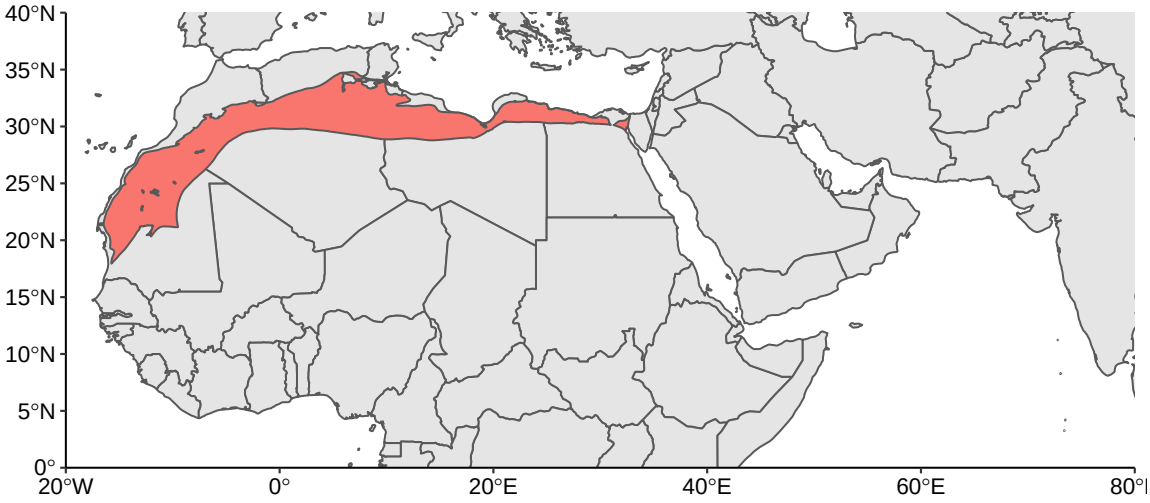

Outbreak (N: 569)
Number of observations
40
30
20
10
0
2003
2008
2013
2018
Year

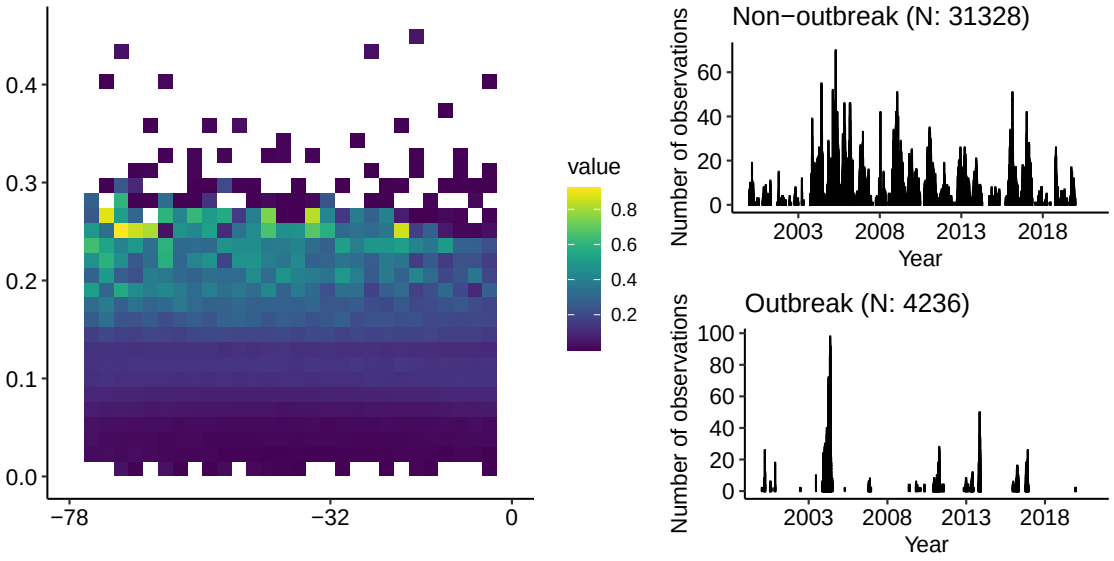

Spring
Summer
Autumn
Winter
0.5
0.4
0.3
0.2
0.1
0.0
−78
−32
0
value
0.3
0.2
0.1

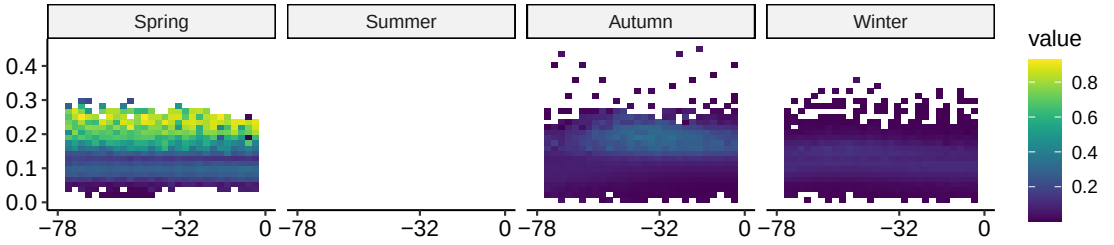
APPENDIX J

SUPPLEMENTARY FIGURE 15 FOR CHAPTER 5

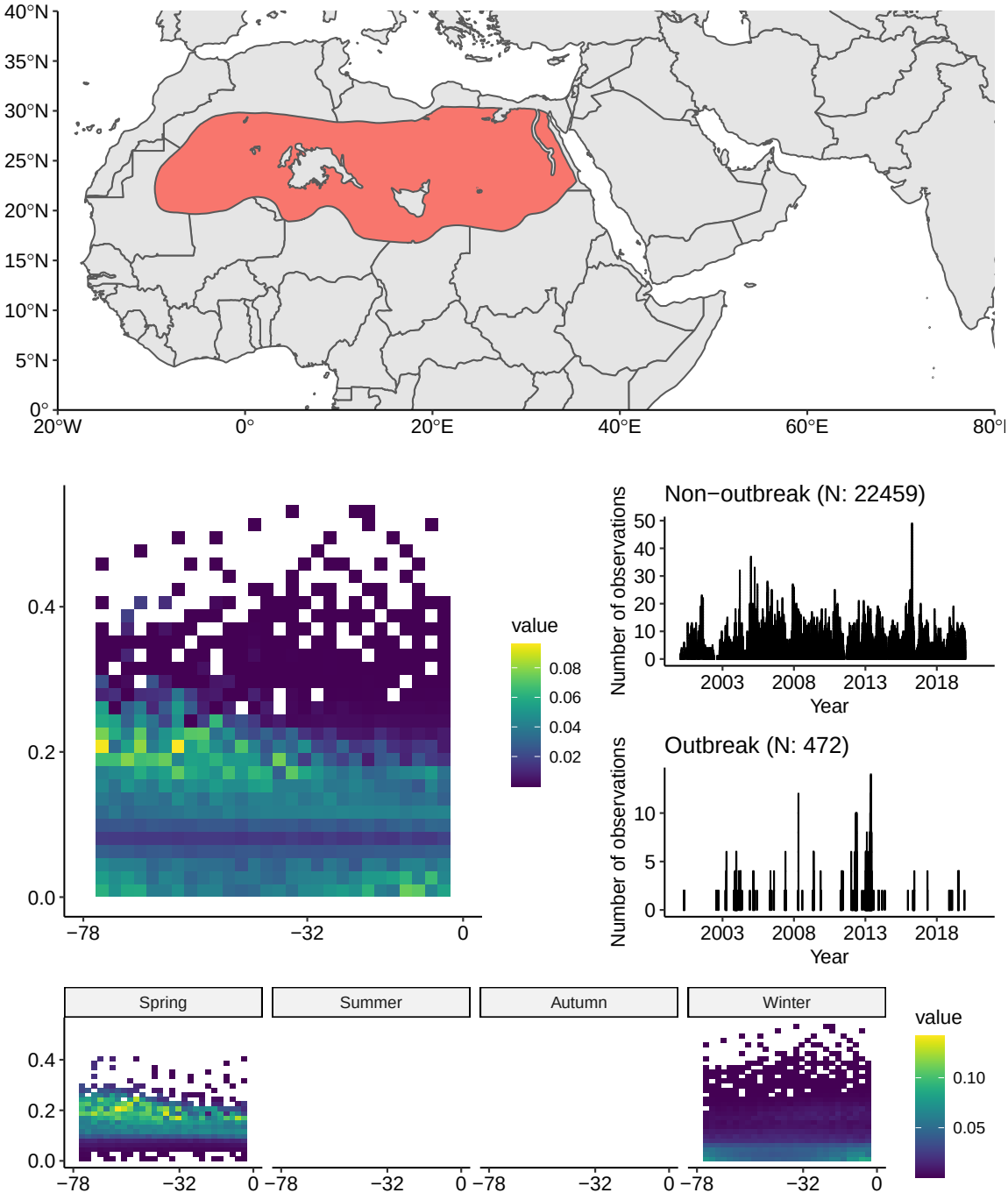
North Saharan steppe and woodlands



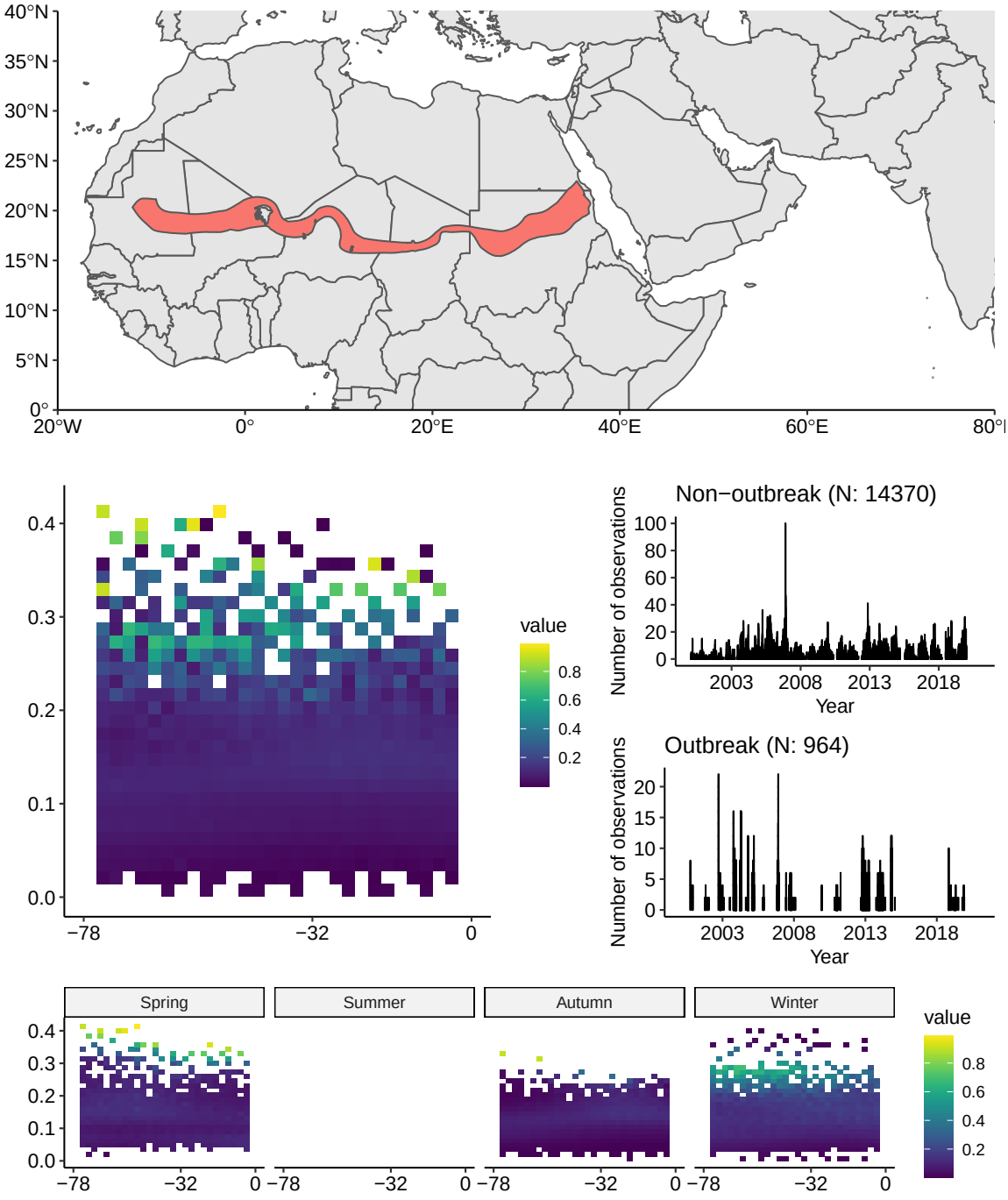




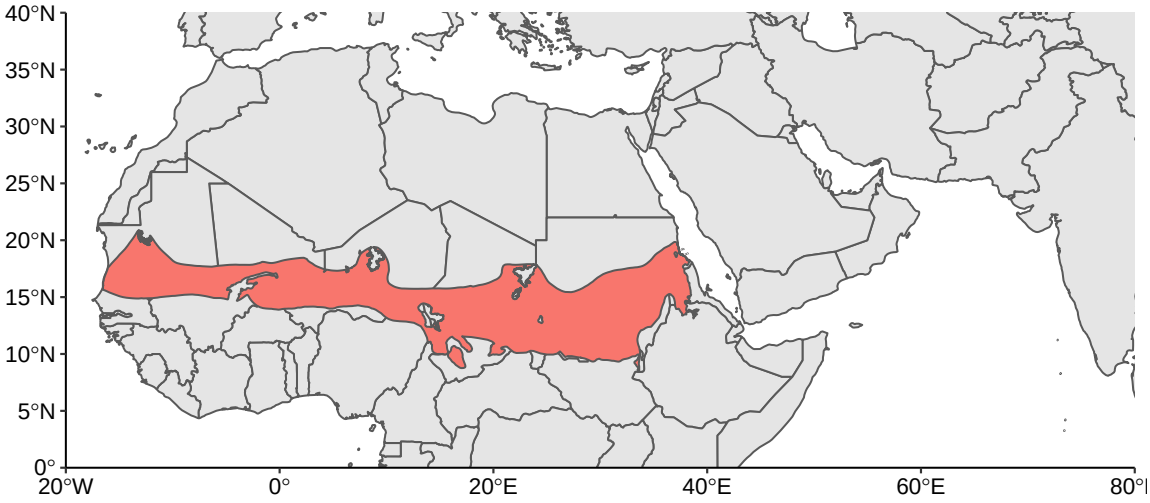
Sahara desert

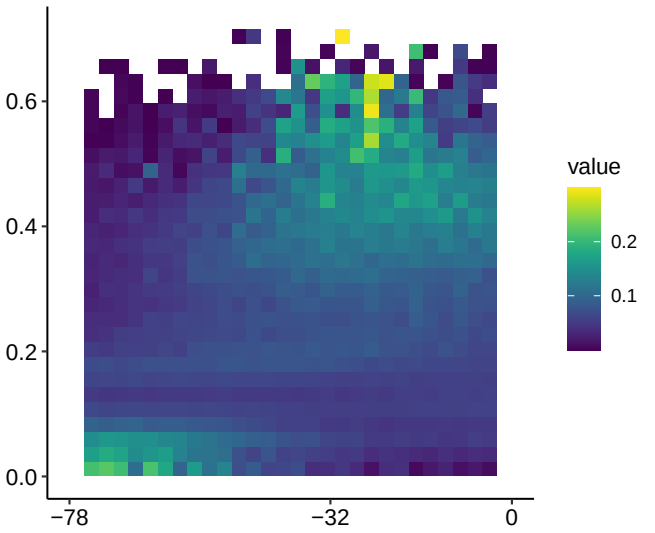


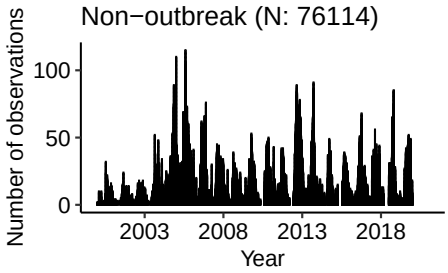
South Saharan steppe and woodlands

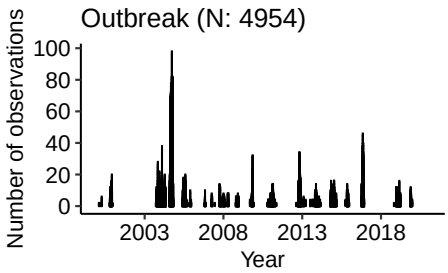


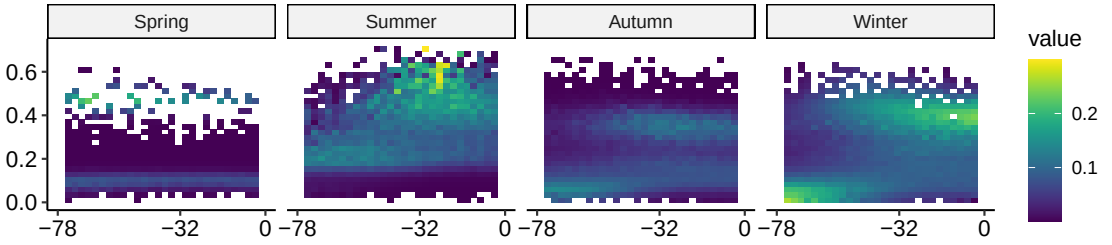
Sahelian Acacia savanna



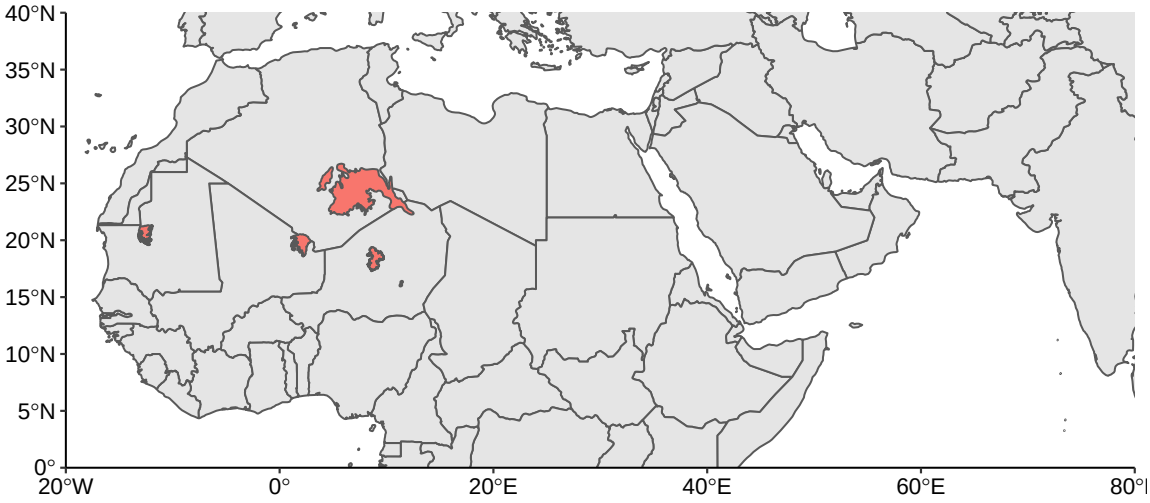


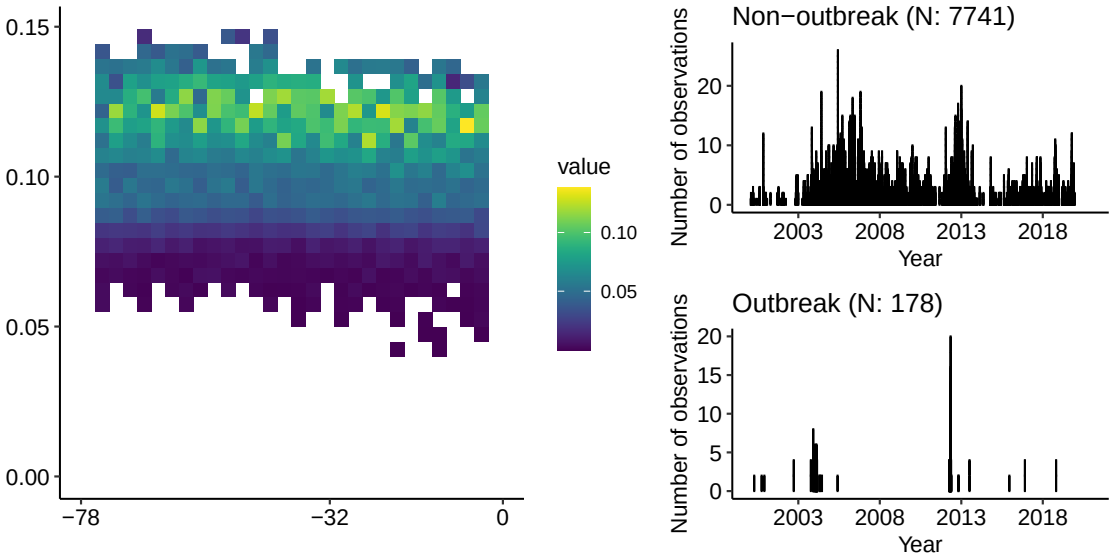


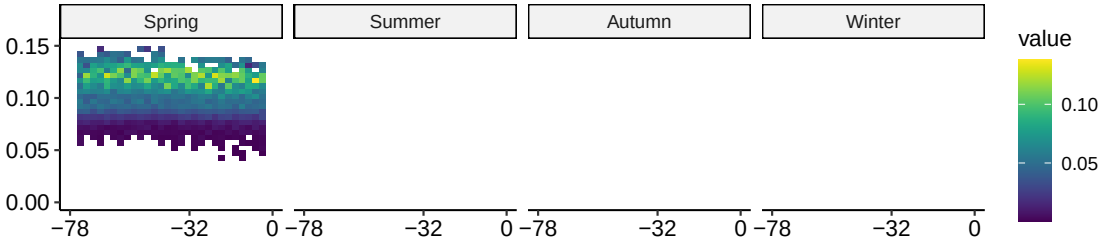


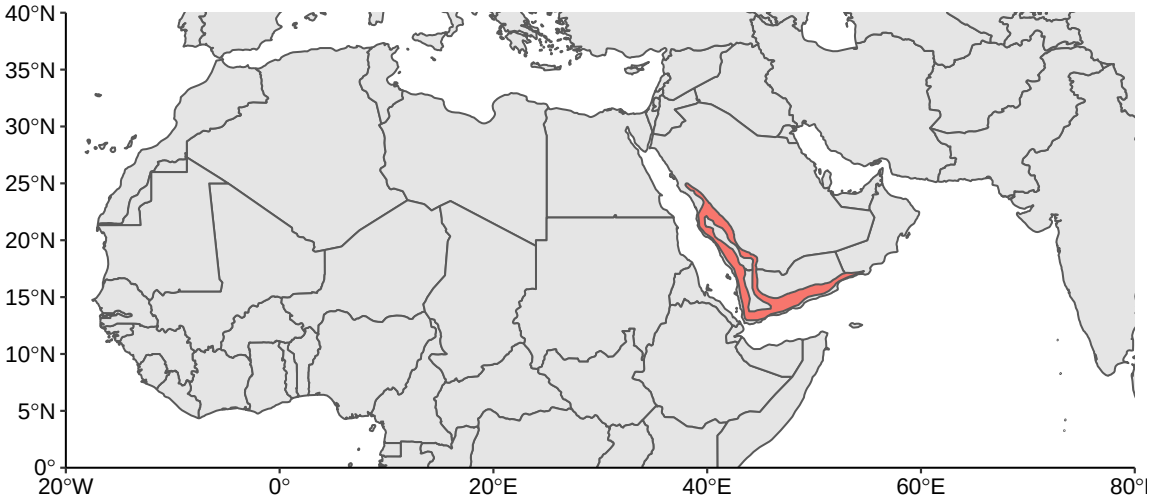


West Saharan montane xeric woodlands





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35°N
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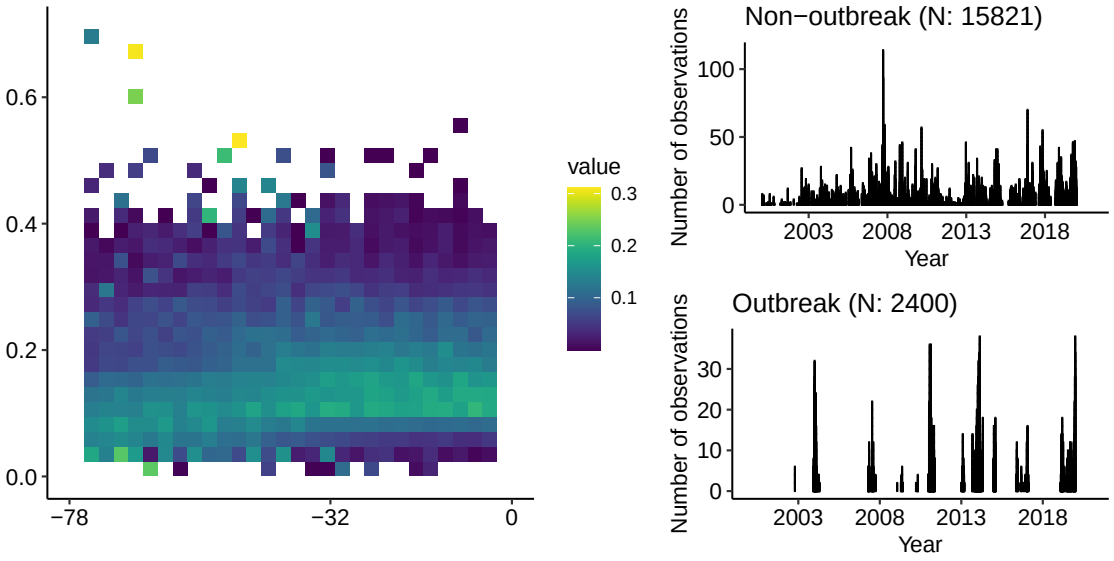
25°N
20°N
15°N
10°N
5°N
0°
20°W
0°
20°E
40°E
60°E
80°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−32
0
value
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0.2
0.1
Non−outbreak (N: 15821)
Number of observations
100
50
0
2003
2008
2013
2018
Year
Outbreak (N: 2400)
Number of observations
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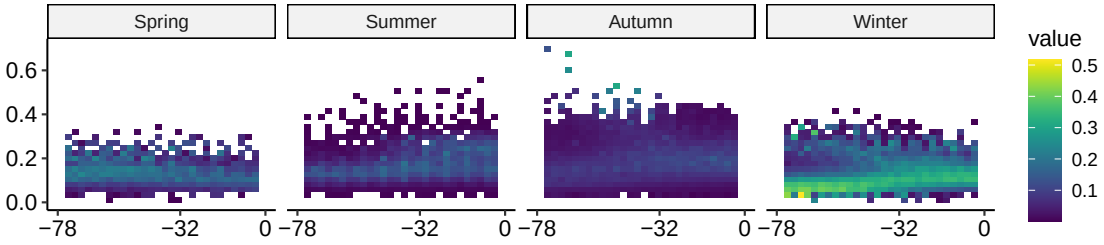
20
10
0
2003
2008
2013
2018
Year


Spring
Summer
Autumn
Winter
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0.4
0.2
0.0
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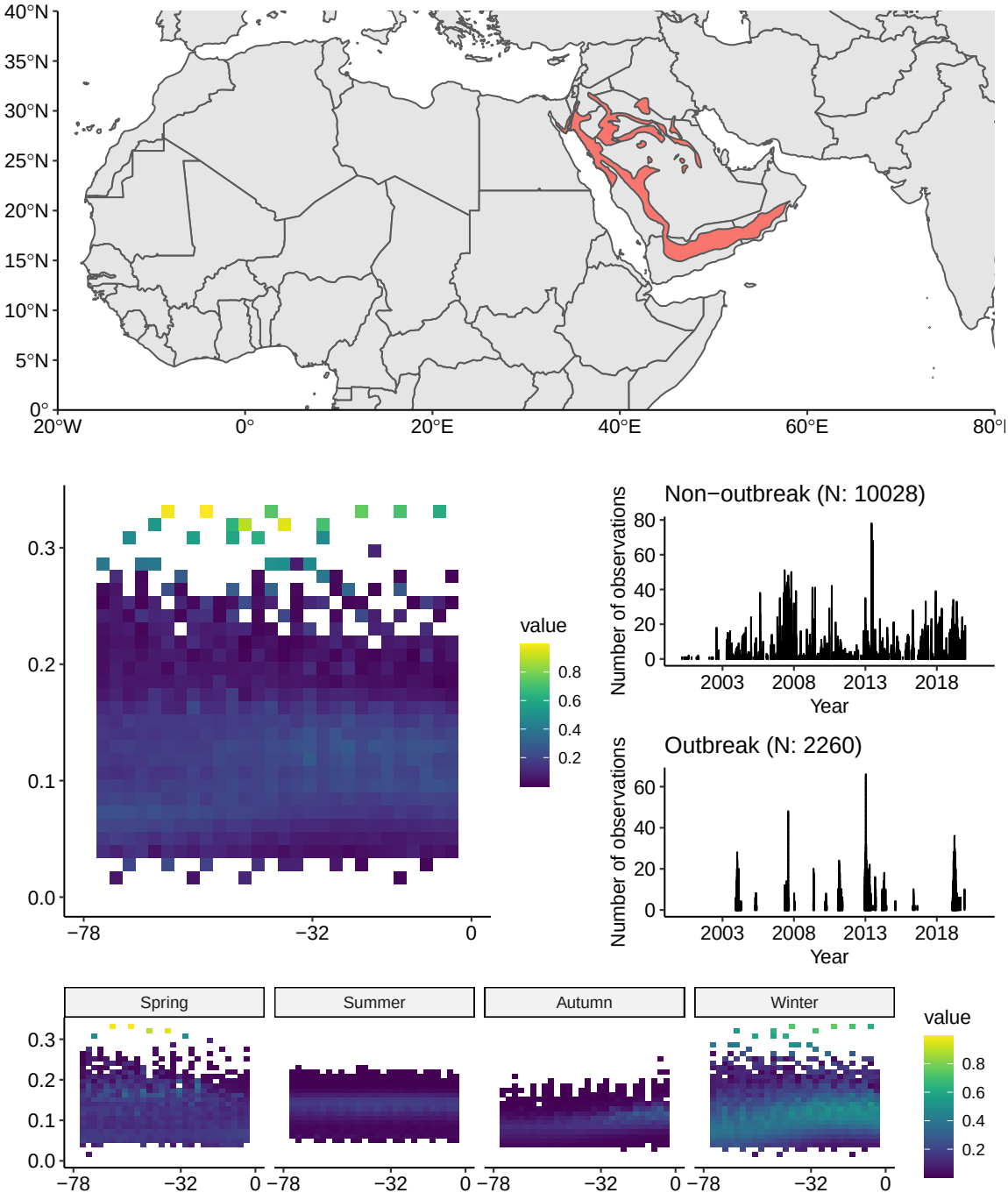
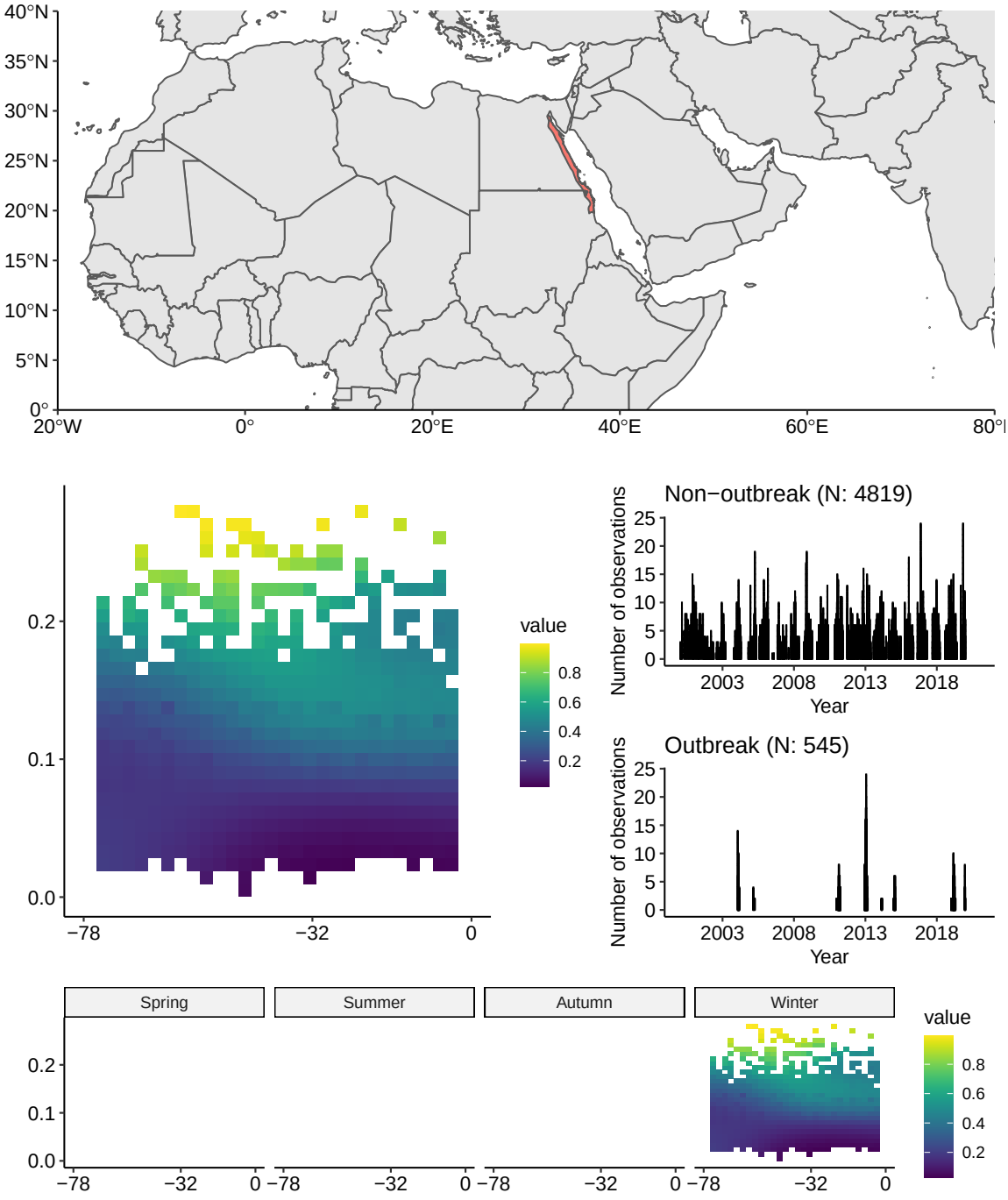
−32
0
value
0.5
0.4
0.3
0.2
0.1

Red Sea Nubo−Sindian tropical desert and semi−desert

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30°N
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15°N
10°N
5°N
0°
20°W
0°
20°E
40°E
60°E
80°
0.2
0.1
0.0
−78
−32
0
value
0.8
0.6
0.4
0.2
Non−outbreak (N: 4819)
Number of observations
25
20
15
10
5
0
2003
2008
2013
2018
Year
Outbreak (N: 545)
Number of observations
25
20
15
10
5
0
2003
2008
2013
2018
Year
Spring
Summer
Autumn
Winter
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−32
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value
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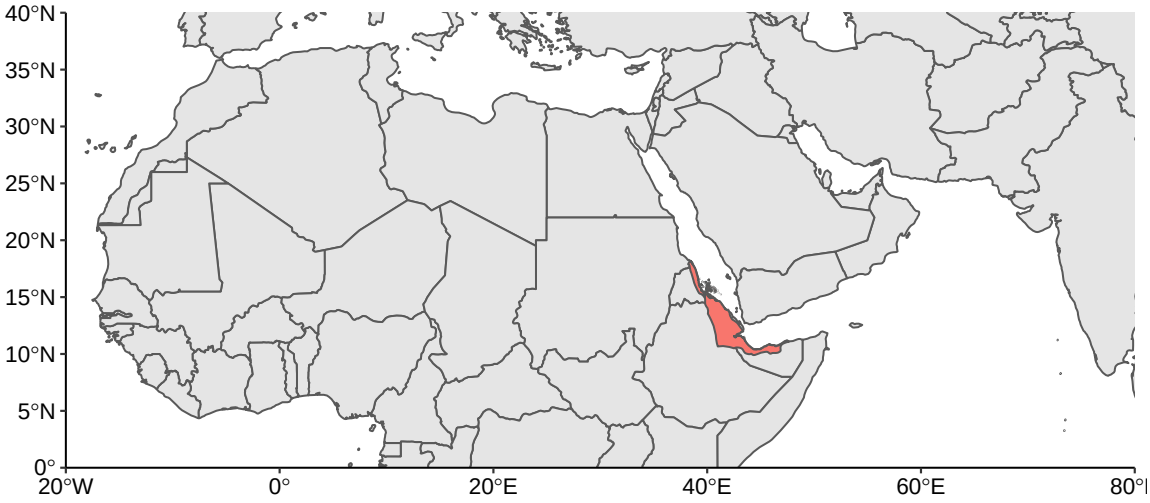
0.4
0.2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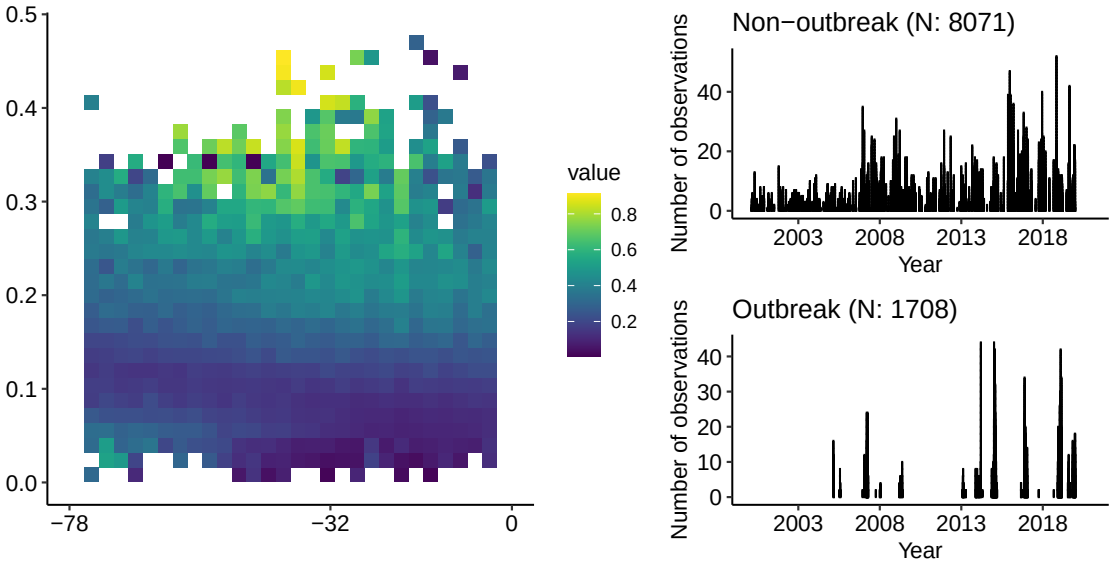
15°N
10°N
5°N
0°
20°W
0°
20°E
40°E
60°E
80°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0.3
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0.1
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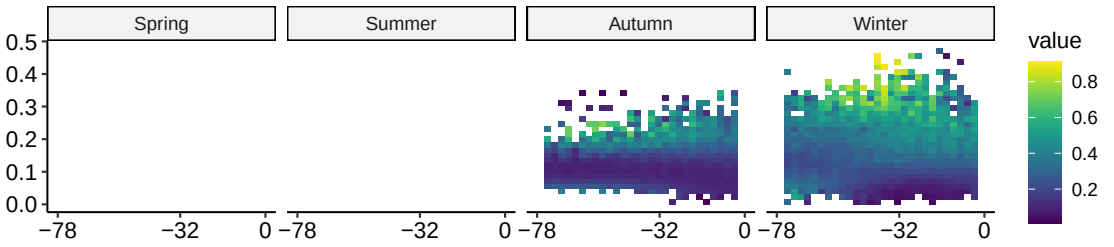
−32
0
value
0.8
0.6
0.4
0.2
Non−outbreak (N: 8071)
Number of observations
40
20
0
2003
2008
2013
2018
Year
Outbreak (N: 1708)
Number of observations
40
30
20
10
0
2003
2008
2013
2018
Year


Spring
Summer
Autumn
Winter
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0.3
0.2
0.1
0.0
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−32
0
value
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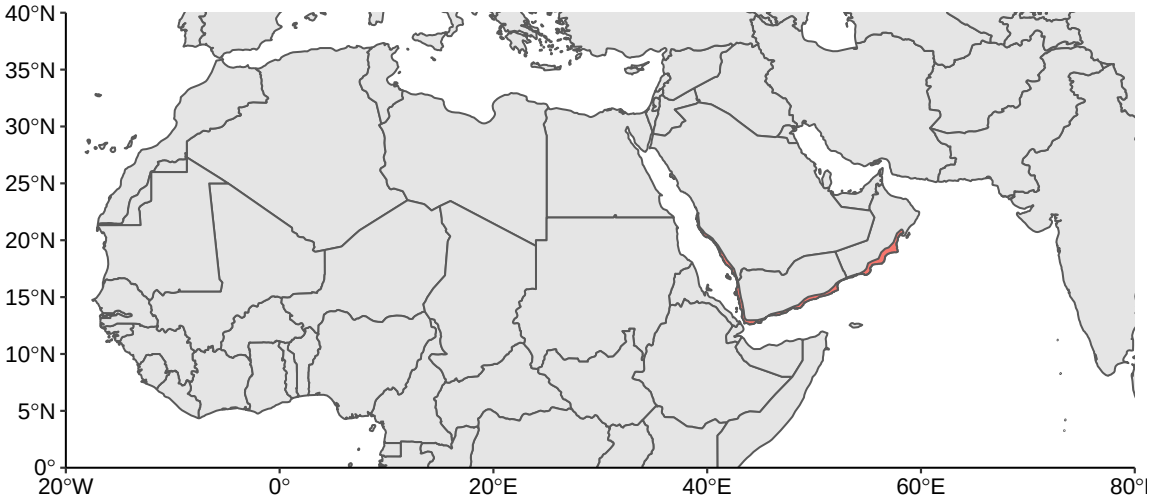
0.6
0.4
0.2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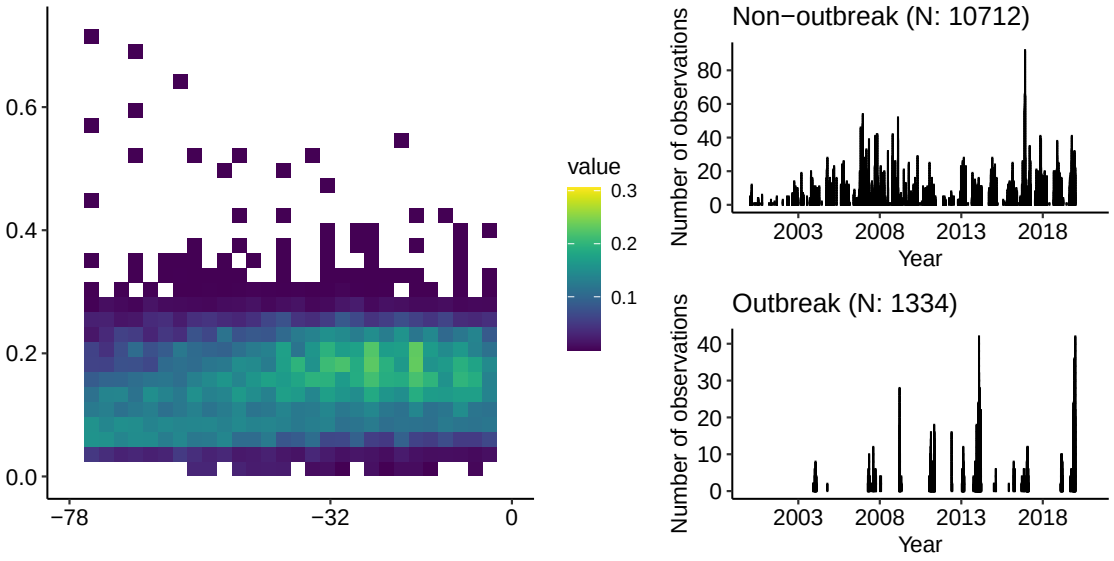
5°N
0°
20°W
0°
20°E
40°E
60°E
80°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value
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0.2
0.1
Non−outbreak (N: 10712)
Number of observations
80
60
40
20
0
2003
2008
2013
2018
Year
Outbreak (N: 1334)
Number of observations
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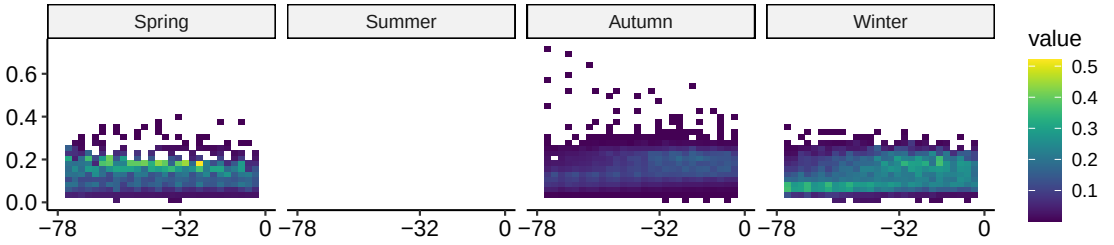
30
20
10
0
2003
2008
2013
2018
Year


Spring
Summer
Autumn
Winter
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0.2
0.0
−78
−32
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value
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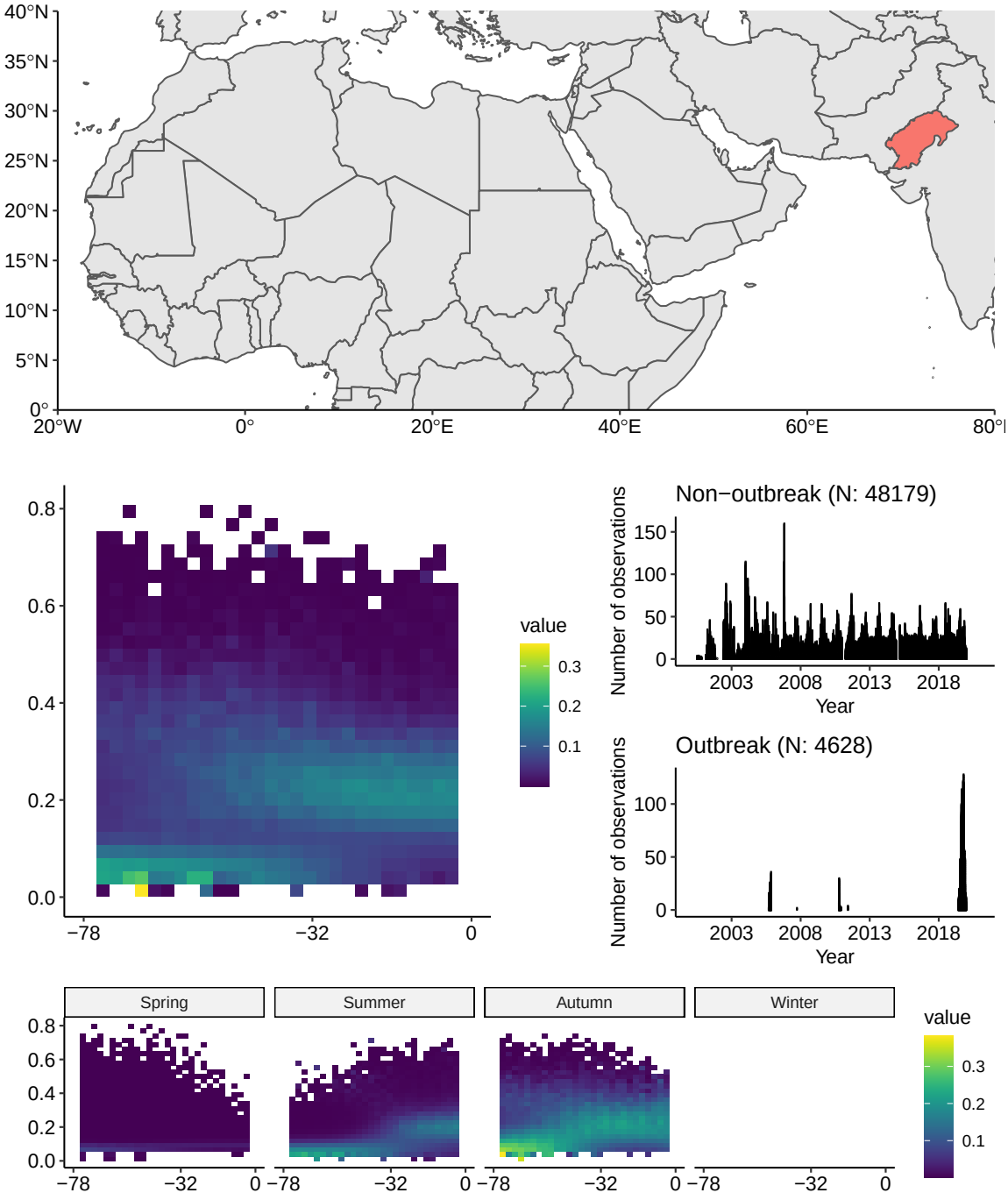
0.2
0.1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35°N
30°N
25°N
20°N
15°N
10°N
5°N
0°
20°W
0°
20°E
40°E
60°E
80°
0.8
0.6
0.4
0.2
0.0
−78
−32
0
value
0.3
0.2
0.1
Non−outbreak (N: 48179)
Number of observations
150
100
50
0
2003
2008
2013
2018
Year
Outbreak (N: 4628)
Number of observations
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50
0
2003
2008
2013
2018
Year
Spring
Summer
Autumn
Winter
value
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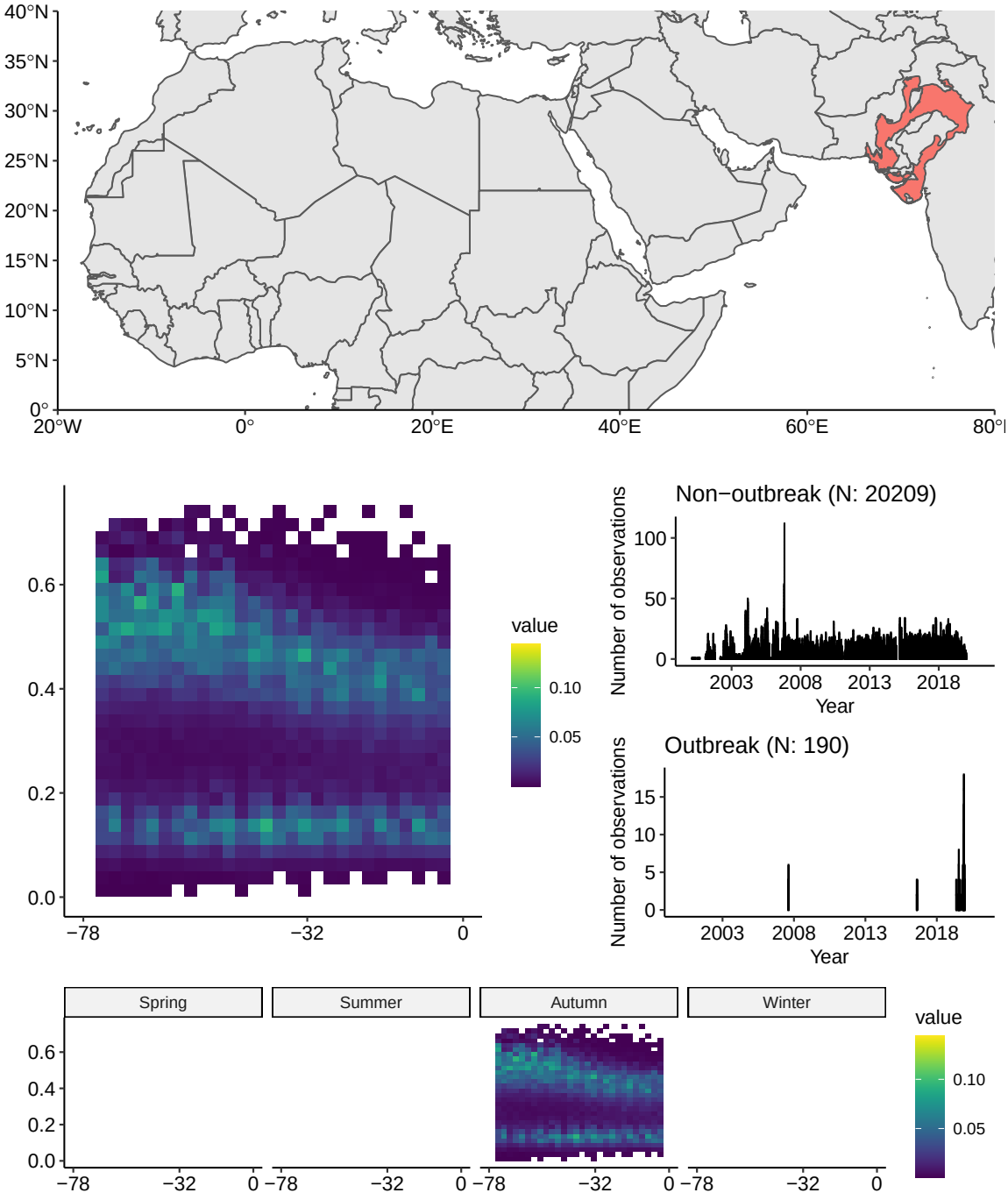
0.2
0.1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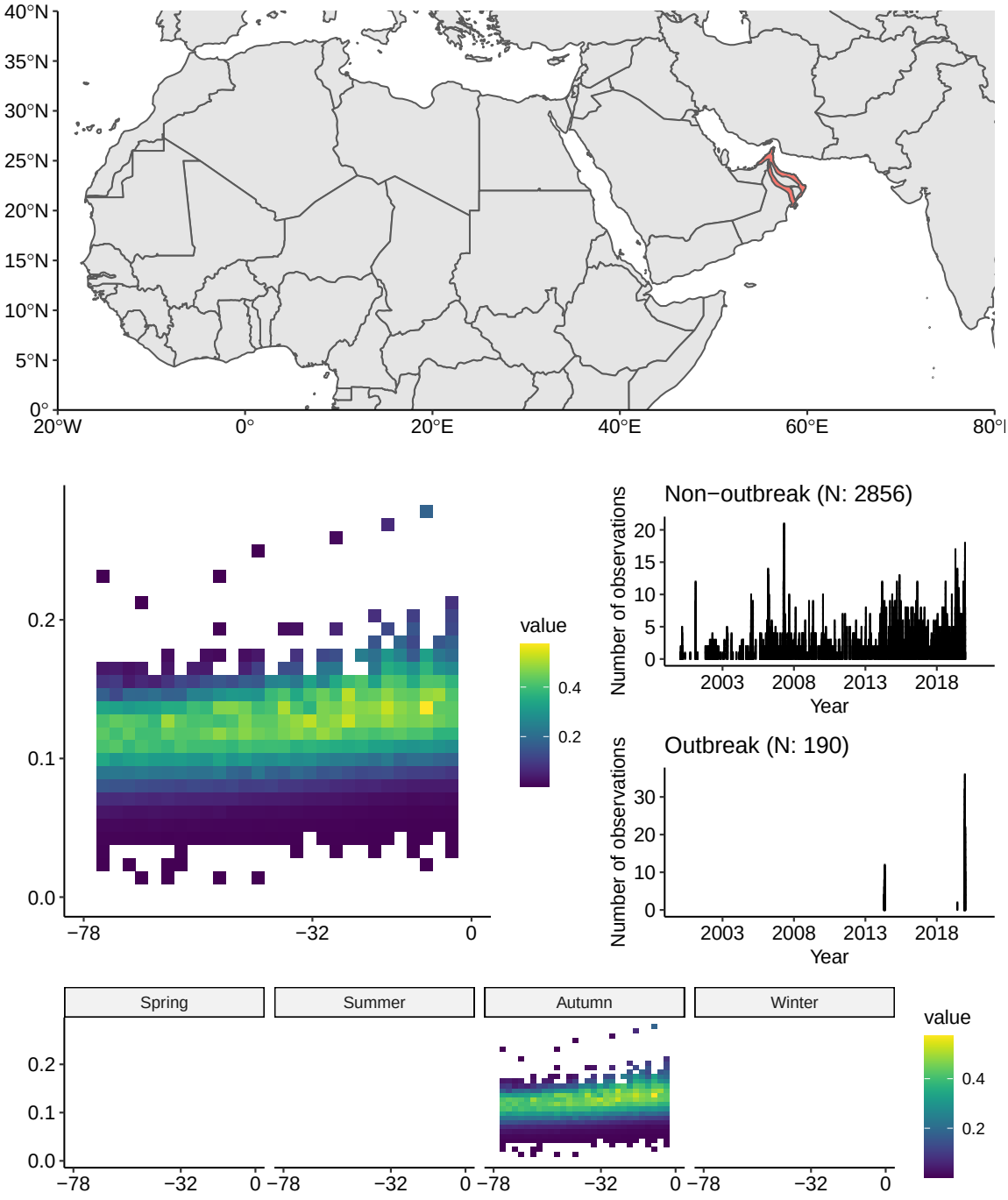
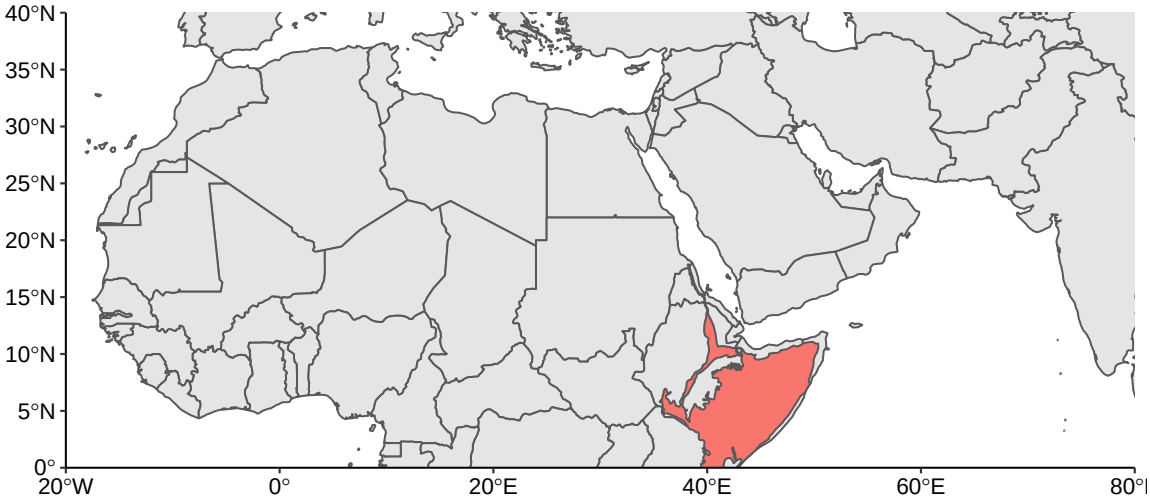
25°N
20°N
15°N
10°N
5°N
0°
20°W
0°
20°E
40°E
60°E
80°
0.6
0.4
0.2
0.0
−78
−32
0
value
0.10
0.05
Non−outbreak (N: 20209)
Number of observations
100
50
0
2003
2008
2013
2018
Year
Outbreak (N: 190)
15
10
5
0
Spring
Summer
Autumn
Winter

Gulf of Oman desert and semi−desert

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35°N
30°N
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5°N
0°
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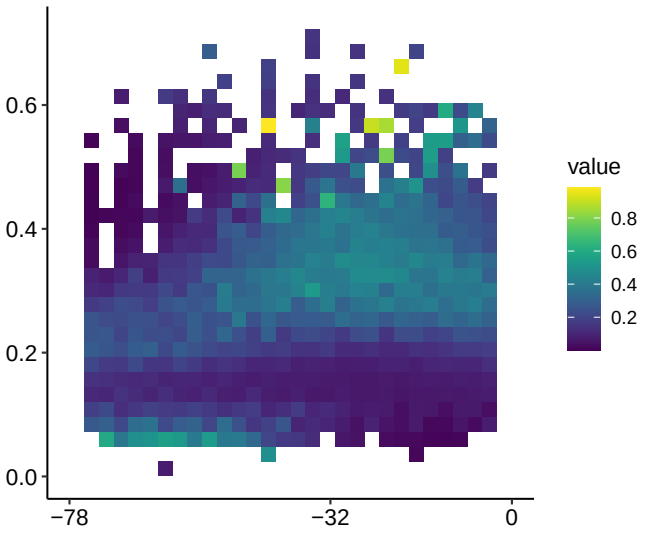
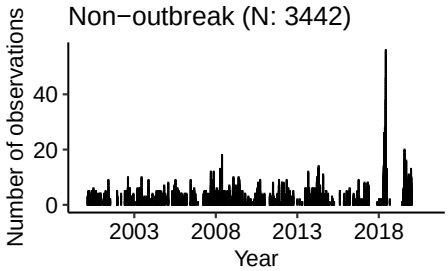
0°
20°E
40°E
60°E
80°


0.6
0.4
0.2
0.0
−78
−32
0
value
0.8
0.6
0.4
0.2


Non−outbreak (N: 3442)
Number of observations
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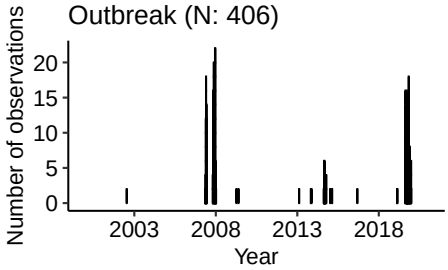
20
0
2003
2008
2013
2018
Year


Outbreak (N: 406)
Number of observations
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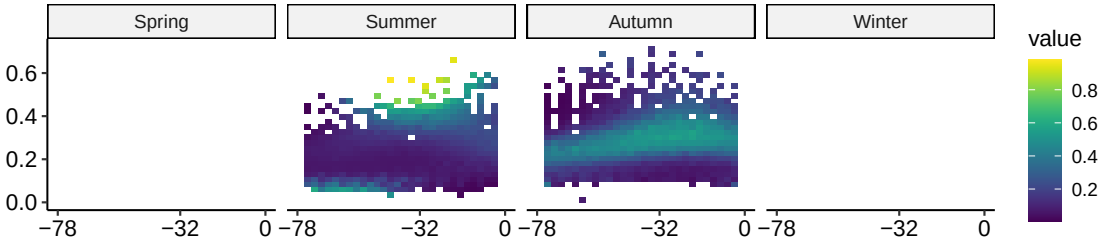
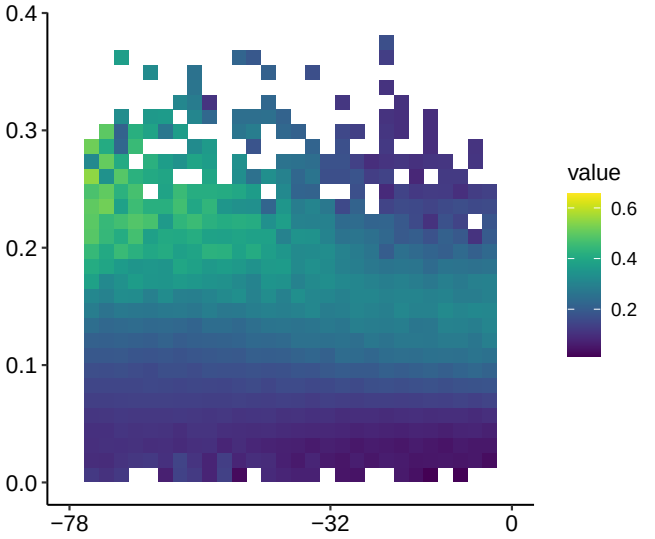
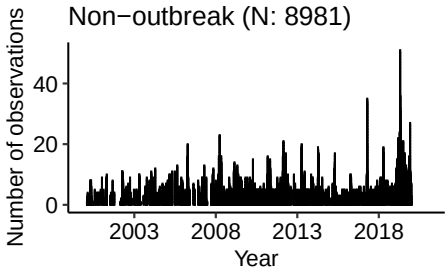
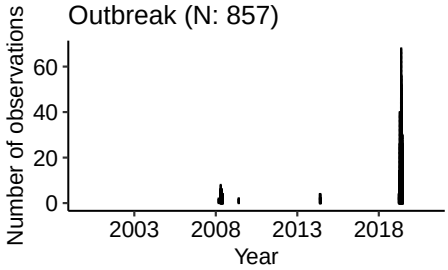
15
10
5
0
2003
2008
2013
2018
Year

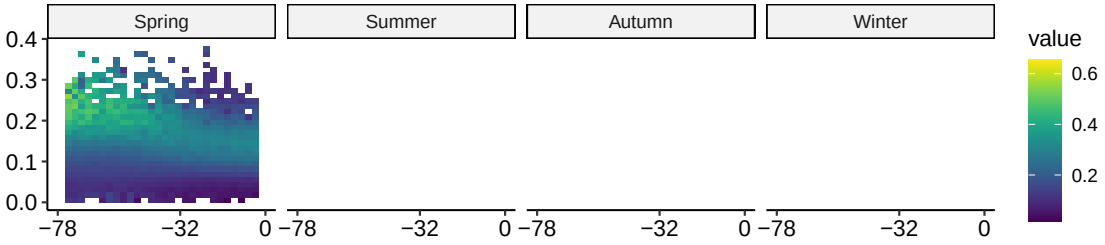

Spring
Summer
Autumn
Winter
0.6
0.4
0.2
0.0
−78
−32
0
value
0.8
0.6
0.4
0.2

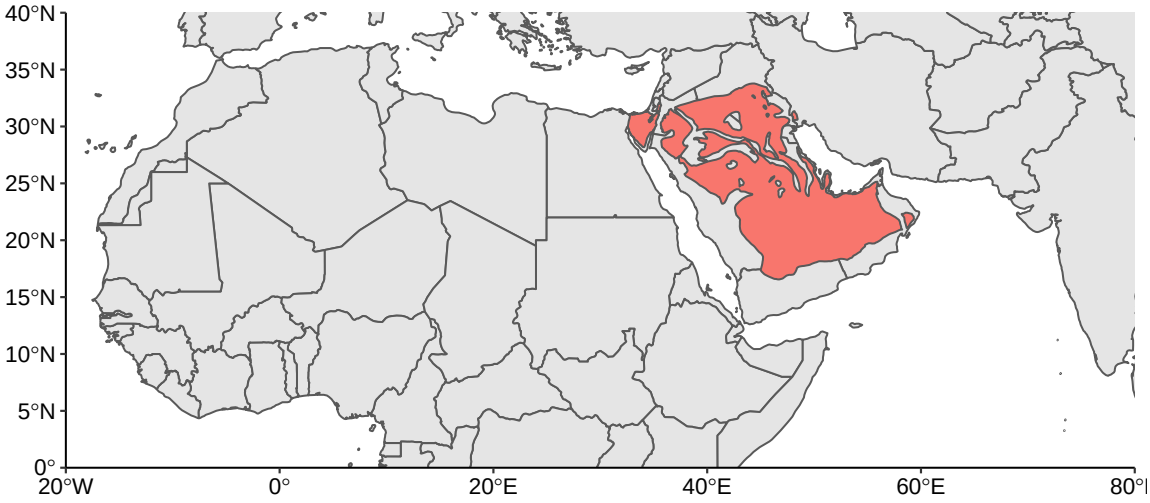
South Iran Nubo−Sindian desert and semi−desert

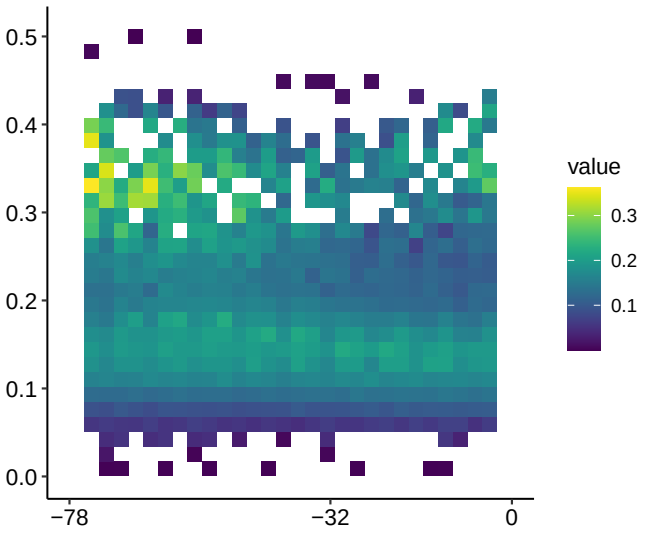


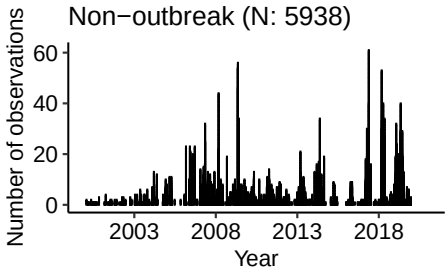


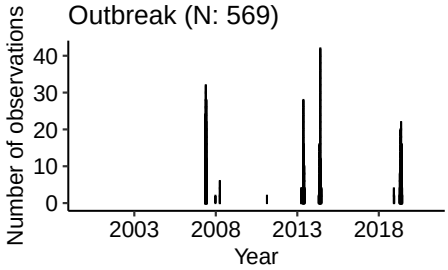


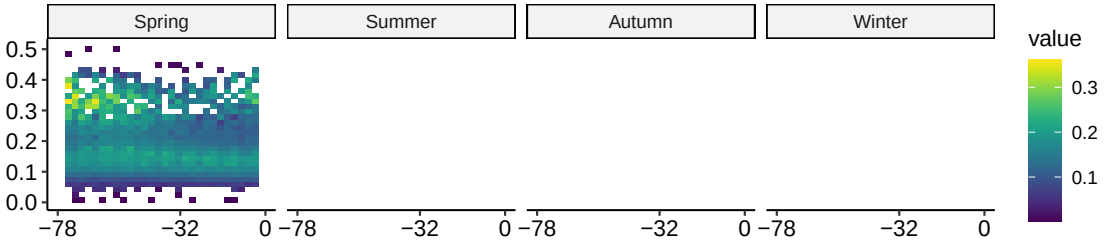



40°N
35°N
30°N
25°N
20°N
15°N
10°N
5°N
0°
20°W
0°
20°E
40°E
60°E
80°


0.5
0.4
0.3
0.2
0.1
0.0
−78
−32
0
value
0.3
0.2
0.1


Non−outbreak (N: 5938)
Number of observations
60
40
20
0
2003
2008
2013
2018
Year


Outbreak (N: 569)
Number of observations
40
30
20
10
0
2003
2008
2013
2018
Year


Spring
Summer
Autumn
Winter
0.5
0.4
0.3
0.2
0.1
0.0
−78
−32
0
value
0.3
0.2
0.1