

**Biodiversity assessments using remote sensing and integrative modelling
for improved conservation management**

by

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Declaration

By submitting this dissertation electronically, I declare that the entirety of the work contained therein is my own, original work, that I am the sole author thereof (save to the extent explicitly otherwise stated), that reproduction and publication thereof by Stellenbosch University will not infringe any third party rights and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

This dissertation includes one original paper published in a peer-reviewed journal or book and two unpublished publications. The development and writing of the papers (published and unpublished) were the principal responsibility of myself and, for each of the cases where this is not the case, a declaration is included in the dissertation indicating the nature and extent of the contributions of co-authors.

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General summary

Insect diversity is declining globally, threatening ecosystem collapse and human well-being. Accurate information on biodiversity dynamics is needed to guide landscape management. This is important within actively managed production landscapes (especially forestry and agriculture), where land use change and habitat degradation impacts biodiversity, which in turn influences ecological resilience.

Satellite remote sensing allows for collection of data over time, which enables a greater understanding of species distributions and drivers of change. Combining satellite-derived variables with advanced integrative modelling approaches, such as time series analysis, habitat suitability modelling, functional connectivity analysis and deep learning image fusion, allows for better understanding of biodiversity dynamics to guide landscape management.

In this dissertation, I focus on grasshoppers, indicators of high-quality grasslands, and study their diversity within grassland corridors between plantation forests, to gain a greater understanding of how plantation landscapes can be managed (e.g. prescribed burning, invasive plant management, tree harvesting) to ensure ecological resilience.

Satellite time series showed that changes in grassland structure can have a lasting positive impact on grasshoppers for up to three years. Prescribed burning, measured using historic Normalised Burn Ratio index, helps maintain high-quality grasshopper habitat, while also influencing functional connectivity of grassland corridors. Normalised Difference Vegetation Index (NDVI) was a useful tool to monitor grassland corridor condition and to assist with planning of prescribed burning. Large corridors with an elevation gradient support diverse assemblages and should be prioritised for conservation.

Deep learning image fusion classified American bramble (*Rubus cuneifolius*), an aggressive invasive species in South African grasslands, with high accuracy compared to conventional satellite imagery. Bramble had negative impact on plant species richness, larger-sized grasshopper species, as well as species of conservation concern. Bramble invaded riparian areas more frequently, threatening Ensifera grasshopper species habitat. Harvesting timber compartments and prescribed burning increased bramble cover within the landscape. Active management of plantation tree saplings after harvesting can lead to enhanced functional landscape connectivity and reduced bramble cover.

Grassland corridors have high vegetation heterogeneity caused by prescribed burning, which contribute to high species turnover. Corridors should be burned every 2-3 years. Using NDVI will help foresters to identify where and when to burn corridors, thereby maintaining high-quality grasshopper habitat and functional connectivity.

Rotational harvesting of timber compartments is recommended, as logging only some compartments will have positive impact on functional connectivity as well as helping prevent bramble invasion through the landscape. I recommend combining prescribed burning with grazing by domestic cattle to control bramble invasion. Special attention is needed to control bramble two years after harvesting, as this is when bramble cover is highest.

This dissertation demonstrated that grassland corridors maintain biodiversity within actively managed production landscapes when management incorporates biodiversity response to disturbance. This motivates for the maintenance and protection of grassland corridors in other parts of the world to conserve biodiversity and help address insect decline. Lastly, the techniques used here provide valuable insights into biodiversity response to actively manage landscapes, and can therefore be applied to other vegetation types for protecting biodiversity.

Algemene opsomming

Insekdiversiteit verminder wêreldwyd wat ekosisteem ineenstorting en menslike welstand bedreig. Ons benodig akkurate inligting op biodiversiteitsdinamika om landskapbestuur te lei. Dit is belangrik in produksielandskappe wat aktief bestuur word (veral bosbou en landbou), omdat verandering in grondgebruik en habitatdegradasie biodiversiteit impak, wat dan ekologiese veerkragtigheid beïnvloed.

Satelliet-afstandwaarneming versamel data oor tyd, wat vir ons 'n beter begrip van spesieverspreidings en hul drywers verskaf. Die gebruik van satelliet-afgeleide veranderlikes en geïntegreerde modelleringsbenaderings, soos tydreeksanalise, habitatgeskiktheids-modellering, funksionele konnektiwiteitsanalise en diep-leer beeldsamesmelting, laat toe vir beter begrip van biodiversiteitsdinamika om landskapbestuur te lei.

In hierdie tesis, fokus ek op sprinkaane, aanwysers van hoë kwaliteit grasvelde, en bestudeer hul diversiteit binne grasveldgange tussen plantasielandskappe, om 'n beter begrip te kry van hoe plantasielandskappe bestuur kan word (bv. Voorgeskrewe veldbrande, indringerplantbestuur, boomoes) om ekologiese veerkragtigheid te verseker.

Satelliettydreeks wys dat veranderinge in grasveldstruktuur 'n blywende positiewe impak op sprinkane het tot en met drie jaar. Voorgeskrewe veldbrande, gemeet deur die historiese "Normalised Burn Ratio" indeks, help om hoë-gehalte sprinkaanhabitat te handhaaf, terwyl dit ook funksionele konnektiwiteit van grasveldgange beïnvloed. "Normalised Difference Vegetation Index" (NDVI) is 'n nuttige hulpmiddel om grasveldgang toestand te monitor en om te help met beplanning van voorgeskrewe brande. Groot grasveldgange met 'n hoogtegradiënt ondersteun diverse springkaan gemeenskappe en moet geprioritiseer word vir bewaring.

Diep-leer beeldsamesmelting het Amerikaanse braambos (*Rubus cuneifolius*), 'n aggressiewe indringerspesie in Suid-Afrikaanse grasvelde, met hoë akkuraatheid geklassifiseer in vergelyking met konvensionele satellietbeelde. Braambos het 'n negatiewe impak gehad op plantegroei, groter sprinkaanspesies sowel as sprinkane van belang vir bewaring. Braambos het oewergebiede gereeld binnegeval, wat Ensifera sprinkaanspesies se habitat bedreig. Die oes van houtkompartemente en voorgeskrewe brande het braambedekking in die landskap verhoog. Aktiewe bestuur van plantasie

boomsaailinge na die oes van bome kan 'n positiewe impak hê op funksionele landskapkonnektiwiteit sowel as om braambedekking te velaag.

Grasveldgange het hoë plantegroei-heterogeniteit wat veroorsaak is deur voorgeskrewe brande, wat bydra tot hoë spesie-omset. Grasvelde moet elke 2-3 jaar gebrand word. Die gebruik van NDVI sal bosbouers help met tydsberekening en bepaling van brande in grasveldgange, wat dan help om hoë kwaliteit sprinkaanhabitat en funksionele konnektiwiteit te handhaaf.

Rotasie-oes van houtkompartemente word aanbeveel, aangesien die afkap van sommige houtkompartemente 'n positiewe impak op funksionele landskapkonnektiwiteit sal hê, as ook om braambos verspreiding deur die landskap te voorkom. Ek beveel aan dat voorgeskrewe brande en beweiding deur mak beeste gebruik word om braambos te beheer. Spesiale aandag is nodig om braambos te beheer twee jaar na die oes van houtkompartemente, omdat braambos bedekking dan hoog is.

Hierdie tesis demonstreer dat grasveldgange biodiversiteit binne produksielandskappe bewaar wanneer bestuur biodiversiteitsreaksie op versteuring inkorporeer. Dit motiveer die instandhouding en beskerming van grasveldgange in ander dele van die wêreld om biodiversiteit te bewaar, wat help om insekafname te voorkom. Hierdie tegnieke bied waardevolle insigte op biodiversiteitsreaksie binne produksielandskappe, en kan dus toegepas word op ander plantegroei tipes vir die beskerming van biodiversiteit.

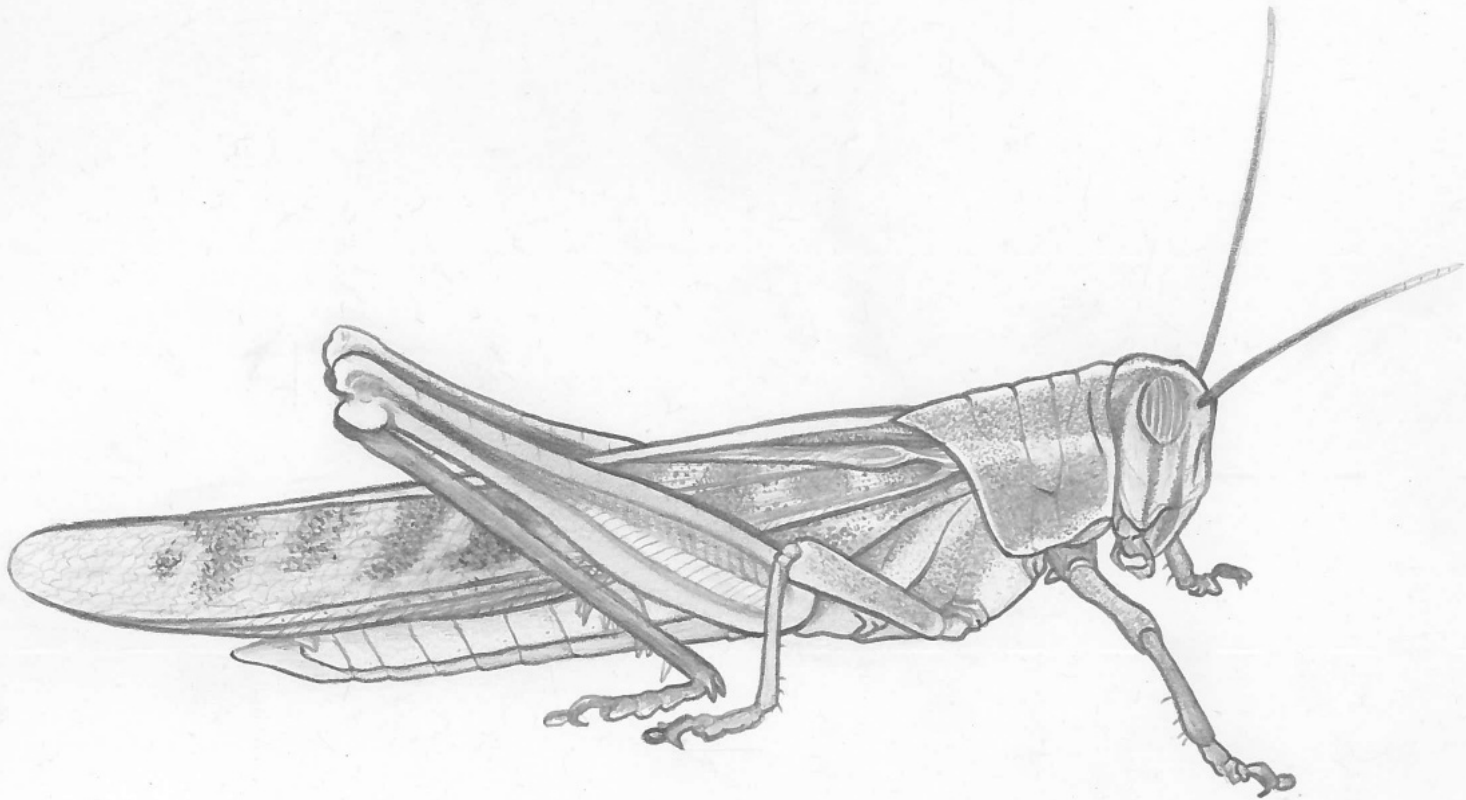
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Your legacy reaches far and wide.



DRJB

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Chapter 1: General introduction

1.1. Importance of insects

Insects are among the most speciose lifeforms on Earth, with an estimated 7 million insect species, forming the bulk of multi-cellular life on our planet (Stork 2018). They have a long evolutionary history, being associated with the earliest land plants some 303 million years ago (Labandeira 2006). Over this time, insects have evolved and diversified with a remarkable array of anatomical traits allowing them to successfully dominate most of the planet (Scudder 2017). This remarkable diversity has made them fundamental to the functioning of ecosystems, as they provide numerous ecosystem services. Insects are responsible for the creation of soil, regulation of water quality, dispersal of seeds, prevention of erosion, decomposition, dung removal, and much more (Noriega et al. 2018). Humans rely on services provided by insects, specifically within agroecosystems, where insects provide services such as pollination, nutrient and energy cycling, and pest suppression (Schowalter et al. 2018). Furthermore, insects contribute to ecosystem function regionally, as insects utilise air currents to disperse over great distances, connecting far-off fragmented habitats and influencing biogeochemistry (Hu et al. 2016).

The great importance of insects to humanity is, unfortunately, still largely unknown to science, considering that most insects are still undiscovered (Stork 2015), with only around 1 million described species (Footitt and Adler 2017). However, this undiscovered potential is being lost, as insects are going extinct at alarming rates, caused principally by rapid anthropogenic developments (Cardoso et al. 2020). The loss of insect diversity impacts human well-being, and the need for humanity to conserve insect diversity and maintain ecological integrity has never been more important (Samways 2020).

1.2. Drivers and consequences of insect decline

The rate of declining insect abundance and species richness, accompanied by the cascading disruptions in ecosystem services, has received substantial attention in recent years, not only within the scientific literature, but also among the public and media outlets (Montgomery et al. 2020), causing insect conservation to rapidly gain global attention (Samways 2020). Although the rate of insect decline and extinction is not the same across the globe (Saunders et al. 2020), with complex patterns of species decline existing within local regions (Wagner et al. 2021a), there is a general consensus that insect diversity is

declining, especially specialist species (Wagner et al. 2021b). Anthropogenic drivers causing habitat loss and fragmentation, pollution, spread of alien invasive species, and climate change, has been identified as among the main drivers causing insect population decline and extinction globally (Cardoso et al. 2020).

Furthermore, these drivers are escalating, which threatens the historic functioning of ecosystems (Dirzo et al. 2014).

Climate change, a major challenge facing humanity, has a disproportionately large negative impact on montane adapted species, as these species cannot move to higher elevations to escape warming climates (Halsch et al. 2021). Furthermore, agricultural expansion and intensification is another challenge, having devastating effects on insect biodiversity. In response to this challenge, we need to find sustainable ways to balance food production while conserving biodiversity (Raven and Wagner 2021). Even though these individual stressors have major negative impacts on insect abundance and diversity, there is still uncertainty with respects to their potential interactions, with recent studies demonstrating a cumulative effect between multiple stressors best explaining insect decline (Wagner et al. 2021b).

Conveying the consequences of insect biodiversity loss to the public and to increase conservation awareness is a daunting challenge. Most services provided by insects have indirect impact on our daily lives, yet insects are not often regarded as important conservation targets. To address these challenges, researchers attempted to place monetary values on insect services. To date, the most comprehensive economic assessment of insect services was done by Losey and Vaughan (2006), who calculated a total amount of \$57 billion for pollination, dung burial, pest control and wildlife nutrition services in the United States alone. More recently, pollinators in the commercial apple orchards of South Africa, were shown to have a substantial influence on fruit yield and quality, with a gross return of R941 million (c. \$50 million) across the region (Ratto et al. 2021).

Unfortunately, ecologists and entomologists have to date not fully conveyed the great importance of insects to the public, as globally the general perception towards insects are overwhelmingly negative (Fukano and Soga 2021). Without insects, a multitude of animals, specifically birds, bats, reptiles, amphibians, small mammals, and fish, would disappear, causing the collapse of terrestrial and freshwater food webs (Goulson 2019). Furthermore, about 75% of edible crops require pollination by insects, and it would therefore not be possible to feed the global human population without them (Noriega et al. 2018).

There is an urgent need to incorporate the importance of insects in education systems to change human perception towards insects to help protect them (Boileau and Russell 2018). Additionally, innovative solutions are needed to increase the amount of habitat being protected for conserving insect biodiversity.

1.3. Conservation in production landscapes

Protected areas are the cornerstone of biodiversity conservation (Coetzee et al. 2014). However, most of Earth's protected areas are poorly connected, preventing effective gene flow, restricting genetic diversity, and hampering eco-evolutionary dynamics (Saura et al. 2018). Models also predict a 50% reduction of intact vegetation within protected areas by 2050, if current agricultural and climate pressures continue unchanged (Habel et al. 2019). Protected areas alone can therefore not conserve all biodiversity, especially as large amounts of biodiversity occur outside protected areas (Gray et al. 2016). This has sparked a long-standing debate about effectiveness of conserving biodiversity within actively managed production landscapes (i.e. agricultural land), which is known as the land sharing-land sparing spectrum (Sidemo-Holm et al. 2021). Land sharing involves environmentally friendly practices within production landscapes to conserve biodiversity, as opposed to land sparing, which involves preserving intact natural vegetation patches alongside actively managed land for biodiversity conservation (Sidemo-Holm et al. 2021).

The sparing of natural vegetation within production landscapes has great potential for biodiversity conservation, compared to land sharing (Balmford et al. 2018), and the formal protection of these areas are critically important for safeguarding biodiversity (Dudley et al. 2018). Incorporating key areas into the protected area network will greatly improve landscape connectivity to sustain biological functioning (Kullberg et al. 2019). This is achievable, as 37% of the world's eco-regions have sufficiently large amounts of intact natural habitat outside of protected areas (Dinerstein et al. 2017). For example, throughout the timber plantation mosaic of South Africa, large-scale grassland corridors are maintained for biodiversity conservation and support a variety of arthropod taxa (Samways and Pryke 2016). These corridors are crucial for insect diversity conservation under global change (Samways et al. 2020), and when managed correctly, they support arthropod diversity at a similar level as in neighbouring protected areas (Pryke and Samways 2012).

The dynamic nature of production landscapes impacts biodiversity in several ways (Vasseur et al. 2013), and we need to improve our understanding of how management, and timing of management, impacts biodiversity, allowing us to optimise conservation programmes within production landscapes (Jung et al. 2019). The grassland corridors in KwaZulu-Natal, for example, are subject to invasion by alien plants, especially American bramble (*Rubus cuneifolius*) impacting pollination networks (Hansen et al. 2018), as well as uncontrolled cattle grazing, where heavy grazing impacts grasshopper assemblages (Joubert-van der Merwe and Pryke 2018). Furthermore, because these grassland corridors occur between commercial forestry plantations, active fire management is needed, not only for biodiversity, but for the protection of the timber compartments. Fortunately, prescribed burning within the grassland corridors has beneficial outcomes for plants, grasshoppers, and butterflies (Joubert et al. 2014, 2016; Gaigher et al. 2019). However, the efficacy of grassland corridors for protecting biodiversity into the future has been raised previously (Samways and Pryke 2016), and empirical evidence is now needed to quantify the longevity of grassland corridors for arthropod conservation. Furthermore, robust methods for monitoring the status of grassland corridors are needed.

1.4. Technology for monitoring and understanding insects

Monitoring of biodiversity has been recognised as vital for informed management decisions by multiple monitoring and reporting frameworks, such as the United Nations' Sustainable Development Goals, as well as the Aichi biodiversity targets and the Post-2020 Global Biodiversity Framework of the Convention on Biological Diversity (Pettorelli et al. 2016; Vihervaara et al. 2017). Management decisions derived from monitoring programmes need to be based on high-quality data that provide information on the state of, and pressures on, biological diversity across space and time. As conventional field-based observations are limited to small spatial scales, satellite remote sensing (SRS) has become an important tool for monitoring biodiversity over large spatial scales and over time (Rocchini et al. 2016). Advances in integrated cloud computing platforms, such as Google Earth Engine, allows more users to access SRS data, thereby increasing our understanding of the changing planet (Gorelick et al. 2017). Furthermore, SRS is increasingly being used to guide management decisions for promoting conservation (Randin et al. 2020), arising from increasingly open access of satellite data (Zhu et al. 2019).

Satellite sensors record electromagnetic radiation reflected from objects on the Earth's surface. This reflected radiation provides important information about those objects. Spectral data derived from satellite imagery are then used to study relationships between local biodiversity and the property being measured by the satellite. For example, the Normalised Difference Vegetation Index (NDVI) is a measure of plant greenness, calculated using red and near infrared spectral bands, and constitutes an informative proxy for photosynthesis, and has been used to study patterns in arthropod diversity (Lafage et al. 2014; Sweet et al. 2015; Miller et al. 2017).

Remote sensing scientists rely on the environmental data recorded by satellites, such as plant productivity or microclimate, and how this relates to arthropods, to design effective monitoring programmes (Rhodes et al. 2021). Furthermore, alongside using SRS to study patterns in arthropod diversity, recent advances in non-parametric classification algorithms combined with SRS has allowed us to map alien invasive plant species with high accuracies (Royimani et al. 2019; Rebelo et al. 2021), which is of fundamental importance for designing conservation programmes for protecting biodiversity (Pyšek et al. 2020).

Alternative to satellites as a remote sensing platform, unmanned aerial vehicle (UAV) technology has grown considerably over the last few years (Horning 2018; Singh and Frazier 2018), allowing us to capture imagery at very high resolution (cm), which can be used for plant species classification or deriving environmental data at a relevant scale for insects. Unfortunately, local legislation around operating UAV is a significant challenge in many regions, which substantially hampers the adoption of UAV (Dash et al. 2019). However, recent developments in deep learning have provided new opportunities for creating imagery with high resolution through image fusion (Palsson et al. 2018; Latte and Lejeune 2020). Image fusion using deep learning involves the joining of imagery with different properties (spectral and spatial) to create a new data product with the desired resolution. This technique is also known as image super-resolution, where a neural network learns to enhance the resolution of imagery by identifying relationships between low- and high-resolution pixels (Dong et al. 2016). Deep learning image fusion provides exciting opportunities for studying biodiversity patterns using SRS.

Effective management of biodiversity within production landscapes also entails a thorough understanding of species distributions and factors which might influence their distribution. Species

distribution modelling (SDM) is critical for this, as it can help us study a species potential distribution as well as identifying the drivers. This is done by correlating environmental variables with species occurrence data and making predictions based on the strength of these correlations. Species distribution modelling has been used to study the potential distribution of endemic grasshoppers within the wine growing region of the Western Cape, South Africa (Adu-Acheampong et al. 2017), as well as to predict the risk of establishment and spread of non-native pest species (Lantschner et al. 2019). It is also increasingly being used to study insect habitat (Koch 2021).

Predictions made by SDM can be greatly improved through using SRS data, especially time series data, allowing us to study how dynamic production landscapes impacts species distribution over time (Leitão and Santos 2019; Randin et al. 2020). This is especially important, as historic events have a stronger influence than current events on shaping local species assemblages (Jung et al. 2019), which highlights the importance of timing management practices to benefit future biodiversity.

Analogous to SDM, landscape connectivity modelling has become an invaluable tool for mapping how animals move within a landscape and allowing areas to be identified where connectivity needs to be improved (McRae et al. 2008). How the landscape impacts the ability of animals to move through it is known as functional connectivity (Tischendorf and Fahrig 2000), which works on the premise that different landscape features provide varying challenges for species, either allowing them to move freely, restricting movement by filtering species/traits, or by completely preventing movement. Recent integration of electrical circuit-theory into conservation and landscape connectivity research has provided new opportunities for studying functional connectivity (Dickson et al. 2019), through the development of *Circuitscape* software (McRae et al. 2008). *Circuitscape* has been used to estimate the value of restoring grassland patches for improving the flow of important insect predators that contribute to biological control in the Midwest United States (Koh et al. 2013), as well as for identifying areas for habitat restoration to improve habitat connectivity for various endemic arthropods of Azores (Aparício et al. 2018). Furthermore, the number of articles where *Circuitscape* is used to study connectivity for arthropods are increasing, compared to other taxa like birds (Dickson et al. 2019).

Unfortunately, most studies that utilise SDM and functional connectivity analysis for conservation management tend to focus on a single species (Ahmadi et al. 2017; Dufлот et al. 2018), leaving other

dimensions of biodiversity, such as beta diversity, overlooked. Beta diversity is a measure of diversity that represents compositional differences between local species assemblages. It is central to our understanding of how species diversity is maintained or impacted throughout the landscape (Socolar et al. 2016). High beta diversity, or species turn-over, thus indicates large changes in species assemblages between locations. Modelling beta diversity is therefore valuable for conservation assessments (Ferrier et al. 2007), as it provides information on the uniqueness of local biodiversity patterns. For example, Deacon et al. (2020) used species turn-over calculations to identify drivers of dragonfly diversity patterns across South Africa, whereas van Schalkwyk et al. (2020) used species turn-over calculations to determine arthropod spillover within orchards in the Kogelberg Biosphere Reserve, South Africa. Through combining SRS with SDM, functional connectivity, and species turn-over calculations, we can get an improved understanding of how natural vegetation contributes to biodiversity conservation within production landscapes.

1.5. Satellite remote sensing of insects

There are considerable challenges and limitations when trying to study insects remotely. Most noticeable is the importance of satellite image resolution, both spatially and temporally, for insect remote sensing (Rhodes et al. 2021). Insects are much smaller than the spatial resolution of remotely sensed data products, barring the use of drone technology, making direct observation currently extremely difficult. Also, the short life cycles of insects mean that most remote sensing data with low temporal resolution will miss key phenomena important for direct monitoring of insects. This means that the use of SRS for insects relies on indirect relationships between easily measurable properties of the landscape, such as vegetation productivity (NDVI), vegetation type, land cover type, and topography, to name a few, and how these landscape properties relate to insect diversity. For example, grassland productivity measured through NDVI has been used as a proxy for food availability and correlates strongly with arthropod biomass in spring, allowing the inference of arthropod biomass in relation to NDVI in remote areas (Fernández-Tizón et al. 2020). The establishment of such indirect relationships are extremely important for insect remote sensing and mostly achieved through fieldwork.

Satellite remote sensing has a long history within entomological research, particularly with pest detection in forestry and agriculture. However, considerable potential remains in relation to using SRS for studying insect ecology and conservation (Rhodes et al. 2021).

1.6. Insect bioindicators

Insects are sensitive to changes in their immediate physical and chemical surroundings (Webster and Cardé 2017), as such they are often used to indicate the state or quality of the local environment (Gerlach et al. 2013). The presence, or absence, of a specific insect indicator species can serve as an early warning sign of environmental change or indicate the level of taxonomic diversity at a site (Gerlach et al. 2013). Insect indicators thereby help determine the stress levels in an ecosystem, or the rate of recovery after the specific stressor has been mitigated, which is particularly useful in monitoring the impact of change/disturbance on biodiversity within production landscapes (Samways et al. 2020).

For this dissertation, grasshoppers were specifically selected as study organisms to validate patterns derived from SRS, as they are effective indicators of high quality grassland habitat (Bazelet and Samways 2011; Fartmann et al. 2012), constitute a significant proportion of invertebrate diversity in grassland (Little et al. 2013), and are sensitive to changes in local environment (Löffler and Fartmann 2017).

1.7. Research gaps

Previous studies has shown that sparing of natural vegetation within production landscapes has great potential for biodiversity conservation (Pryke and Samways 2012, Samways and Pryke 2016). However, there is little support for their longevity and the ability to support long-term biodiversity. There is also no clear guidelines for using remote sensing tools for monitoring grasslands habitat to guide management. Within the grassland corridors in KwaZulu-Natal, research has mostly focused on the structural nature of the corridors, and overlooked if these corridors also promote functional connectivity. There is also a lack of clear guidelines for land managers to use when prioritising restoration efforts for conservation. Furthermore, there are no adequate methods to monitor the spread of invasive shrubs, like bramble, and we have little understanding of bramble invasion dynamics, which are needed to help control the spread and conserve biodiversity.

1.8. Overall aims

This dissertation aims to contribute to our growing understanding of how grassland corridors conserve arthropod diversity under global change using SRS and other modelling procedures to improve conservation management of production landscapes. Grassland corridors within South Africa are ideal study areas, as these grassland ecosystems are highly threatened yet support high levels of biodiversity (Samways and Pryke 2016). I specifically aim to 1) provide insight into grassland corridor longevity by performing time series analysis, 2) link satellite-derived NDVI with grasshopper diversity for remote monitoring, 3) identify drivers of grasshopper distribution using stacked species distribution modelling and species turnover calculations, 4) assess whether corridors promote functional connectivity using Circuit-theory, 5) use super-resolution imagery derived from machine learning to map the distribution of bramble, and 6) to gain valuable insight into bramble invasion dynamics by performing landscape analysis.

This dissertation will be presented as a series of connected and overlapping articles, investigating various aspects of grassland corridors for grasshopper conservation. This research will also contribute to the global literature on grassland conservation and management.

1.9. Dissertation outline and chapter aims

In chapter 2, I investigated the longevity of grassland corridors for conserving biodiversity by studying how past management impacts current patterns in grasshopper diversity. This is important as biodiversity is directly linked to appropriate management of these corridors, with accumulating evidence showing that past grassland management has a lasting impact on biodiversity (Perring et al. 2018; Löffler et al. 2020; Poniatowski et al. 2020). Furthermore, recent change (past five years) is also important (Jung et al. 2019), as it directly affects species fitness and progeny (O'Connor et al. 2014). To gain insight into this, I examined how historic grassland photosynthetic activity (25-year NDVI time series) shaped current grasshopper diversity and assemblage structure. Vegetation characteristics measured in the field was used to understand the potential mechanisms driving grasshopper response. Lastly, I explored the efficacy of SRS for monitoring grasshopper habitat. By doing this, I aimed to answer the following questions: 1) How does variation in grassland photosynthetic activity through time affect grasshopper diversity? 2) Which local

patch-level variables influence grasshopper diversity? 3) What is the relationship between grassland photosynthetic activity and grasshopper diversity? From this work I aimed to gain a better understanding of how current management within grassland corridors will impact future biodiversity, which will help optimise planning of management activities for conserving biodiversity.

Understanding the relationship between grassland photosynthetic activity and grasshopper diversity can provide new insights into how the landscape functions to support species. To take this further, chapter 3 examined how grassland corridors maintain ecological resilience by studying the distribution of high-quality grasshopper habitat. However, effectively protecting high-quality grasshopper habitat can only be achieved by understanding how the landscape facilitates ecological processes, such as species movement, as well as what impacts the ability of a species to move through the landscape (Wurtzebach and Schultz 2016). Therefore, to better understand how the managed landscape is affecting biodiversity, and which management practices provide opportunities for biodiversity conservation, I combined stacked-species distribution modelling, functional landscape connectivity analysis, and species turn-over calculations. In doing this, I aimed to answer the following questions: 1) What is driving the distribution of high-quality grasshopper habitat? 2) How connected are high-quality habitats, and where should connectivity be restored? 3) What are the drivers causing changes in grasshopper species richness and beta diversity throughout the landscape? 4) How similar are these patterns among species with different conservation priorities? Answering these questions allowed a better understanding of the variables important for maintaining high-quality habitat for grasshopper conservation, variables important for increasing beta diversity, identifying crucial corridors for maintaining functional connectivity, how the landscape can be managed to improve functional connectivity, and where to prioritise restoration within the landscape to improve functional connectivity for biodiversity conservation.

Another challenge for conserving biodiversity within production landscapes is the control of alien invasive plant species, which is one of the main drivers of global biodiversity loss (Pyšek et al. 2020). However, our ability to effectively monitor alien invasive plant species, especially shrubs, are limited, and monitoring tools are needed to improve control programmes. In chapter 4, I explored recent advances in deep learning and super-resolution image reconstruction (Latte and Lejeune 2020) for mapping an alien invasive shrub. Specifically, I aimed to map American bramble (*Rubus cuneifolius*) within grassland corridors, which

threatens plant species richness and endemic grassland birds (Reynolds and Symes 2013), dragonflies (Kietzka et al. 2015), pollinating insects (Hansen et al. 2018), soil arthropods and soil recovery (Eckert et al. 2019). Through using super-resolution satellite imagery, I aimed to improve our understanding of bramble invasion dynamics by answering the following questions: 1) How widespread is bramble, and what is causing higher bramble cover? 2) What is the local impact of bramble on other plants and on grasshoppers? 3) How will uncontrolled bramble invasion impact the landscape? By answering these questions, I aimed to improve our understanding of the influence of image resolution for mapping alien invasive shrubs, elucidating the mechanisms driving bramble invasion within production landscapes, and determining the impact of bramble on landscape and local biodiversity, as well as providing management recommendations for controlling the spread of bramble.

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Chapter 2: Identifying managerial legacies within grassland corridors using remote sensing and grasshoppers as bioindicators

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2.1. Abstract

Biodiversity conservation under global change requires effective management of key biodiversity areas, even areas not under formal protection. Natural grassland corridors between plantation forests are such areas, as they improve landscape connectivity, mitigate the impact of landscape fragmentation, and conserve biodiversity. However, empirical evidence is required to identify the extent to which past management actions promote effectiveness of grassland corridors into the future. I address this issue using grasshoppers, which are well-established indicators of habitat quality. In particular, I assess grasshopper response within corridors to historic grassland photosynthetic activity using a 25 year Normalised Difference Vegetation Index (NDVI) time series. I then use vegetation characteristics measured in the field to understand the potential mechanisms driving grasshopper response. Furthermore, I explore the efficacy of satellite remote sensing for monitoring grasshopper habitat using additive models. I found that grasshopper evenness responded positively to deviation in NDVI within a three-year period, whereas assemblage composition responded positively over a shorter time of two years. Grasshopper richness and evenness responded strongly to the local vegetation height and bare ground, whereas grasshopper assemblage composition also responded to plant species richness. I found a major negative impact of the invasive alien bramble (*Rubus cuneifolius*) on large-sized grasshoppers and species of conservation concern. Overall, the results illustrate the importance of maintaining primary high-quality habitat for conserving grasshopper diversity, alongside removal of invasive bramble. I recommend prescribed burning to maintain high-quality habitat heterogeneity, with sites burned within three years. Furthermore, high-resolution satellite imagery is effective for monitoring grasshopper richness and assemblage composition response to changes in vegetation within the corridors. Grassland corridors do conserve biodiversity, although effective management and monitoring needs to be in place to ensure biodiversity resembles that of neighbouring protected areas.

Keywords: fire; lag effect; monitoring; NDVI; Orthoptera; time series

2.2. Introduction

Protected areas alone cannot conserve all biodiversity, as large amounts of biodiversity occur outside these areas (Gray et al. 2016). Conserving unprotected areas is therefore critically important for safeguarding biodiversity (Dudley et al. 2018), especially as insect extinctions are increasing globally at alarming rates (Cardoso et al. 2020). Most of Earth's protected areas are poorly connected, preventing effective gene flow, restricting genetic diversity, and hampering eco-evolutionary dynamics (Saura et al. 2018). This means that effective biodiversity conservation under global change requires improved connectivity between areas of irreplaceable biodiversity. This can be achieved by extending the protected area network to include unprotected key biodiversity areas (Kullberg et al. 2019). Fortunately, this is possible, as 37% of the world's eco-regions have sufficiently large amounts of intact natural habitat outside of protected areas that should be protected (Dinerstein et al. 2017). Protecting these key biodiversity areas, and increasing connectivity between them, is crucial for insect diversity conservation under global change (Samways et al. 2020).

Within South Africa, the commercial timber production landscape has converted large parts of the natural environment to plantation forests (mostly *Pinus* and *Eucalyptus* species), predominately within KwaZulu-Natal and Mpumalanga provinces. These plantations cover approximately 2.1 million ha, making up 1.6% of land in South Africa (Thompson 2019). Between the plantation blocks large amount of mostly intact remnant habitat still resides, forming structurally connected grassland corridors, which are set aside for biodiversity conservation (Samways and Pryke 2016). These grassland corridors are recognised as playing a critical role in protecting biodiversity under global change, as this land falls outside formally protected areas (Samways et al. 2020). Corridors also extend the reaches of neighbouring protected areas by improving connectivity of the timber plantation landscape (Pryke and Samways 2012a), which helps to mitigate the adverse effects of landscape fragmentation on biodiversity (Samways and Pryke 2016).

Correct management of the timber plantation landscape is needed for maintaining biodiversity within grassland corridors. For example, prescribed burning used to reduce grassland fuel load for protecting timber compartments against wildfires, helps maintain stable grassland plant populations within this fire adapted ecosystem (Joubert et al. 2014) and promote grasshopper and butterfly diversity (Joubert et al. 2016; Gaigher et al. 2019). However, invasion of the alien invasive plant *Rubus cuneifolius* (American bramble) into grasslands, has severe negative impacts on grassland bird diversity (Reynolds and Symes 2013), flower

visiting insects (Hansen et al. 2018), as well as on the restoration success of grasslands (Eckert et al. 2019). Furthermore, domestic cattle roam throughout these corridors, causing some excessive grazing of the landscape, as manifested by changes in grasshopper assemblage composition (Joubert-van der Merwe and Pryke 2018).

When corridors are managed correctly, they are able to conserve endemic and threatened grassland plants (Joubert et al. 2014), a variety of arthropod taxa (Pryke and Samways 2015), as well as grassland specialists birds (Lipse and Hockey 2010). This is possible because of how resources, important for survival, are distributed throughout the corridors, which helps improve landscape functional connectivity (Tischendorf and Fahrig 2000).

The efficacy of corridors to conserve biodiversity into the future has been raised previously (Samways and Pryke 2016), but more empirical evidence is needed to quantify the long-term effectiveness of corridors for biodiversity conservation. Developing resilience should be a key priority when developing management recommendations for protecting biodiversity within grassland corridors. This is especially important as biodiversity is directly linked to appropriate management of these corridors, with accumulating evidence showing that past management has a lasting impact on biodiversity (Perring et al. 2018; Löffler et al. 2020; Poniatowski et al. 2020a). Furthermore, recent change (past five years) is also important (Jung et al. 2019a), as it directly affects species fitness and progeny (O'Connor et al. 2014a). Understanding how management decisions can continue to impact and shape biological patterns into the near future will provide important information to help mitigate any negative biological consequences, thereby ensuring effective protection for biodiversity within production landscapes.

To investigate potential management legacies, it is imperative to monitor biodiversity over time. Monitoring of biodiversity is recognised as vital for informed management decisions by multiple monitoring and reporting frameworks (Pettorelli et al. 2016). As conventional field-based observations are limited to small spatial scales, satellite remote sensing (SRS) has become an important tool for creating predictions of biodiversity over large spatial scales and through time (Rocchini et al. 2016). SRS can guide management decisions for promoting conservation (Randin et al. 2020), especially through more ready open access of satellite data (Zhu et al. 2019) and cloud computing (Gorelick et al. 2017).

Satellite sensors record electromagnetic radiation reflected from objects on the Earth's surface. This reflected radiation provides us with important information about those objects. Indices derived from satellite data have been used to predict mountain plant richness and rarity (Levin et al. 2007), as surrogates for ground beetle richness and abundance (Lassau and Hochuli 2008; Lafage et al. 2014), predict arthropod biomass (Sweet et al. 2015), model patterns of pollinator species richness and diversity (Hofmann et al. 2017), as well as forecast presence of the desert locust (Piou et al. 2018). These functional links between plant structure and health to their primary consumers (Miller et al. 2017), are utilised for studying arthropod diversity with SRS.

Here I investigate the overall value of SRS for improved forest practices within corridors to conserve biodiversity under global change. I aim to address 1) how management decisions in the past affect current biodiversity, 2) the mechanisms of change, and 3) how to monitor the change. Grasshoppers were selected as study organisms as they are easily captured, and they constitute a significant proportion of invertebrate biomass in South African grasslands (Little et al. 2013). They are also an important food source for many other organisms, are effective indicators of high quality grassland habitat in corridors (Bazelet and Samways 2011) and in general (Fartmann et al. 2012), and are sensitive to changes in local environment (Löffler and Fartmann 2017). Using grasshopper bioindicators to validate patterns derived from SRS, I specifically aim to address the following: 1) How does variation in grassland photosynthetic activity through time affect grasshopper diversity? 2) Which local patch-level variables influence grasshopper diversity? 3) What is the relationship between grassland photosynthetic activity and grasshopper diversity?

To answer these questions, the effect of historic grassland photosynthetic activity on grasshoppers is determined using a time series analysis. This time series will provide insight into how long it takes for changes in grassland photosynthetic activity to manifest in current grasshopper diversity. This is important as changes in photosynthetic activity over time can lead to changes in species assemblages (Jung et al. 2019a, 2019b). Furthermore, the influence of the local environment, measured through vegetation characteristics, will provide information on the potential mechanisms of change, and how grasshoppers respond to this change. Finally, the effectiveness of SRS for monitoring grasshopper habitat are explored using additive models, at various scales, to provide recommendations for better landscape management. These results can then guide current management towards consideration of how past practices shape future diversity patterns.

2.3. Methods

2.3.1. Study area and design

This study took place in four commercial timber estates within the KwaZulu-Natal Midlands of South Africa (Fig. 2.1). These estates cover about 21 400 ha of highly threatened grasslands of the Maputaland-Pondoland-Albany Hotspot (Dinerstein et al. 2017). About 60% of these estates comprise alien tree plantations, and the remaining 40% of land is set aside for conservation. This temperate region has austral summer rainfall (September-April), and a mean annual temperature of 15°C and mean annual precipitation of 900 mm (Mucina and Rutherford 2011). The topography is complex, from steep mountain valleys to rolling grassland hills, ranging in elevation from 800 m to 1750 m above sea level.

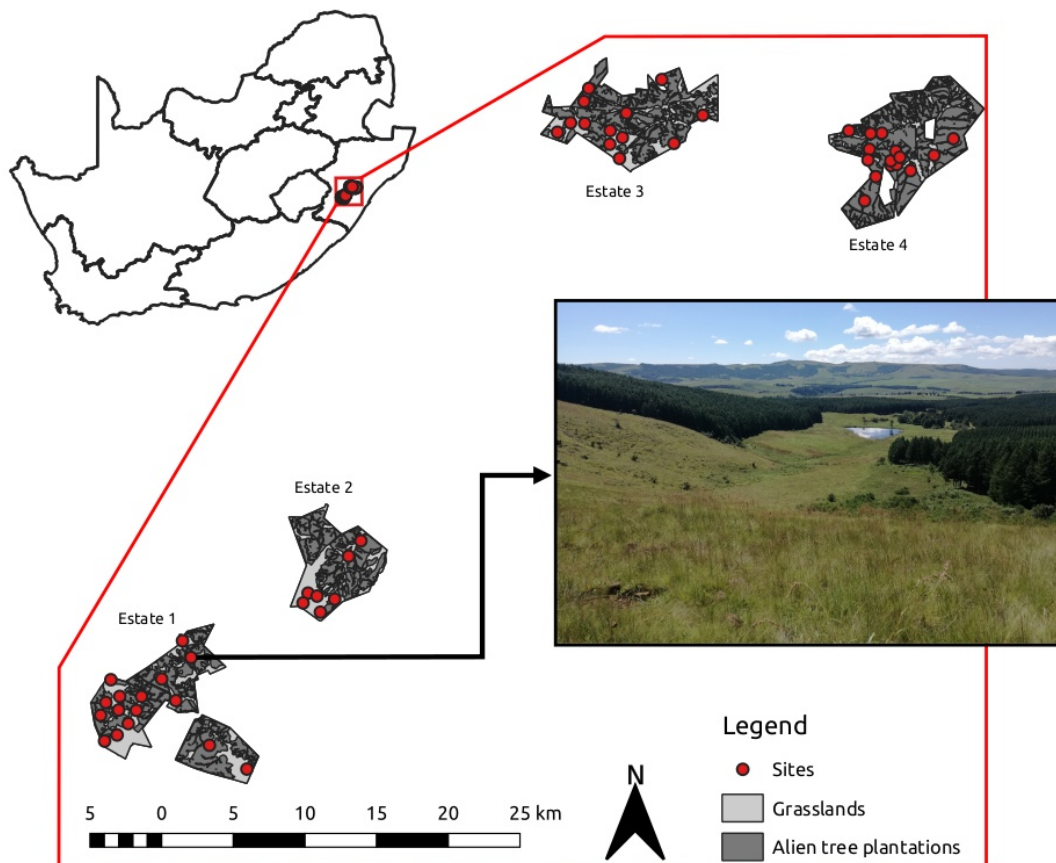


Figure 2.1: Map of site layout in the four commercial timber estates within the KwaZulu-Natal Midlands of South Africa. Photo on the right illustrates the structural nature of the grassland corridors throughout the study region.

Sampling took place within the grassland corridors across the four timber estates. Elevation of the sampling locations were similar within estates, but differed between estates. Sites were selected to cover the extent of the corridors, capturing the heterogeneity caused by divergent fire management (Gaigher et al. 2019). Sites were separated by > 1 km within the estates to ensure independence of sampling, except within estate no. 4, where the minimum distance between sites was 400 m due to smaller grassland fragments. A total of 51 sites were sampled.

2.3.2. Grasshopper sampling

Grasshoppers were sampled using a sweep net with a diameter of 0.5 m and depth of 0.7 m. Per site a total of three 100 m transects were placed in parallel separated by 5 m. At every 1 m along the transect, vegetation was swept with a sweep net, using a 180-degree arc movement. A total of 100 sweeps were performed per transect, with an overall total of 300 sweeps per site.

In addition to sweep netting, active searching was employed to capture mobile and elusive species. Two observers simultaneously searched within the sampling area by flushing out and chasing after large-sized grasshoppers. Active searching was performed after sweep netting, and lasted 20 min. A total of 40 min of active searching per site (20 min per observer) took place. Previous research has demonstrated the efficacy of these methods in sampling grasshopper diversity within South African grassland corridors (Bazelet and Samways 2011; Crous et al. 2013; Joubert et al. 2016).

To capture mostly adult grasshoppers, sampling occurred in March 2020, the peak season for adult grasshopper activity in this area (Kinvig 2006). As grasshopper species richness and abundance can remain relatively stable between years (Gebeyehu and Samways 2006), and that I focused on the effect of historic change in grassland photosynthetic activity on current grasshopper richness and diversity, I base my results on biological data from one year only. Sampling was undertaken between 08h30-16h00 on sunny cloudless days with little to no wind, and took place at the centre of fragments, or > 50 m away from edges (Pryke and Samways 2012b). All sampled grasshoppers were transferred to re-sealable bags. They were later placed in a freezer prior to sorting. Immatures were not included owing to identification difficulties, and all adults collected were pooled per site for analysis. Adult grasshoppers were identified using a museum reference collection, as well as guidelines from Cigliano et al. (2009).

2.3.3. Response variables

Species richness and exponent Shannon diversity index were used as response variables and calculated using caeliferan grasshoppers (i.e. excluding tettigoniids) so as to focus on dry grassland species. Exponent Shannon diversity index was calculated using the *diversity* function within the *vegan* package (Oksanen et al. 2019). Species accumulation curves were calculated to assess sampling effort and completeness of sampled grasshoppers, using the *specaccum* function within *vegan*. Spatial autocorrelation was investigated at the univariate and multivariate levels using the *ade4* package (Dray and Dufour 2007) by calculating the Moran's I and Monte-Carlo tests, respectively.

2.3.4. Vegetation surveys

To obtain information on the local environment, vegetation data were collected after grasshopper sampling using 1 m² quadrats. At each site, a total of 24 quadrats were randomly placed within the sampling area to obtain an average representation of the vegetation at each site. Plant richness, abundance, mean height, and percentage cover was recorded per plant growth form (tree, shrub, succulent, fern, sedges, forb, bulb, grass, and creeper). The invasive alien American bramble (*Rubus cuneifolius*) commonly occurs throughout the sampling area, and so its abundance and percentage cover were determined. Lastly, percentage cover of rockiness and bare ground was also recorded per quadrat, as these are significant for grasshoppers in the region (Crous et al. 2013). Averages were calculated per site for plant richness, growth form richness, vegetation height, bramble cover and abundance, rockiness, and ground cover. These variables were used in statistical modelling to determine grasshopper response at the local patch scale.

2.3.5. Time series analysis

To determine how historic grassland photosynthetic activity affects current grasshopper diversity, a Normalised Difference Vegetation Index (NDVI) time series was extracted from the Landsat surface reflectance imagery archive. NDVI is a widely used index, calculated using the red and near infrared part of the electromagnetic spectrum, which shows high reflectivity over green healthy vegetation. NDVI was selected over other vegetation indices, as previous research demonstrated its importance in predicting grass

biomass within the study region (Shoko et al. 2018). Surface reflectance imagery is preferred for time series over top-of-atmosphere imagery, as surface reflectance imagery is corrected to remove scattering and absorbing effect of atmospheric gases and aerosols, allowing accurate comparison of pixel values over time (Vermote et al. 2016). Furthermore, as I focused on grassland photosynthetic activity, the spatial resolution of the Landsat archive (30 m pixels) allowed me to restrict the time series to within grasslands only, and not the surrounding plantation forests. This was particularly important for smaller grassland fragments.

I used 25 years of images from Landsat 5, 7 and 8 between 1995/01/01 and 2020/03/31. The satellite sensors in the Landsat archive differ slightly. To make accurate comparisons of NDVI values over time, I fitted a spectral transformation function so that the spectral bands of Landsat 5 and 7 more closely resembled that of Landsat 8, using coefficients presented in Roy et al. (2016). A NDVI time series was calculated within a 50 m buffer surrounding each sampling location on all pre-processed imagery using Google Earth Engine (Gorelick et al. 2017). This buffer size was used to capture neighbouring pixels in NDVI calculations for statistical analysis, which helped address the potential mismatch between scale of sampling and sensor footprint.

A total of 1 304 images over the sampling region was used for building the time series, with an average of three images per month. To remove extreme outliers from the NDVI time series, I followed a similar procedure implemented by Jung et al. (2019a). This method was preferred to the native quality assessment data product derived from the CFMask algorithm, to remove outlier pixel values caused by clouds, shadows, or sensor failure, as it allowed me to maintain the greatest number of observations possible over the cloudy sampling region (709 observations with CFMask; 1010 observations without CFMask). Extreme outliers were identified by calculating the absolute difference of all values from the median relative to the total median absolute deviation (MAD) of all values (Leys et al. 2013). Values that deviated by more than two units from the MAD, and was > 99% of all values, were removed from the time series.

Missing values in time series data were imputed using Kalman smoothing, based on an autoregressive integrated moving average model, which considers preceding data when estimating missing values. The *na_kalman* function from the *imputeTS* package was used for imputing missing values (Moritz and Bartz-Beielstein 2017). Kalman smoothing improves Landsat temporal resolution over cloudy areas with high quality (Zhou and Zhong 2020). To remove further noise from time series data while maintaining

natural fluctuation and small abrupt changes, a Savitzky-Golay filter was applied, which relies on adjacent data points to identify noise, and it applies a linear least square model to smooth values. This filter works well for removing noise within NDVI time series data (Chen et al. 2004). The *sgolayfilt* function within the *Signal* package (Signal developers 2014) was used to apply a Savitzky-Golay filter. NDVI time series data were processed in R version 3.6.1 (R Core Team 2019). From these processed NDVI time series data, the standard deviation was calculated for different cumulative years between 1995-2020 (e.g. for one year 2020/03 – 2019/03, four years 2020/03 – 2016/03), and used in statistical analyses to investigate how variance in grassland photosynthetic activity over longer time frames impact current grasshopper diversity.

To model the effect of variation in NDVI over time on grasshopper diversity (*Lag models*) I used linear mixed-effect models from the *lme4* package (Bates et al. 2015) and included timber estate as a random effect to account for spatial autocorrelation. A total of 25 separate single variable *Lag models* were created to compare the variation over the different years. I used the Akaike information criterion (AIC) to rank model importance and compare between them.

2.3.6. Influence of local environmental variables

To identify which local patch variables collected in the field influenced grasshopper diversity, model averaging was performed within the *MuMIn* package (Bartoń 2020) using linear mixed-effect models (*Local models*). Based on a correlation matrix, vegetation growth-form richness and bramble cover were excluded from model building. Variable inflation factor scores, calculated using the *vif* function (Fox and Weisberg 2019), were all below 1.22 indicating low multicollinearity, when performed on a global model containing vegetation height, vegetation richness, bramble abundance, ground cover and rockiness. Model selection was performed on the global model using the *dredge* function, followed by model averaging on the top-performing models ($\Delta < 2$) based on AIC corrected for smaller datasets (AICc) using the *model.avg* function. All data were standardised before modelling in R, using the *standardize* function within *robustHD* package (Alfons 2019).

2.3.7. Monitoring grasshoppers

To investigate the effectiveness of NDVI in monitoring grasshopper habitat, I calculated NDVI from PlanetScope (3 m), Sentinel (10 m) and Landsat (30 m) imagery at three different dates (May 2019, January 2020, and March 2020. Appendix S2: Table S2.1). These dates were selected to determine whether grassland photosynthetic activity had an influence on grasshopper diversity during different stages of their development (egg laying during May, developing juveniles in January, and fully-grown adults in March). Additionally, understanding the impact of spatial resolution will help guide managers to select appropriate imagery.

Sentinel and Landsat NDVI values were calculated from surface reflectance imagery and downloaded using Google Earth Engine, whereas PlanetScope surface reflectance imagery was obtained from Planet Labs (Planet Team 2017) and NDVI calculated using R. NDVI values with respect to all imagery were averaged for 50 m buffers surrounding the sampling locations and used for statistical analyses.

To investigate the relationship between NDVI and grasshopper diversity (*Spectral models*), generalised additive mixed-effect models were used from the *gam4* package (Wood and Scheipl 2020). Timber estate was added as a random effect to account for spatial autocorrelation. Additive models were selected over linear models as the relationship between NDVI and grasshopper diversity was likely non-linear. Multiple single variable *Spectral models* were created to avoid multicollinearity, and AIC was used to rank model importance. Additive models were fitted with a tensor product smooth applied to NDVI, using a cyclic cubic regression spline with four knots.

2.3.8. Grasshopper assemblage composition

To assess grasshopper assemblage composition response to the various variables explained above, I used the *manyglm* function within the *mvabund* package (Wang et al. 2012). This procedure fits multiple generalised linear models with negative binomial distribution to multivariate abundance data. Test statistics were calculated based on residual permutation resampling with 999 permutations on standardised explanatory variables. Fourth corner analysis was used to visualise observed patterns using the *traitglm* function in *mvabund*. The fourth corner models were fitted with subfamily data, instead of trait data, to determine how subfamilies responded to specific explanatory variables, as well as direction of response. All

fourth corner models had a LASSO penalty added to reduce small coefficients to zero. The *Lag*, *Local*, and *Spectral models* were used for *manyglm* and *traitglm* analysis. Timber estate was included as a variable in all models to account for the spatial layout of sampling.

2.4. Results

2.4.1. Sampled grasshoppers

A total of 2 503 adult Caelifera grasshopper individuals from 58 species, 46 genera, 18 subfamilies and 6 families, were collected (Appendix S2: Table S2.2). Species accumulation curves reach near asymptotes (Appendix S2: Figure S2.1). The most diverse and abundant subfamilies were the Gomphocerinae (9 species, 533 individuals), Oedipodinae (9 species, 137 individuals), followed by Acridinae (8 species, 546 individuals). *Eyrepocnemis calceata*, *Anablepia pilosa*, *Pseudoarcyptera cephalica*, and *Dirshia abbreviata*, found in this study are strongly associated with protected areas (Joubert et al. 2016). Furthermore, *Faureia milanjica*, found at three sites, is an indicator of high-quality habitat (Bazelet and Samways 2011). These results compare to previous studies within South African grassland corridors (Bazelet and Samways 2011; Crous et al. 2014; Joubert et al. 2016).

2.4.2. Lag models

Species richness was positively affected by the deviation in NDVI between 2019-2020, whereas exponent Shannon diversity was positively affected by deviation in NDVI between 2019-2020 and 2017-2020 (Fig. 2.2, Table 2.1). This effect was strongest with best fit (AIC) for richness and deviation in NDVI between 2019-2020 (Fig. 2.2, Table 2.1).

When looking at the assemblage composition, variation in NDVI between 2019-2020 and 2018-2020 had a significant influence, where NDVI data between 2018-2020 had the strongest effect and best fit (Table 2.4).

Grasshopper subfamilies showed consistent response between the different cumulative years, with the 2018-2020 NDVI data showing the strongest response (Fig. 2.4). Larger-sized grasshoppers (Pyrgomorphinae and Porthetinae) seem to benefit more than smaller ground hoppers (Tetriginae) (Fig. 2.4).

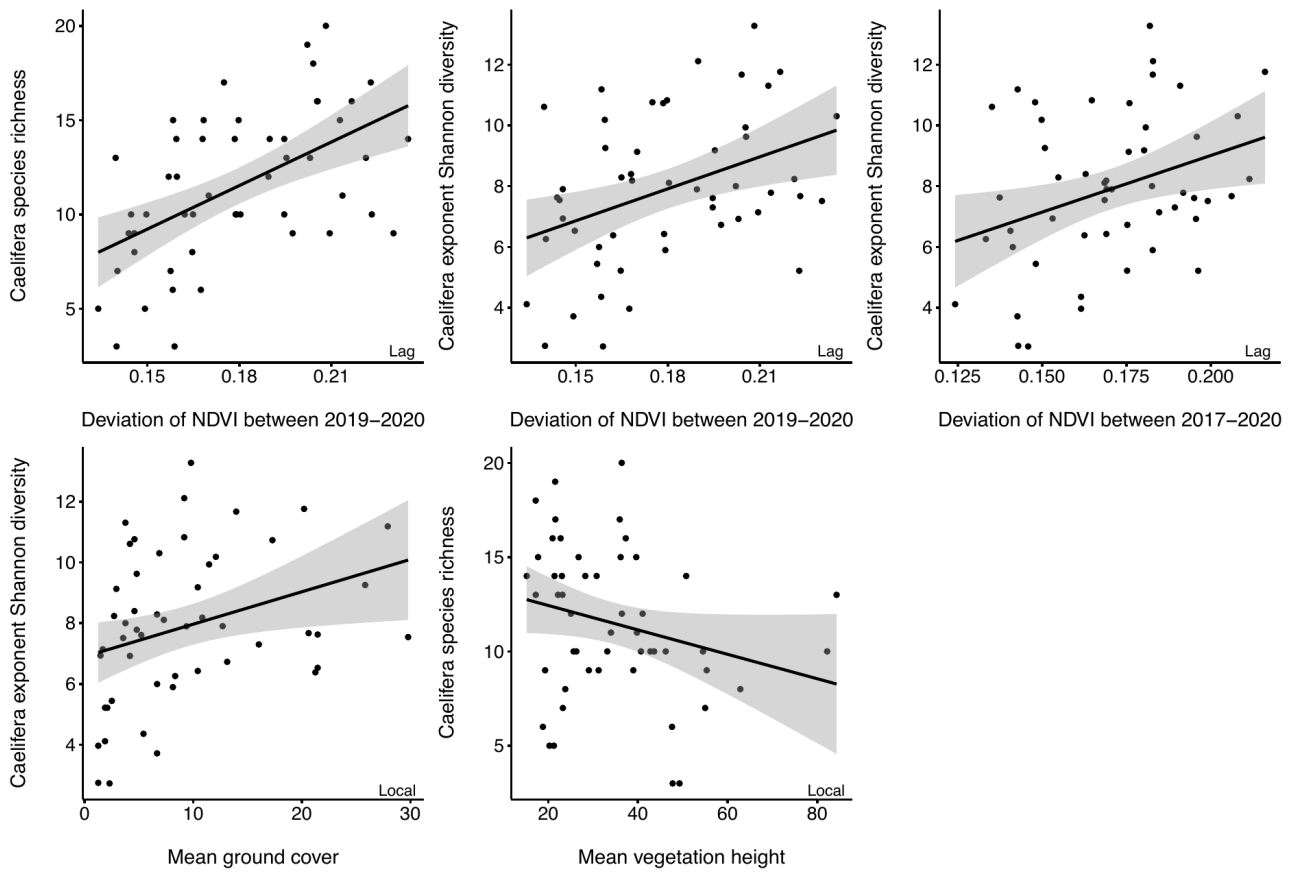


Figure 2.2: Significant results from linear mixed-effect models (*Lag and Local models*) investigating effect of deviation in NDVI between different years, as well as patch variables, on grasshopper richness and exponent Shannon diversity.

Table 2.1: Results from linear mixed-effect models (*Lag models*) investigating effect of deviation in NDVI between different years on grasshopper richness and exponent of Shannon diversity. Results only show significant effects.

Response	Explanatory	beta	se	5%	95%	t-value	AIC
Richness	NDVI 2019-2020	0.455	0.143	0.156	0.771	3.181	138.938
exShannon	NDVI 2019-2020	0.378	0.140	0.134	0.649	2.700	147.677
exShannon	NDVI 2017-2020	0.295	0.148	0.075	0.602	1.996	149.769

2.4.3. Local models

At the local scale, vegetation height had a negative effect on species richness, whereas ground cover had a positive effect on exponent Shannon diversity (Fig. 2.2, Table 2.2).

Furthermore, vegetation height and richness, bramble abundance, and ground cover, all had an influence on grasshopper assemblage composition (Table 2.4). Rockiness only had a marginal effect on the assemblage composition (Table 2.4).

Vegetation height showed a consistent positive influence on multiple subfamilies, whereas subfamilies responded differently to plant species richness (Fig. 2.4). Bramble abundance showed a strong negative influence on larger-sized grasshoppers (Pyrgomorphinae) as well as species of conservation concern (Thericleinae) (Fig. 2.4). Rockiness showed an overall positive influence on multiple subfamilies, but with a negative influence on flightless species (Lentulinae) (Fig. 2.4). Ground cover showed a similar pattern compared to rockiness (Fig. 2.4).

Table 2.2: Model-averaged estimates (conditional average) of local patch variables (*Local models*) predicting grasshopper richness and exponent Shannon diversity. Significant variables in bold. RI = relative importance, #models = number of containing models.

Response	Explanatory	beta	se	5%	95%	RI	#models	AICc
Richness	Mean Veg Height	-0.269	0.128	-0.526	-0.012	0.37	1	140.708
	Mean Ground Cover	0.222	0.124	-0.029	0.472	0.20	1	141.981
exShannon	Mean Ground Cover	0.360	0.131	0.097	0.623	1.00	2	146.131
	Mean Veg Height	-0.232	0.133	-0.500	0.035	0.30	1	147.780

2.4.4. Spectral models

NDVI calculated from PlanetScope in May 2019 and January 2020, as well as from Sentinel in May 2019, January 2020, and March 2020, had a significant relationship with species richness (Fig. 2.3, Table 2.3). NDVI calculated from Landsat in March 2020 had only a significant relationship with exponent Shannon diversity (Fig. 2.3, Table 2.3). NDVI calculated during January 2020 showed the strongest relationships, whereas Sentinel data had the best fit (Fig. 2.3, Table 2.3). Per image, the species richness or exponent Shannon diversity was highest at NDVI values in the third quartile range (Fig. 2.3).

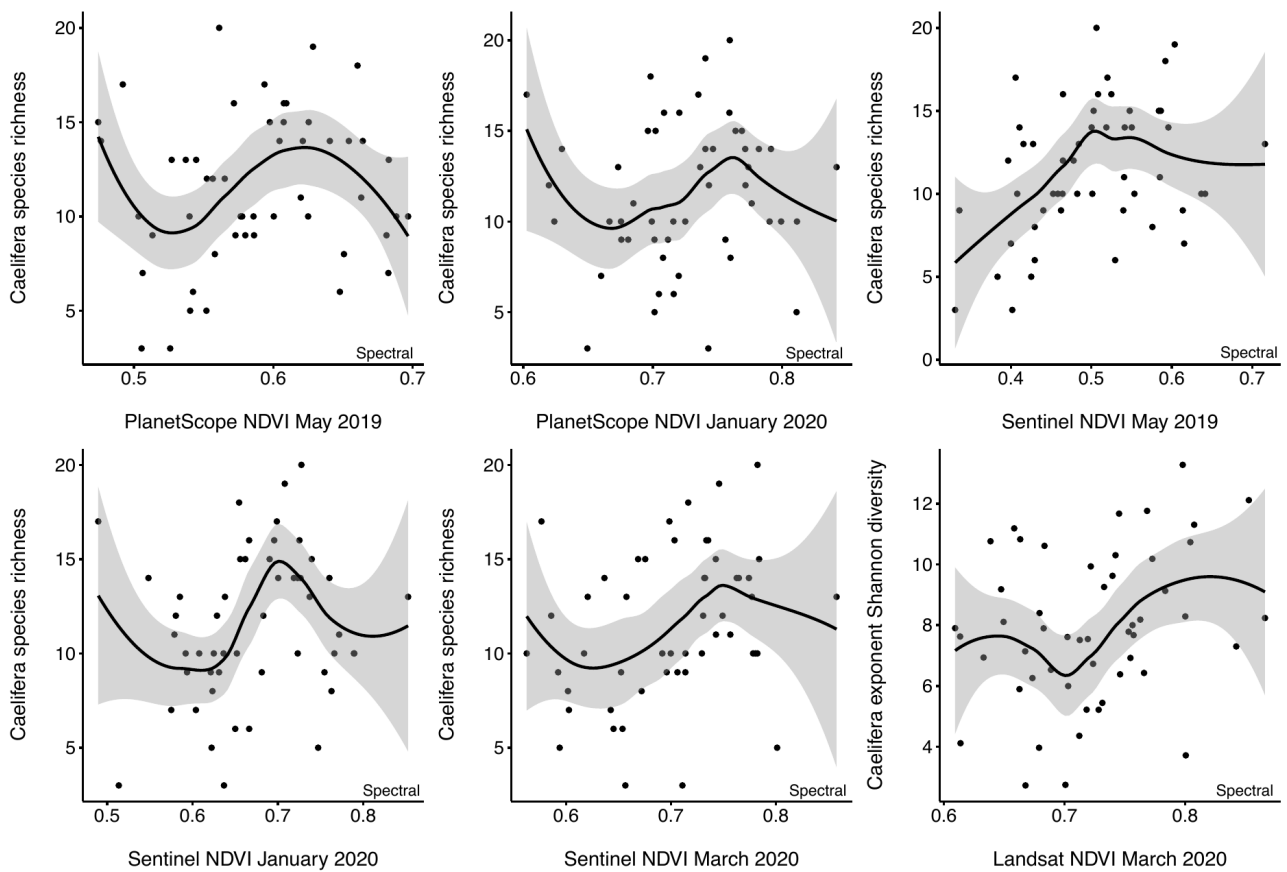


Figure 2.3: Significant results from generalised additive mixed-effect models (*Spectral models*) investigating the relationship between NDVI calculated from PlanetScope (3 m), Sentinel (10 m) and Landsat (30 m) in three different influential times, on grasshopper richness and exponent Shannon diversity.

Table 2.3: Results from generalised additive mixed-effect models (*Spectral models*) investigating the relationship between NDVI calculated from PlanetScope (3 m), Sentinel (10 m) and Landsat (30 m) in three different influential times, on grasshopper richness and exponent Shannon diversity. Results only show significant effects.

Response	Explanatory	edf	f-value	p-value	AIC
Richness	PlanetScope NDVI May 2019	1.409	3.681	0.032	140.153
Richness	PlanetScope NDVI January 2020	1.532	4.879	0.022	138.709
Richness	Sentinel NDVI May 2019	1.459	4.378	0.036	138.981
Richness	Sentinel NDVI January 2020	1.533	5.564	0.020	138.385
Richness	Sentinel NDVI March 2020	1.381	3.200	0.048	139.879
exShannon	Landsat NDVI March 2020	1.426	3.181	0.035	148.324

At the assemblage level, NDVI calculated from PlanetScope in May 2019 and from Landsat in May 2019, had an significant influence, whereas NDVI calculated from Landsat in May 2019 showed the strongest influence (Table 2.4). However, NDVI calculated from PlanetScope in May 2019 showed the best fit (Table 2.4).

Grasshopper subfamilies responded differently to spatial resolution, where a more prominent effect was detected with NDVI calculated from PlanetScope imagery (Fig. 2.4).

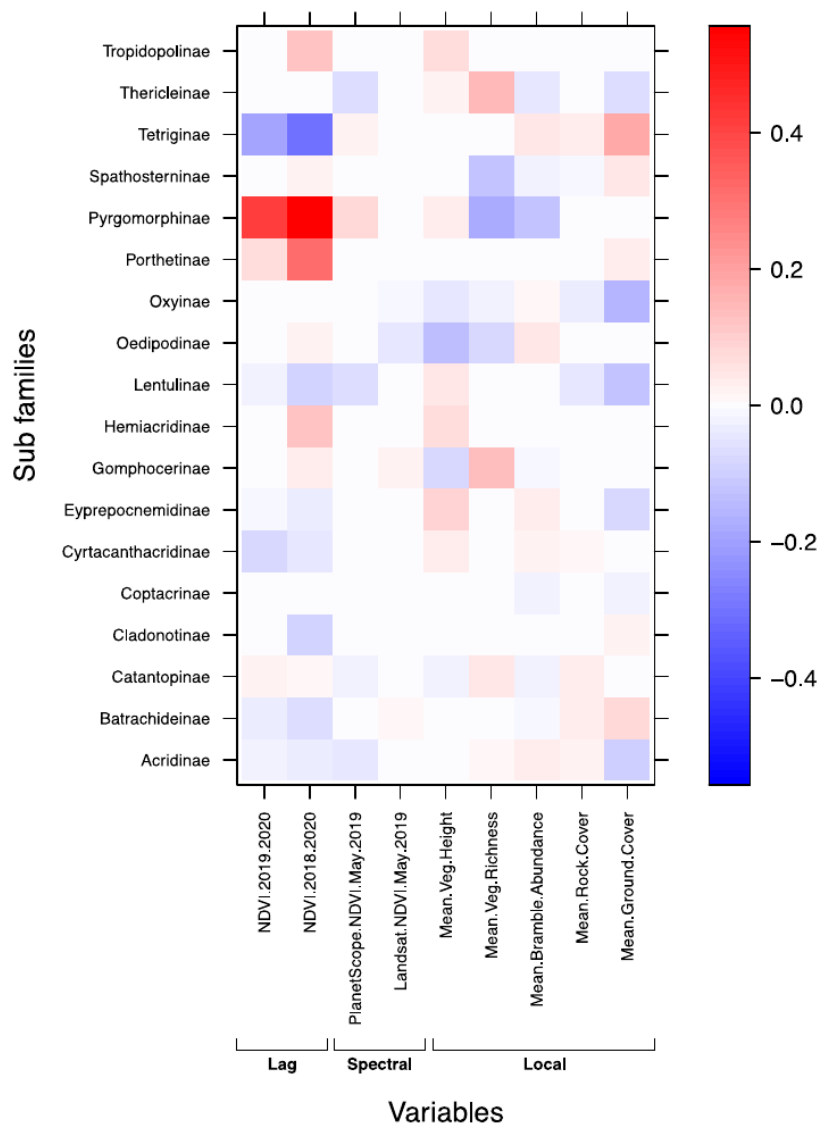


Figure 2.4: Fourth corner analysis showing variable-subfamily coefficients for all models (*Lag*, *Spectral* and *Local models*). Coefficients were calculated using different models but visualised together.

Table 2.4: Aggregated results from all the *manyglm* analysis. Results for the *Lag* and *Spectral models* has been reduced to only show significant effects. Score = Score-Test statistic from the *manyglm* model.

Model	Variable	Score	p-value	AIC
<i>Lag</i>	NDVI 2019-2020	70.186	0.045	4863.254
	NDVI 2018-2020	74.787	0.025	4825.943
<i>Spectral</i>	PlanetScope NDVI May 2019	71.761	0.050	4828.464
	Landsat NDVI May 2019	84.178	0.011	4869.580
<i>Local</i>	Mean Veg Height	115.55	0.001	4751.916
	Mean Veg Richness	104.30	0.002	
	Mean Bramble Abundance	64.70	0.021	
	Mean Rock Cover	56.22	0.084	
	Mean Ground Cover	85.59	0.002	

2.5. Discussion

2.5.1. Management legacies

My results show that recent changes in vegetation condition within grassland corridors have a beneficial effect on current grasshopper evenness over a three-year period, while assemblages only responded to change within a two-year period. These results are similar to a long-term study focusing on grassland disturbance regimes on grasshoppers (Chambers and Samways 1998). This also corresponds with other research demonstrating how ecological integrity links to past management (Perring et al. 2018; Jung et al. 2019a, 2019b; Löffler et al. 2020; Poniatowski et al. 2020a), highlighting the effect of past management practices on the next generation of biodiversity. Changes in vegetation condition, through alterations in vegetation health or structure, have an immediate effect on species assemblages directly, leading to their change. Depending on a species' life history, developmental stage and physiological state, the effect can be either positive or negative, resulting in species or populations getting a head start the following season or falling behind (O'Connor et al. 2014a).

With disturbance being a dominant process in human-managed landscapes, it can be a significant factor in maintaining high levels of certain insect populations (Schowalter 2012), especially as organisms

often depend on disturbance to maintain their habitat (Roxburgh et al. 2004). Grasshoppers tend to thrive under moderate disturbance, and when these disturbances are excluded, or when high-quality habitat is not maintained, grasshopper diversity decreases and assemblage structure changes (Chambers and Samways 1998; Fartmann et al. 2012). Changes in grasshopper assemblages over time can lead to changes within the ecosystem, affecting grassland functioning over many years (Belovsky and Slade 2018). Furthermore, when, where, and how change occurs within a production landscape will greatly influence how organisms interact with their local environment through changing access to needed resources (Sitters and Di Stefano 2020). This change, in turn, affects local population persistence by altering colonisation and extinction dynamics (Jackson and Sax 2010). Landscape planning should therefore incorporate the temporal aspect of biological response to changes in the landscape, which will ultimately improve the conservation success of grassland corridors.

2.5.2. Drivers of change

Previous research aimed at understanding the drivers of variation in grassland photosynthetic activity illustrated the importance of grassland plant species richness and functional trait composition in explaining variation in photosynthetic activity (van 't Veen et al. 2020). Thus, any driver that can cause changes in local vegetation structure and assemblage composition can therefore lead to variation in photosynthetic activity over time. For example, invasion by alien plants can greatly alter local plant structure and diversity through biotic homogenization (Olden et al. 2004, Vilá et al. 2011). Overgrazing by domestic cattle has a severe negative impact on local plant species richness and assemblage composition, which leads to simplified grass species composition (Fedrigo et al. 2018). Fire, through prescribed burning, helps to maintain native plant species diversity within a fire-adapted landscape (Joubert et al. 2014). Lastly, climate change can reduce resilience of native vegetation assemblages, allowing opportunities for alien invaders to colonise (Leishman and Gallagher 2015).

Grasshoppers within grassland corridors respond strongly to the local vegetation structure and available bare ground (Bazelet and Samways 2011; Joubert-van der Merwe and Pryke 2018). My results also support this by showing that local plant species richness, vegetation structure and bare ground has a significant influence on grasshopper assemblage composition. However, grassland structure is closely linked

to the management of disturbance regimes. Little et al. (2015) showed that annual burning and heavy grazing leads to a distinct plant community dominated by disturbance specialists, thereby impacting local vegetation structure and plant diversity in grasslands of Mpumalanga, South Africa. These findings are also supported by research in Kansas, USA, where fire and grazing are the main drivers of vegetation structure and assemblage composition and within tallgrass prairies (Collins and Calabrese 2012). These findings show that prescribed burning and controlled grazing are the main drivers contributing to changes in vegetation structure and composition, leading to variation in photosynthetic activity within grasslands.

Fire, through prescribed burning, is used annually in some of parts of the corridors to reduce the grassland fuel load as protection for the plantation trees against large intense wildfires. Fortunately, prescribed burning of corridors has beneficial outcomes for plants, grasshoppers and butterflies (Joubert et al. 2014, 2016; Gaigher et al. 2019). Fire is a fundamental natural disturbance within grasslands, where many plants and animals require fire for their survival (Kelly and Brotons 2017). Fire has such a prominent impact on the landscape, that in most cases, it overrides the effect of grazing in maintaining birds and arthropods within grasslands (Little et al. 2013). Thus, the exclusion of fire, or the inappropriate use of prescribed burning, has large cascading impacts on grassland ecosystems, by allowing alien weeds and woody shrubs to encroach (O'Connor et al. 2014b).

The American bramble (*Rubus cuneifolius*) is one of the most problematic invasive plant species in grasslands of South Africa (Henderson 2007). Where bramble invades, the local plant communities become more characteristic of woodlands, thereby threatening specialists grassland taxa (Henderson 2007). Furthermore, bramble within the corridors has severe negative impacts on biodiversity, with previous research indicating negative impacts on birds (Reynolds and Symes 2013), dragonflies (Kietzka et al. 2015), flower visiting insects (Hansen et al. 2018), as well as topsoil and leaf litter arthropods (Eckert et al. 2019). In add to this by showing that bramble negatively impacts larger-sized grasshopper species (especially Pyrgomorphinae), as well as species of conservation concern (mainly Thericleinae). Fortunately, the removal of bramble can enhance bird diversity (Reynolds and Symes 2013), positively influence pollination networks (Hansen et al. 2018) and promote grassland restoration success (Eckert et al. 2019).

However, under global change, how biodiversity responds to their local environment will vary. In the case of tallgrass prairie in North East Kansas, USA, climate warming affects grasshopper host-plant

populations, which indirectly changes grasshopper diversity (Welti et al. 2018). Additionally, drought in one year can cause a significant change in grasshopper assemblage composition the following year (Bruckerhoff et al. 2020). Under climate warming, substantial range expansions are expected for the large marsh grasshopper in Germany (Leins et al. 2021). Furthermore, in Germany, Orthoptera are resilient to climate warming in primary grasslands of high quality (Löffler et al. 2019; Fumy et al. 2020), although climate change can affect the distribution of grasshopper assemblages, especially in previously transformed landscapes (Löffler et al. 2019; Fumy et al. 2020; Poniatowski et al. 2020a). Understanding the complexities of ecosystem response to global change is critically important (Bruckerhoff et al. 2020), and more research is needed to understand the impact of climate change, especially on stable climatic refugia, such as the grassland corridors within the Maputaland-Pondoland-Albany Hotspot of South Africa (Harrison and Noss 2017).

2.5.3. Monitoring tools

Monitoring of insects has never been more important than in current times (Cardoso et al. 2020; Samways et al. 2020), and SRS has become an invaluable tool for monitoring biodiversity (Rocchini et al. 2016). Spectral information derived from satellite imagery is usually based on attributes of the local environment, which is directly or indirectly linked to either a species, population, or an ecosystem service, which is then used to guide management recommendations (Vihervaara et al. 2017). The spatial resolution of satellite imagery will impact the ability of spectral information to explain patterns of local biodiversity. Finer pixel sizes tend to outperform coarser ones in explaining this relationship (Wang et al. 2017). High resolution imagery is able to capture more complexity of the local environment, and is a good predictor of local biodiversity. My results confirm this by showing that high resolution PlanetScope satellite imagery performed best, compared to coarser resolution imagery, in predicting patterns in grasshopper diversity. Other research also supports this by demonstrating that high resolution imagery outperformed medium resolution imagery in modelling grassland bird communities in southwestern France (Sheeren et al. 2014), as well as plant communities in Tasmania, Australia (Melville et al. 2018).

Furthermore, I demonstrate the relationship between the satellite derived vegetation index NDVI, and grasshopper richness and assemblage composition. Grasshopper richness was highest at moderately high

NDVI values, which reflects their preference towards structurally simplistic grasslands with available bare ground. However, the strength of these relationships was rather weak, and more research is needed to establish stronger links between SRS and local grasshopper diversity. Nevertheless, Klein et al. (2020) demonstrated a similar NDVI and grasshopper relationship in Europe, and used this to predict grassland habitat with high grasshopper richness, illustrating the effectiveness of NDVI as a widely-applicable monitoring tool for grasshoppers. I also show that there is a three-month lag in this relationship, which corresponds with juvenile activity in January. This three-month lag also occurs in butterflies (Valtonen et al. 2013). Using NDVI at the appropriate time to monitor grasshopper diversity can provide valuable insight into when and where to burn grassland corridors for biodiversity conservation.

Alongside monitoring plant condition for grasshopper conservation, other local factors such as rockiness can influence the quality of habitat needed to sustain grasshopper populations (Crous et al. 2013). Rockiness within grassland corridors is a surrogate for predicting plant, butterfly and grasshopper diversity (Crous et al. 2013). However, here, rockiness had an overall weak positive influence on multiple grasshopper subfamilies. Crous et al. (2014) suggested that grasshoppers are not necessarily correlated directly with rockiness, but rather the underlying environmental correlates of rockiness, such as plant richness. Here, multiple grasshopper subfamilies responded positively to plant species richness.

2.5.4. Management recommendations

Primary high-quality areas with surface rockiness, diverse grass assemblages, and no bramble, should be the focal habitat for grasshopper conservation. The active removal of bramble is strongly encouraged, especially as this landscape is a global priority for ecosystem restoration (Strassburg et al. 2020), and that it can take hundreds to thousands of years for plant diversity to resemble primary state (Nerlekar and Veldman 2020). Bramble must be removed from all sites, focusing on secondary habitat where landscape functional connectivity can be restored to benefit biodiversity (Poniatowski et al. 2018, 2020b). Research from Germany showed that restoring calcareous grasslands benefits biodiversity (Poniatowski et al. 2020b), inhibits future species extinctions (Löffler et al. 2020), and safeguards them against climate warming (Fumy et al. 2020).

More research is needed to identify exact drivers causing variation in grassland photosynthetic activity important for maintaining grasshoppers within grassland corridors. Because fire is actively used within these corridors, I consider it a major source of the variation in grassland photosynthetic activity that manifests a beneficial impact on grasshoppers. Research shows that prescribed burning maintains high-quality habitat and creates heterogeneity, thereby conserving habitat specialists (Poniatowski et al. 2018). As variation in grassland photosynthetic activity had an influence on grasshoppers for up to three years, I recommend that these grassland corridors should not be left unburned for more than three years, especially as habitat specialists benefit most from early grassland successional stages (Fartmann et al. 2012). This recommendation is similar to that from previous research, which aims to prevent woody plant encroachment into grasslands (Gaigher et al. 2019). Furthermore, as fire overrides the impact of grazing on birds and arthropods (Little et al. 2013), it should be prioritised as a management action over grazing. Prescribed burning should be used consistently, as excluding fire from an area for more than three years has negative consequences for biodiversity (McLauchlan et al. 2020). How fire impacts functional connectivity within the landscape should also be critically considered when identifying sites to burn (Sitters and Di Stefano 2020), as this will ultimately impact meta-population dynamics and influence viability of future generations (Jackson and Sax 2010).

Lastly, high resolution PlanetScope data are recommended for monitoring grasshopper richness and assemblage composition response to changes in vegetation within the corridors. These grassland corridors have the potential to conserve biodiversity, however, management and monitoring needs to be in place to ensure biodiversity resembles neighbouring protected areas (Pryke and Samways 2012a).

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Chapter 3: Assessing grassland corridors between plantation forests for biodiversity conservation through measuring species distribution, turnover and functional connectivity

**Under review in Landscape Ecology.*

3.1. Abstract

Context Grassland corridors are set aside for biodiversity conservation within the commercial timber plantation landscape of South Africa. However, the impact of the production landscape on functional connectivity within these corridors has not been investigated.

Objectives I combine stacked species distribution modelling, functional connectivity analysis, and species turnover calculations, to improve our understanding of how grassland corridors contribute to functional connectivity and biodiversity conservation within plantation landscapes.

Methods Grasshoppers, which are reliable indicators of grassland quality, were used as model organisms and sampled within grassland corridors. Remote sensing and machine learning was used to gain insight into the conservation potential of grassland corridors.

Results Grassland corridors maintain much high-quality grasshopper habitat, characterised by vegetation structure and topoclimate. Large corridors with an elevation gradient supported diverse assemblages, with generalists occurring in edge habitat, while specialists preferred grassland interiors. Less frequent fires within corridors helped maintain high-quality habitat and functional connectivity. Grasslands were critical for increasing functional connectivity and can be monitored using NDVI to assist with prescribed burning. Shrublands establishing after tree harvesting also contributed to functional connectivity, but only in the short term.

Conclusions Prescribed burning should be used to maintain vegetation structural heterogeneity and functional connectivity. I recommend less frequent fires, burning every 2-3 years, guided by NDVI. Large corridors at high elevation are priority. Management of plantation tree saplings should be incorporated into conservation plans, as it can enhance functional connectivity. Focusing on maintaining functional connectivity within corridors helps improve long-term biodiversity.

Keywords: Grassland mosaics; Grassland management; Plantation management; Land sparing; Grasshoppers; South Africa

3.2. Introduction

Remnant habitat within production landscapes is important for biodiversity conservation under changing climate and disturbance regimes (Dudley et al. 2018), requiring critical evaluation for ensuring long-term effectiveness for biodiversity conservation (Wurtzebach and Schultz 2016). This is especially important for insect diversity and abundance, as insects are declining at alarming rates (Wagner et al. 2021). Insect assemblages depend on natural disturbance regimes, such as fire and grazing within the landscape for maintaining healthy populations (Schowalter et al. 2012). However, disturbances within production landscapes, such as commercial timber plantation forests, can be more frequent than natural systems (Betts et al. 2021), which can have a lasting impact on long-term insect diversity (Jung et al. 2019; Theron et al. 2021). One way to ensure that the management of remnant habitat within dynamic landscapes conserves biodiversity, is to model the complexities of biodiversity through use of predictive models (Pollock et al. 2020). Specifically, use of species distribution modelling (SDM) and functional connectivity analysis are being used to monitor biodiversity within remnant habitat to prioritise conservation management (Villero et al. 2017; Dickson et al. 2019).

Species distribution modelling is a valuable tool for conservation, as it combines observations of species occurrence with environmental estimates of the local environment to predict suitable habitat within a larger geographic region to gain insight into the drivers of species distribution (Elith and Leathwick 2009). Understanding how the environment shapes species distributions is critical for conservation management, and recent developments in SDM has grown considerably due to advances in machine learning (Gobeyn et al. 2019), which has made these tools more accessible to researchers (Villero et al. 2017). A common use of SDM in conservation is the delineation of protected areas (Domisch et al. 2019; Velazco et al. 2020). However, incorrect selection of environmental variables reduces the effectiveness of SDM (Domisch et al. 2019; Velazco et al. 2020), which can lead to undesired conservation outcomes. This has particular importance for commercial timber plantation forests where prescribed burning is a common management practice (Betts et al. 2021).

Identifying and protecting habitat with valuable biodiversity alone is not enough to maintain ecological resilience (i.e., the ability of an ecosystem to resist disturbance and recover quickly) within production landscapes. Understanding how the landscape facilitates ecological processes, such as species

dispersal, is essential for ensuring resilient ecosystems (Wurtzebach and Schultz 2016), as reductions in functional connectivity can affect meta-population dynamics (Sitters and Di Stefano 2020). Recent integration of electrical circuit-theory into conservation and landscape connectivity research provides such insights (Dickson et al. 2019). Electrical circuit-theory applied to ecology gives a deeper understanding of how the landscape affects animal movement (McRae et al. 2008), relying on the concept of functional connectivity, which links the behavioural response of animals to the landscape (Tischendorf and Fahrig 2000). For example, fire creates heterogeneity in resource availability, and functional connectivity analysis can be used to monitor the response of biodiversity to prescribed burning (Sitters and Di Stefano 2020), which is very important for conservation within production landscapes (Doherty and Driscoll 2017).

Production landscapes are dynamic systems, arising from various management activities, such as prescribed burning and tree harvesting, which affect biodiversity in many ways. Combined use of SDM and functional connectivity analysis provides better understanding of how the managed landscape is affecting biodiversity, and which management practices provide opportunities for biodiversity conservation. Furthermore, restoration activities can be prioritised by using SDM and functional connectivity analysis to identify remnant habitat important for maintaining functional connectivity, as well as assessing the contribution made by different land cover types to sustain functional connectivity (Dufлот et al. 2018). This provides much needed evidence on the importance of conserving remnant habitat within production landscapes (Sidemo-Holm et al. 2021).

Most studies that utilise SDM and functional connectivity analysis for conservation management tend to focus on a single species (Ahmadi et al. 2017; Dufлот et al. 2018). A single species approach to conservation can help protect other species or communities as well, but only if protecting the target species habitat has been shown to protect other species habitats (Breckheimer et al. 2014). However, for insects a single species approach is not always insightful for insect assemblages as a whole, due to their high diversity and greatly varying specific habitat requirements among the different species (Gerlach et al. 2013). Furthermore, focusing on a single species ignores other important aspects of biodiversity, specifically, species diversity, which relates to functioning of ecosystems (Thompson et al. 2017).

Modelling species distributions and the degree of functional connectivity between remnant patches will not provide a full picture of how remnant habitat sustains ecological functioning into the future.

Managing a landscape for improved functional connectivity might negatively impact some species over others, leading to changes in species diversity and functioning of ecosystems (Pliscoff et al. 2020).

Researchers in the past have relied on modelling beta diversity, or more specifically species turnover, to gain deeper insight into how the landscape is contributing to changes in species assemblages, which is of immense value for conservation assessments (Ferrier et al. 2007). Understanding what affects species distribution and how this impacts species diversity and functional connectivity is needed to ensure that remnant habitat is managed for ecological resilience.

Throughout the endangered grasslands of KwaZulu-Natal and Mpumalanga provinces, South Africa, a great deal of natural forest and grassland has been converted into commercial timber plantation forests, consisting mostly of *Pinus* and *Eucalyptus* species. However, much mostly intact remnant grassland habitat remains between plantation forests and are set aside for biodiversity conservation in the form of large-scale grassland conservation corridors (Samways and Pryke 2016). Yet to date, the degree to which these corridors facilitate functional connectivity has not been formally investigated. To assess the conservation value these grassland corridors, I explore the usefulness of SDM, functional connectivity analysis, and species turnover calculations. I specifically focus on grasshoppers, which are indicators of high-quality grassland habitat (Fartmann et al. 2012; Löffler and Fartmann 2017) to answer the following questions: 1) What is driving the distribution of high-quality grasshopper habitat? 2) How connected are high-quality habitats, and where should connectivity be restored? 3) What drives grasshopper species richness and beta diversity throughout the landscape? 4) How similar are these patterns among species with different conservation priorities?

Answering these questions will allow a better understanding of the variables important for maintaining high-quality habitat for grasshopper conservation and how this impacts species turnover. Furthermore, through identifying corridors important for maintaining functional connectivity and how the landscape can be managed to improve functional connectivity, I can identify priority restoration sites within the landscape to improve functional connectivity for biodiversity conservation.

3.3. Methods

3.3.1. Study area and design

This study took place in four commercial timber estates within the KwaZulu-Natal Midlands of South Africa (Fig. 3.1). These estates cover about 21 400 ha of highly threatened grasslands of the Maputaland-Pondoland-Albany Hotspot (Dinerstein et al. 2017), where about 60% of land is used for plantation forests, and the remaining land is set aside for conservation. Dominant vegetation types include the Mooi River Highland Grassland, Midlands Mistbelt Grassland, Southern KwaZulu-Natal Moist Grassland, as well as Southern Mistbelt Forests. This temperate region, with a summer-dominant rainfall between December to March, has a complex topography with steep mountain valleys to rolling grassland hills, ranging in elevation from 800 m to 1750 m above sea level.

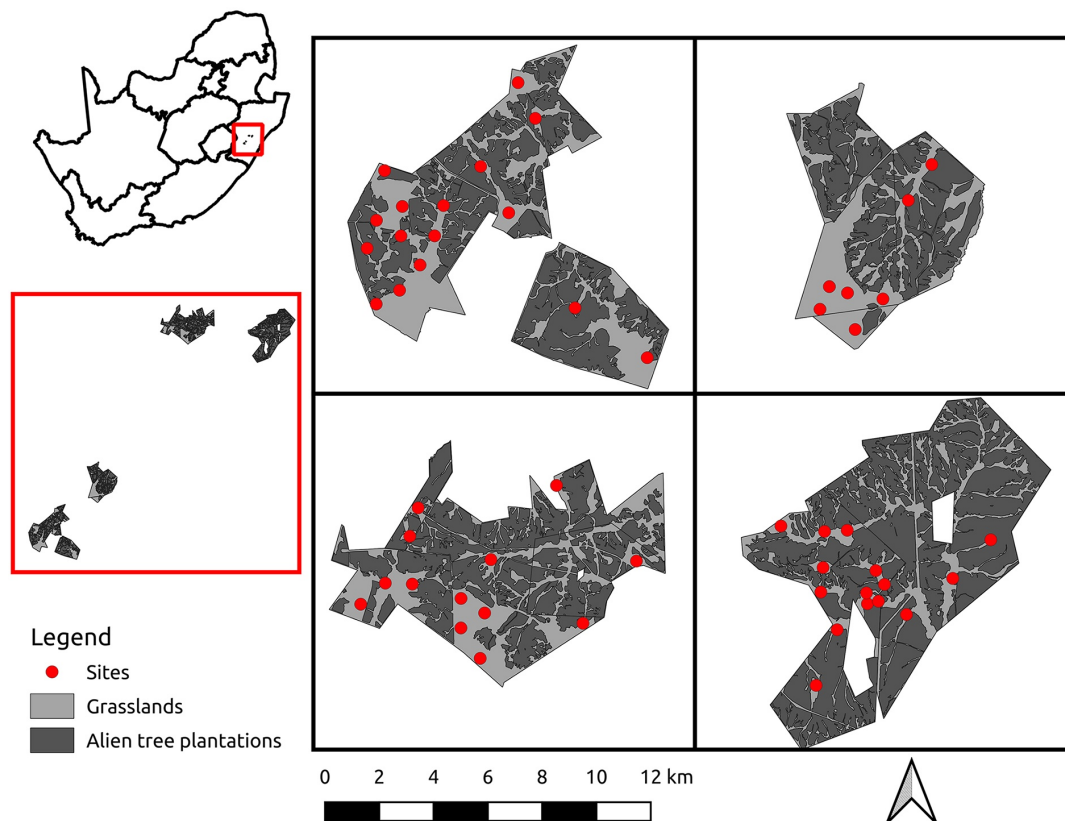


Figure 3.1: Map of the study area. Left hand side shows the four timber plantation estates located within KwaZulu-Natal, South Africa. Right hand side shows the sampling sites within each estate, located throughout grassland corridors/remnants of varying shapes and sizes.

Grassland corridors occur throughout the plantation estates and of different sized remnant corridors and nodes affecting the degree of structural connectivity (Fig. 3.1). Sampling sites were selected within grassland corridors based on a scoring and prioritisation methodology (Appendix S3.1). Land cover types were scored based on grasshopper preference, and all land cover types were then summed within larger grids to identify high and lower value habitat. Sites were selected with high and low habitat value scores, and to cover the geographic extent of the four estates, capturing much heterogeneity caused by divergent fire management (Gaigher et al. 2019). Sites were separated by > 1 km within the estates to ensure independence of sampling, except within estate no. 4, where the minimum distance between sites was 400 m due to smaller remnant areas. A total of 51 sites were sampled.

3.3.2. Grasshopper sampling

Grasshoppers were sampled using a sweep net, with a diameter of 0.5 m and depth of 0.7 m. Each site had a total of three 100 m transects, placed in parallel separated by 5 m. At every 1 m along the transect, vegetation was swept with a sweep net, using a 180-degree arc movement. A total of 100 sweeps were performed per transect, with an overall total of 300 sweeps per site.

In addition to sweep netting, active searching was employed to capture mobile and elusive species. Two observers simultaneously searched throughout the sampling area by flushing out and chasing after large-sized grasshoppers, lasting 20 min. A total of 40 min of active searching per site (20 min per observer) was undertaken.

To capture mostly adult grasshoppers, sampling was in March 2020, peak season for adult grasshopper activity in this area (Kinvig 2006). Sampling was undertaken between 08h30-16h00 on sunny cloudless days with little to no wind and took place at the centre of the corridors, or > 50 m away from edges (Pryke and Samways 2012a). All sampled grasshoppers were transferred to re-sealable bags. They were later placed in a freezer prior to sorting. Immatures were not included owing to identification difficulties, and all adults collected were pooled per site for analysis.

3.3.3. Response variables

Species accumulation curves were plotted to assess sampling effort and completeness of sampled grasshoppers using the *specaccum* function within the *vegan* R package (Oksanen et al. 2020). Species richness and exponent Shannon diversity index was used as response variables for all univariate analyses, calculated using caeliferan grasshoppers (i.e., excluding tettigoniids) to focus on dry grassland species. Previous research indicates low grasshopper diversity within other land cover types (Pryke and Samways 2012a), which further motivates my focus on caeliferan grasshoppers, which show preference towards dry grassland habitat. Furthermore, exponent Shannon diversity index was specifically used here as it accounts for rarity and commonness of species at each site (Roswell et al. 2021).

Grasshoppers were also scored as low (score of 3 and 4), intermediate (5 and 6) and high (7 and 8) conservation priority following guidelines of Matenaar et al. (2015). These scores were based on three parameters, specifically, species rarity, endemism, and mobility. This was done to investigate differences in response between species groupings with different adaptations. Each parameter had different classes, and the sum of all classes was used to classify grasshoppers (Appendix S3.2: Table S3.2.1). A species with a high conservation priority is one that is a local endemic, only occurred at \leq five sites, and flightless. In contrast, a low conservation-priority species is one that has a wide geographic distribution and occurs outside South Africa, occurred at $>$ 10 sites, and is fully capable of flight. Species used in this study did not show wing-dimorphism, and mobility was characterised based on wing characteristics seen in the field and in the lab.

Species richness and exponent Shannon diversity index were calculated for the three different species grouping (low, intermediate, and high) derived from the scoring system above and used as additional response variables alongside overall richness and diversity for univariate analysis. Furthermore, the overall assemblage and the species groupings were used for SDM, functional connectivity analysis, and predicting species turnover.

3.3.4. Raster processing

In preparation for SDM, functional connectivity analysis, and species turnover calculations, various raster data variables were generated. For details on variable source, processing, importance and how it was used in which analysis, see Appendix S3.1: Table S3.1.1.

3.3.5. Species distribution modelling

To identify high-quality habitat for grasshoppers within grassland corridors, I used stacked species distribution modelling (S-SDM) from the *SSDM* package (Schmitt et al. 2017). This procedure models the distribution of multiple species together, allowing us to make inference on species assemblages. This is done by summing up the probabilities for all species occurring at a specific location (using individual SDM) to produce a species richness map. This richness map can be interpreted as areas of highest quality habitat to support diverse grasshopper assemblages.

Uncertainty in predictions made by different algorithms used for SDM can have great impact on land use planning, due to differences in model results (Gritti et al. 2013). To overcome this limitation, I used an ensemble approach, thereby exploring the range of projections across the Random Forest and Support Vector Machines algorithms, by averaging the derived results from these algorithms and avoiding bias from relying on one model only (Gritti et al. 2013).

Furthermore, per species, each algorithm was repeated 10 times and only accurate models were retained for stacking. This filtering was done using the Area Under the Receiver Operating Characteristic Curve (AUC) accuracy statistic, which is a widely used accuracy metric in machine learning derived from a confusion matrix. Only models with an AUC score of 0.7 or higher were used. To evaluate the performance of the final stacked model, I split the grasshopper data into training (70%) and testing (30%) sets. The algorithms learned to make accurate prediction using the training data, and this learning was validated using the testing data (cross-validation). This is done by comparing modelled species assemblages with independent species inventories observed in the field, and then calculating multiple evaluation statistics. Specifically, S-SDM calculates 1) the species richness error, which is the difference between the predicted and observed species richness in the field, 2) assemblage specificity, which is the proportion of correctly predicting when a species is absent, 3) assemblage sensitivity, which is the proportion of correctly predicting when a species is present, and 4) the Jaccard index, which is a metric used to demonstrate community similarity. Lastly, S-SDM measures the relative contribution of environmental variables for predicting species distribution, which is done through evaluating the change in model accuracy between a full model and models where each environmental variable was omitted in turn (Schmitt et al. 2017). The test statistics,

as well as the relative contribution of environmental variables, are averaged over the different modelling repeats (Schmitt et al. 2017).

Most SDM requires species presence and absence data. However, in the situations where absence data is not obtained, or is not reliable, pseudo-absence data can be generated. Pseudo-absence data are locations where a species is assumed to be absent, based on the combination of environmental data provided to the algorithm. For the S-SDM, I grouped species per site and generated pseudo-absence data using species occurring at > 3 sites. This decision was made based on potential bias in my sampling design, as I only sampled grasslands (Phillips et al. 2009), the difficulty capturing elusive and mobile grasshopper species, the relatively low amount of occurrence records for some species (Pearson et al. 2007), and the difficulty in obtaining true absence records (Mackenzie and Royle 2005). Following recommendations from Barbet-Massin et al. (2012), pseudo-absence data were repeatedly generated per algorithm run to obtain best performing models.

To fit the stacked models, only environmentally relevant variables were used, based on previous research within the study region. Specifically, I included Normalised Difference Vegetation Index (NDVI), land cover, distance to corridor edge, maximum Normalised Burn Ratio (maxNBR), topographic aspect, and cold air drainage. NDVI, which shows high reflectivity over green healthy vegetation, influences grasshopper diversity in this region, and was calculated using Sentinel-2 image in January 2020 (Theron et al. 2021). Land cover type (Appendix S3.3) was included to help the algorithm generate accurate pseudo-absence data, as I only sampled within grasslands, allowing me to accurately predict over the entire study area. Distance to corridor edge influences the strength of edge effects on arthropods (van Schalkwyk et al. 2020). I therefore include it here to stand as a proxy for corridor size due to the different sized corridors sampled. Prescribed burning, which is highly significant for plant and grasshopper diversity within this region (Joubert et al. 2014, 2016), was included in the model and measured using the NBR index. This index is used to study fire severity and intensity (Keeley 2009), and ranges from -1 (high burn intensity, low vegetation cover) to +1 (low burn intensity, high vegetation cover). The maximum NBR index was calculated from Landsat imagery dating back three years from grasshopper sampling using Google Earth Engine (Gorelick et al. 2017). Selecting the maximum NBR pixel values over 3 years allows us to map the frequency of burns within the grassland corridors, where lower NBR values indicate areas of recent recurring

burns, with higher NBR values indicating longer burn intervals or where it has not burned recently (within the last three years). Lastly, I included cold air drainage, which has a significant influence on grasshopper abundance, alongside aspect (Samways 1990). Cold air drainage was processed as a distance matrix. More information on S-SDM with preliminary results and variable selection is given in Appendix S3.4.

3.3.6. Functional connectivity

To model functional connectivity and to identify areas where connectivity should be re-established, I used the *Circuitscape* package in the *Julia* coding language (Anantharaman et al. 2020), as well as least-cost path models from the *leastcostpath* R package (Lewis 2021).

Circuitscape is based on electrical circuit-theory, where electrical current will flow through areas with high conductance or low resistance (McRae et al. 2008). This can translate to animal movement within a landscape, where animals struggle to move through a land cover with high resistance values (Dickson et al. 2019). The resulting map that *Circuitscape* produces shows the density of electrical current, which represents the probability of use by a random walker (Doyle and Snell, 1984), and can be interpreted as functional connectivity (McRae et al. 2008).

On the other hand, least-cost path models identify the shortest possible path between two locations based on the extent to which the landscape hinders movement (Adriaensen et al. 2003). These models assume that the shortest distance between areas is the best solution for animals moving between high-quality habitats (McClure et al. 2016). Least-cost path models therefore highlight corridors important for maintaining functional connectivity and can be used to identify areas where connectivity needs to be restored.

Performing accurate functional connectivity analysis requires suitable resistance/conductance surfaces (Peterman 2018). As the type of surface can influence the resulting connectivity map, I produced connectivity maps using three different conductive surfaces. Details on the different conductance surfaces used for connectivity modelling can be found in Appendix S3.5. As functional connectivity analysis is computationally intensive, I rescaled the conductance surfaces to 20 m resolution before performing the *Circuitscape* analysis to save on processing time without compromising resulting connectivity maps (McRae et al. 2008).

To run *Circuitscape* and least-cost path models, grasshopper source patches had to be determined. Source patches is defined here as the highest quality habitat for sustaining grasshopper populations, and areas from which species can disperse. Previous research demonstrated that suitable habitat derived from species distribution models is a cost-effective method to build functional connectivity models (Valerio et al. 2019). Thus, source patches were delineated by selecting the top 5% of high-quality habitat from S-SDM. Source patches were filtered to only include areas ≥ 1 ha, as this is the minimum size for supporting large grasshopper populations (Theuerkauf and Rouys 2006). However, for estate no. 4, which contains smaller remnants, source patches were filtered to include areas ≥ 0.5 ha.

The *Circuitscape* analysis was performed using conductance surfaces in pairwise mode, which measures connectivity for every source node pair combination, and was run separately per estate, as well as per conductance surface. To gain insight into which land cover types are most important to maintain functional connectivity, I averaged the three resulting connectivity maps and selected the top 15% of current within the map, before overlying the selected current onto a land cover data product and identifying underlying land cover types. Similar threshold values have identified the most important areas for maintaining functional connectivity (Duflot et al. 2018).

To identify the least-cost path network that connects source patches, I used the *create_lcp_density* function within the *leastcostpath* R package (Lewis 2021), which calculates the number of times a corridor is used by a random walker moving between source patches. As the conductance surfaces used in *Circuitscape* produced very similar connectivity maps (Appendix S3.5: Figure S3.5.3; Figure S3.5.4), only high-quality habitat from S-SDM was used as a conductance layer in least-cost path models. To gain insight into corridor characteristics of frequently and less frequently used corridors, I selected the top and bottom five most and least used corridors and investigated the underlying landscape features (NDVI, distance to edge, maximum NBR, topographic aspect, cold air drainage, and elevation). These features were averaged per corridor.

To identify sites where connectivity should be improved, I selected the least-cost path network in which the amount of current (*Circuitscape* connectivity map) was $<$ the top 15% of current. This represents areas where functional connectivity is not high enough to maintain connectivity within the landscape, based on research by Duflot et al. (2018). This was done only within the most frequently used corridors per estate (used > 233 times) to prioritise restoration efforts. For this analysis I excluded all paths outside of the estates,

as well as paths that crossed any plantations, so that subsequent recommendations would be focused on grassland corridors within the plantation estates.

3.3.7. Grasshopper beta diversity

To identify the drivers of species turnover I used generalised dissimilarity modelling from the *gdm* R package (Fitzpatrick et al. 2021). Species turnover is a measure of species replacement between locations and is based on dissimilarities in biological composition between pairs of sampled sites. Thus, generalised dissimilarity modelling relates environmental data to dissimilarities in species assemblages, which is calculated from a distance matrix, where greater distances indicate larger dissimilarities (Ferrier et al. 2007).

For fitting my models, I used the Jaccard dissimilarity index, which was selected because it can detect underlying ecological patterns well without relying on abundance data (Oksanen et al. 2020). I decided to use the same presence data in S-SDM for species turnover calculations, to allow better comparisons between methods. The effect of each variable was then evaluated based on range of the partial response plots. These plots show differences between the explanatory variables, and how each effect the response variable (community dissimilarity). The range of response for every variable indicates the strength of the variable in predicting species turnover, and the non-linear curve indicates which portions of that curve would have steeper species turnover.

Alongside the variables used in S-SDM, electrical current maps (*Circuitscape*) and elevation were included as additional variables. To account for the autocorrelation, I included geographic distance between sites as an additional variable in all models. Variable selection was performed to identify important variables affecting species turnover, following a backwards elimination procedure using 100 permutation (*gdm.varImp* function within the *gdm* R package). Only significant variables were used in the final model.

3.3.8. Grasshopper species richness

To identify the drivers affecting local species richness and diversity, I used mixed-effect models. Linear mixed-effect models from the *lme4* R package (Bates et al. 2015) were used for overall richness, exponent Shannon diversity, as well as for low and intermediate conservation-priority species richness and exponent Shannon diversity. Due to the large number of zeros in the high conservation-priority grasshopper

response variables, I decided to use zero-inflated generalised mixed-effect models from the *glmmADMB* R package (Fournier et al. 2012). Specifically, species richness was fitted using Poisson distribution, whereas exponent Shannon diversity, which contained decimal values, was fitted using gamma distribution. For consistency, only species occurring at > 3 sites were used.

To identify most influential variables for the response variables, I performed model selection and averaging using the *MuMIn* R package (Bartoń 2020). This methodology iteratively runs through all possible variable combination (candidate models) and ranks model performance based on Akaike's information criterion (AICc), which accounts for small datasets. Variables used during dissimilarity modelling were also used for mixed-effect modelling, with estate name used as a random effect to account for autocorrelation. Land cover type was excluded from mixed-effect models, as grasshopper richness does not respond strongly to land cover in the surrounding landscape (Bazelet and Samways 2011a). Furthermore, highly correlated variables (± 0.6) were identified using Spearman rank coefficients and excluded from further modelling. Model selection was performed on a global model, containing distance to corridor edge, maxNBR, aspect, elevation, and cold air drainage (VIF < 2.2), using the *dredge* function (Bartoń 2020). Model averaging was then performed using the *model.avg* function (Bartoń 2020) on a subset of the best performing models ($\Delta < 2$), before deriving test statistics. Model averaging incorporates highly influential candidate models into the derived test statistics, which better represents ecological patterns in the data compared to using a single model (Burnham and Anderson 2002).

3.4. Results

3.4.1. Sampled grasshoppers

A total of 2 503 adult Caelifera grasshopper individuals from 58 species, 46 genera, 18 subfamilies and 6 families, were collected, with species accumulation curves reaching near asymptotes (Appendix S2.1: Figure S2.1). On average, 11 species were collected per site (min = 3, max = 20), with a mean number of individuals of 49 (min = 6, max = 186). More information on species richness and abundance per site in Appendix S3.2: Table S3.2.2. Numerous species found in these grassland corridors are associated with protected areas, specifically, *Eyprepocnemis calceata*, *Anablepia pilosa*, *Pseudoarcpytera cephalica*, and

Dirshia abbreviata (Joubert et al. 2016), whereas *Faureia milanjica*, found at three sites, is an indicator of high-quality habitat (Bazelet and Samways 2011b).

A total of 21 grasshopper species with low conservation-priority were collected, with *Oxya hyla*, *Vitticatantops humeralis* and *Pnorisa angulata* being the most abundant species, while a total of 27 grasshopper species with intermediate conservation-priority were collected, with *Lentula obtusifrons*, *Duronia chloronota curta* and *Anablepia pilosa* being the most abundant species. Only 10 grasshopper species with high conservation-priority were sampled, with *Stenoscepa picticeps*, *Dirshia abbreviata* and *Pseudoarcyptera cephalica* being the most abundant species. After removing species occurring at ≤ 3 sites, an overall total of 35 species remained, of which 3, 11 and 21 were high, intermediate, or low conservation-priority species. See Appendix S2. Table S2.2 for full grasshopper species list.

3.4.2. Stacked species distribution modelling

Stacked species distributing modelling performed well in predicting species richness throughout the landscape (Table 3.1). However, for the overall and low conservation-priority species groupings there was relatively high richness prediction error, which decreases substantially with the intermediate and high conservation-priority species groupings, as the number of stacked species decreased (Table 3.1). The models all had high sensitivity, correctly predicting when a species was observed as present, whereas specificity, the ability to correctly predict when a species is observed to be absent, was somewhat lower (Table 3.1). Overall, the models had the ability to correctly predict large proportions of grasshopper assemblage composition (Table 3.1). Additionally, there was high correlation between the two algorithms chosen for the ensemble ($r = 0.77 - 0.88$), indicating overall agreement in the predicted high-quality habitat produced by both algorithms (Appendix S3.4: Figure S3.4.1).

The most influential variables for predicting high-quality habitat for the overall grasshopper assemblage were maxNBR, NDVI, cold air drainage, and aspect, followed by distance to edge and land cover with lower importance (Table 3.2). For low and intermediate conservation-priority species the trend was generally the same (Table 3.2). For species of high conservation-priority, the most influential variables were cold air drainage, aspect, maxNBR, and distance to edge, followed by land cover and NDVI with lower importance (Table 3.2).

Table 3.1: Evaluation statistics for stacked species distribution modelling that were used to identify drivers of high-quality grasshopper habitat for the overall assemblage as well as for the different conservation-priority species groups (Low - High). Spp rich error = species richness error (difference between predicted and observed species richness), Specificity = assemblage specificity (proportion of correctly predicting when a species is absent), Sensitivity = assemblage sensitivity (proportion of correctly predicting when a species is present), and Jaccard = Jaccard index (community similarity). Values represent the mean (\pm SD) of the 10 modelling repeats.

Model	Spp rich error	Specificity	Sensitivity	Jaccard
Overall	16.65 (\pm 10.37)	0.26 (\pm 0.28)	0.74 (\pm 0.31)	0.29 (\pm 0.14)
Low	9.08 (\pm 6.15)	0.24 (\pm 0.29)	0.73 (\pm 0.27)	0.31 (\pm 0.15)
Intermediate	5.63 (\pm 3.57)	0.28 (\pm 0.38)	0.96 (\pm 0.17)	0.38 (\pm 0.24)
High	1.46 (\pm 0.78)	0.19 (\pm 0.38)	1.00 (0)	0.50 (\pm 0.25)

Table 3.2: Relative contribution of environmental variables used in stacked species distribution modelling to predict high-quality grasshopper habitat for the overall assemblage as well as for the different conservation-priority species groups (Low - High). Values represent the mean (\pm SD) of the 10 modelling repeats. NDVI = Normalised Difference Vegetation Index, Drain dist = distance to nearest cold air drainage line, Dist edge = Distance to grassland edge, maxNBR = maximum Normalised Burn Ratio index.

Model	NDVI	Land cover	Drain dist	Aspect	Dist edge	maxNBR
Overall	20.12 (\pm 9.64)	10.73 (\pm 4.93)	17.88 (\pm 5.52)	17.60 (\pm 5.45)	12.23 (\pm 8.02)	21.44 (\pm 6.37)
Low	18.69 (\pm 8.76)	9.83 (\pm 3.60)	17.52 (\pm 3.99)	17.69 (\pm 3.87)	13.02 (\pm 8.56)	23.25 (\pm 6.02)
Intermediate	20.23 (\pm 7.40)	13.44 (\pm 4.50)	17.48 (\pm 5.79)	16.44 (\pm 3.77)	11.20 (\pm 7.13)	21.22 (\pm 6.87)
High	9.54 (\pm 3.00)	9.59 (\pm 5.51)	22.77 (\pm 17.66)	22.29 (\pm 16.21)	14.20 (\pm 7.62)	21.61 (\pm 11.84)

High-quality habitat for the overall assemblage was driven mostly by low conservation-priority species, where the model indicates a preference for grassland edges (Fig. 3.2). Intermediate conservation-priority species also showed a preference for grassland edges, alongside a preference for grassland patch interiors (Fig. 3.2). High conservation-priority species did not prefer grassland edges, as habitat was most suitable in the grassland corridor interior, especially when large in size (Fig. 3.2).

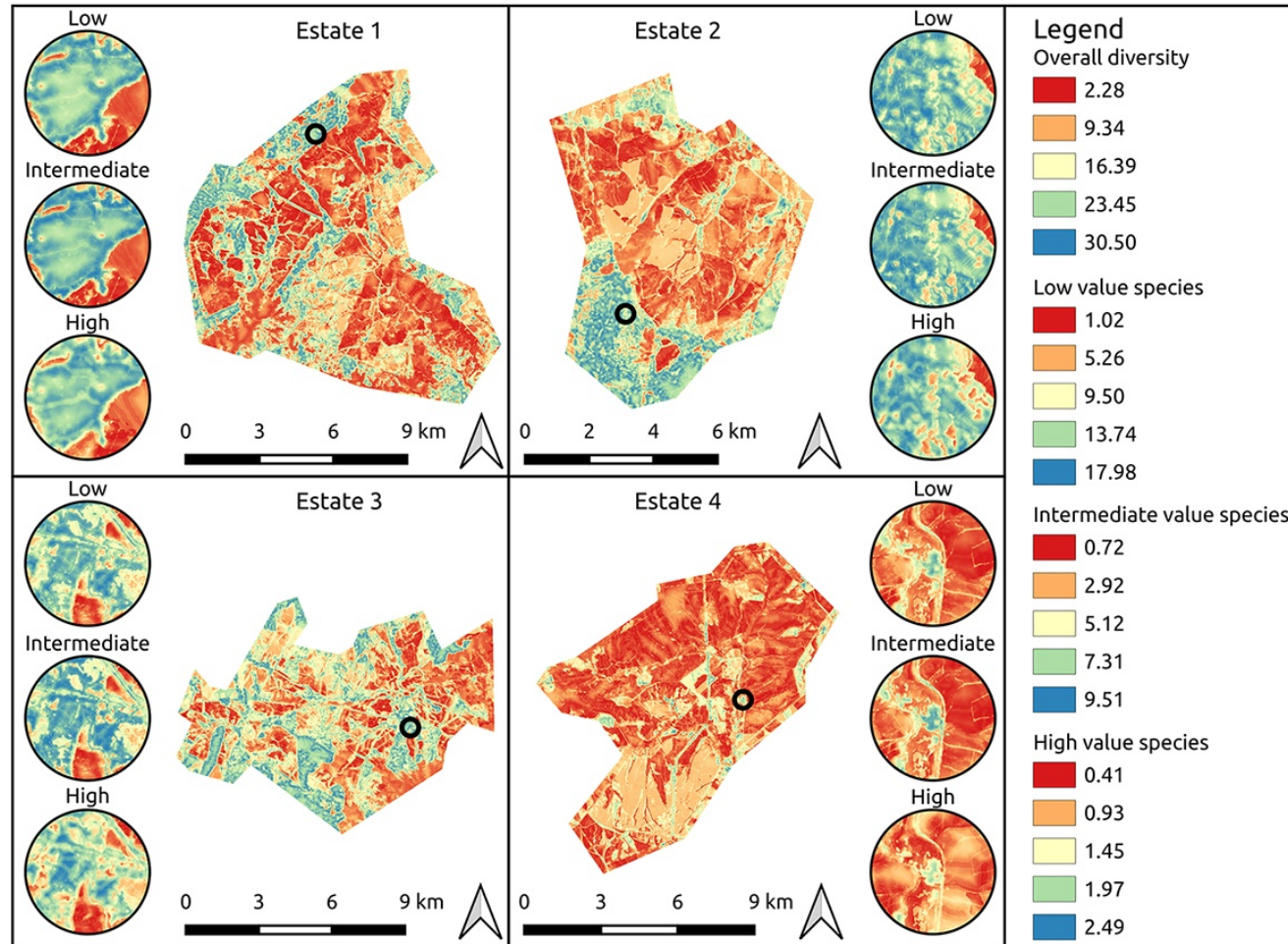


Figure 3.2: Stacked species distribution modelling within the four plantation estates, for overall caeliferan diversity, low, intermediate, and high conservation-priority species groups. Red indicates low-quality habitat with low richness values, whereas blue indicates high-quality habitat with high richness values. Differences between low, intermediate, and high conservation-priority species habitat are illustrated within 700 m buffers (black circle).

The amount of high-quality habitat identified as source patches was generally the same between species groupings, where high conservation-priority species had the lowest amount of source patches available, compared to intermediate conservation-priority species with the largest amount (Fig. 3.3; Appendix S3.4: Table S3.4.3). Additionally, estate no. 4 had the lowest amount of source patches compared to all other estates, with estate no. 1 having the highest amount (Fig. 3.3; Appendix S3.4: Table S3.4.3).

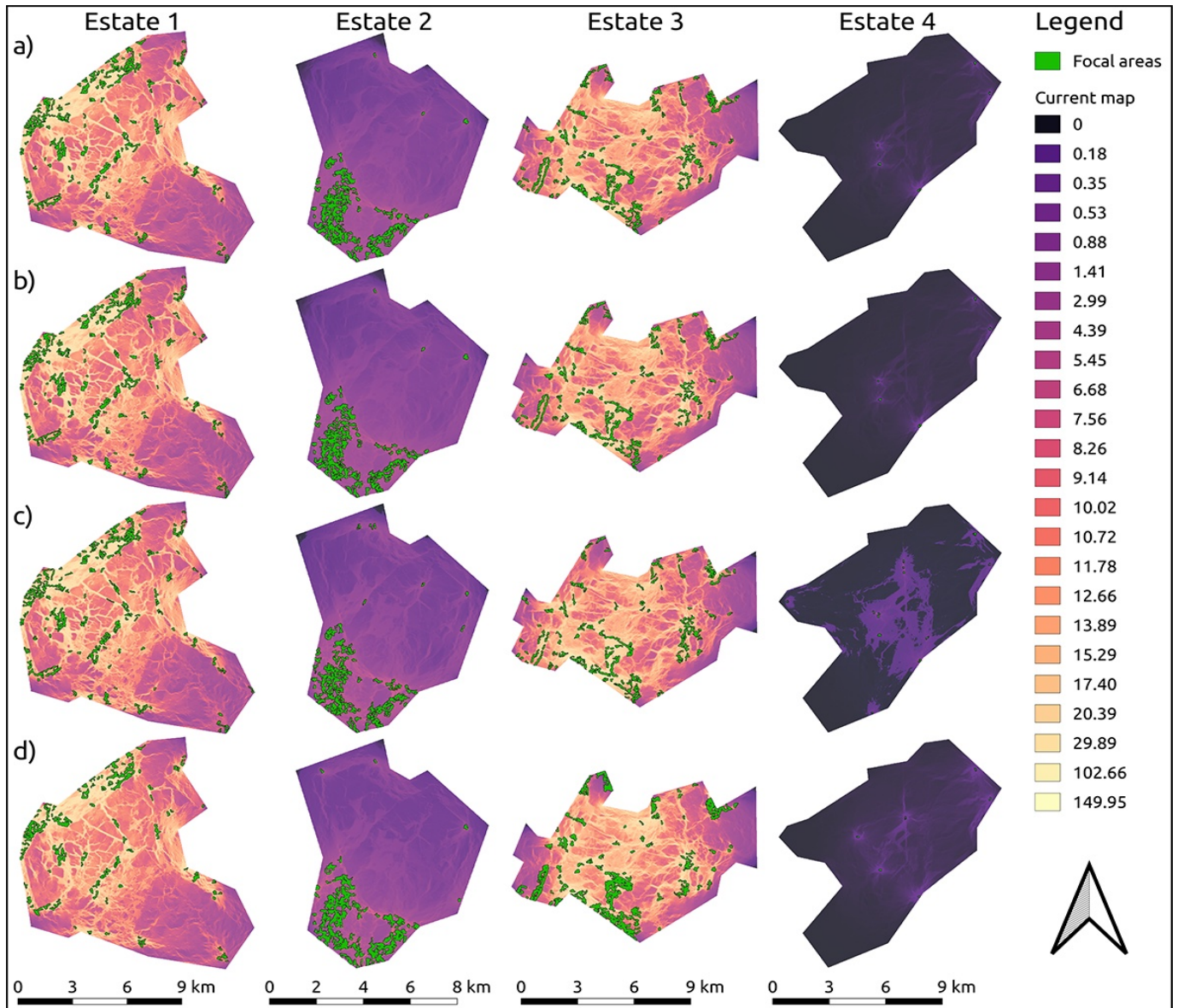


Figure 3.3: Functional landscape connectivity maps for all four estates produced using *Circuitscape*. a) Maps for overall grasshopper assemblage composition, b) low conservation-priority grasshopper species, c) intermediate conservation-priority grasshopper species, and d) high conservation-priority grasshopper species. Green areas indicate grasshopper source patches derived from stacked species distribution modelling.

3.4.3. Functional connectivity

Estate no. 1 and 3 had higher functional connectivity compared to estates no. 2 and 4 (Fig. 3). These estates had large amounts of grasslands compared to timber compartments, and were adjacent to protected areas (Appendix S3.1: Table S3.1.2).

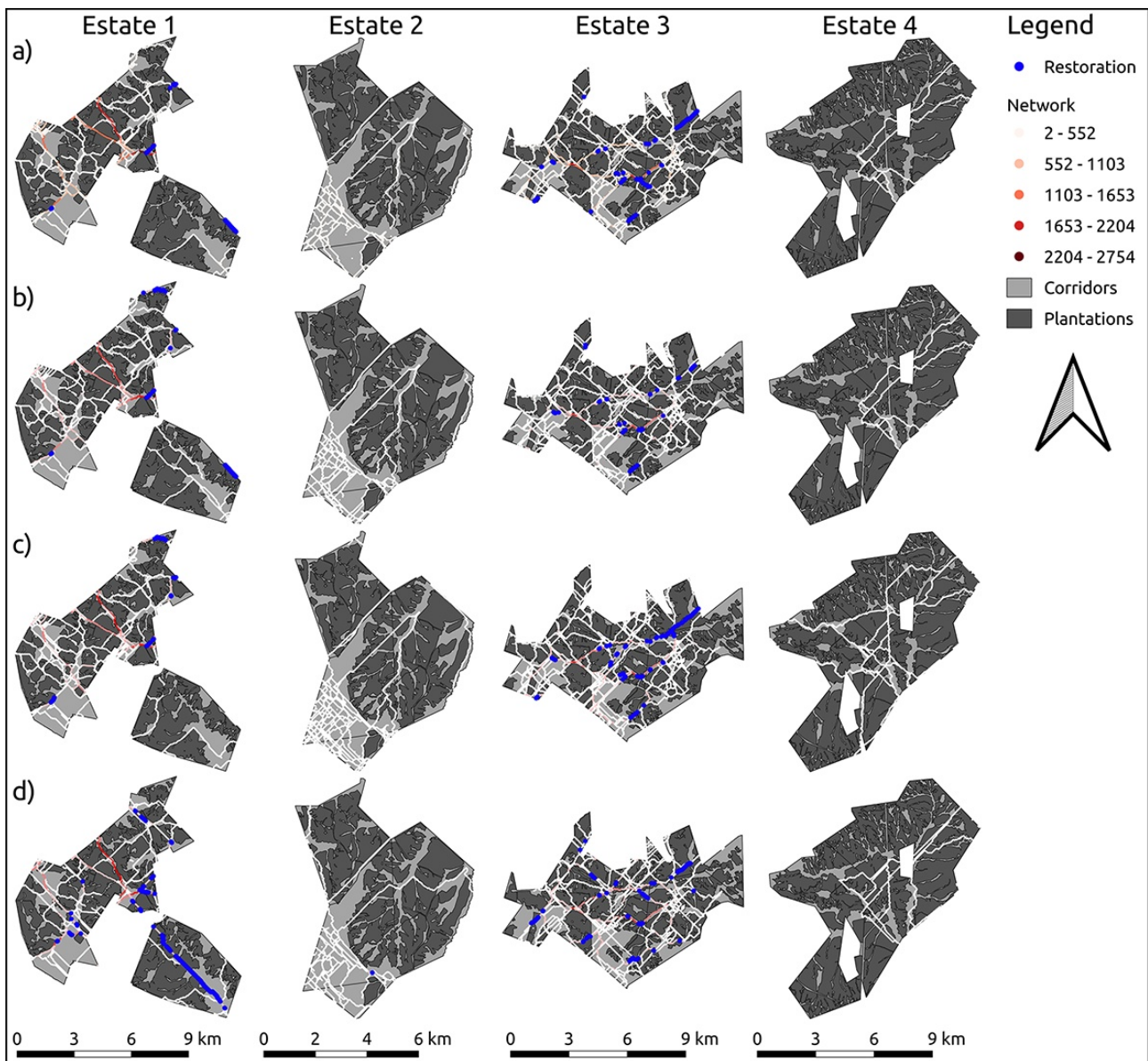


Figure 3.4: Least-cost path networks over all four estates for a) overall grasshopper assemblage composition, b) low conservation-priority grasshopper species, c) intermediate conservation-priority grasshopper species, and d) high conservation-priority grasshopper species. Network path has a colour gradient, where red indicates important corridors frequently used to move between source patches and white shows less frequently used corridors. Blue areas indicate where functional landscape connectivity should be improved within frequently used corridors.

Functional connectivity was generally the same between different species groupings, except for estate no. 4, where functional connectivity improved for intermediate and high conservation species (Fig. 3.3). The most important land cover for maintaining functional connectivity were grassland, followed by shrubland and bare ground with lower importance (Appendix S3.5: Figure S3.5.1).

The least-cost path models identified several highly important corridors, specifically within estates no. 1 and 3 (Fig. 3.4). These important corridors were more often at higher elevation compared to less frequently used corridors (Appendix S3.5: Table S3.5.2). No other features played a major part in identifying important corridors (Appendix S3.5: Table S3.5.2). Between species groupings the least-cost path networks changed, but the highly important corridors stayed constant (Fig. 3.4).

Within the very important corridors, many areas were identified for improving functional connectivity, specifically within estate no. 3 (Fig. 3.4). Corridors within estate no. 1 had fewer restoration sites identified, indicating more suitable functional connectivity (Fig. 3.4). Between species groupings, the number of restoration sites was different, with many sites identified for high conservation-priority species within estate no. 1, as well as for intermediate conservation-priority species within estate no. 3 (Fig. 3.4).

3.4.4. Grasshopper beta diversity

Predicted species turnover of the overall grasshopper assemblage increased steadily with greater distances from grassland edges as well as at higher elevation, whereas little turnover was detected at ≥ 30 km distances between sites (Fig. 3.5). There was a similar pattern for predicted species turnover of low conservation-priority species (Fig. 3.5). For intermediate conservation-priority species, predicted turnover rates increased up until 1 400 m above sea level, above which there was little turnover (Fig. 3.5). For high conservation-priority species, predicted turnover increased rapidly at higher elevations as well as on north-west (warm and sunny) facing slopes (Fig. 3.5).

3.4.5. Grasshopper species richness

Distance to nearest grassland edge had a significant negative effect on local species richness and exponent Shannon diversity for overall grasshopper and low conservation-priority species (Table 3.3). Furthermore, maxNBR had a significant positive effect on exponent Shannon diversity for intermediate

conservation-priority species (Table 3.3). No significant effects were found for high conservation-priority species (Table 3.3).

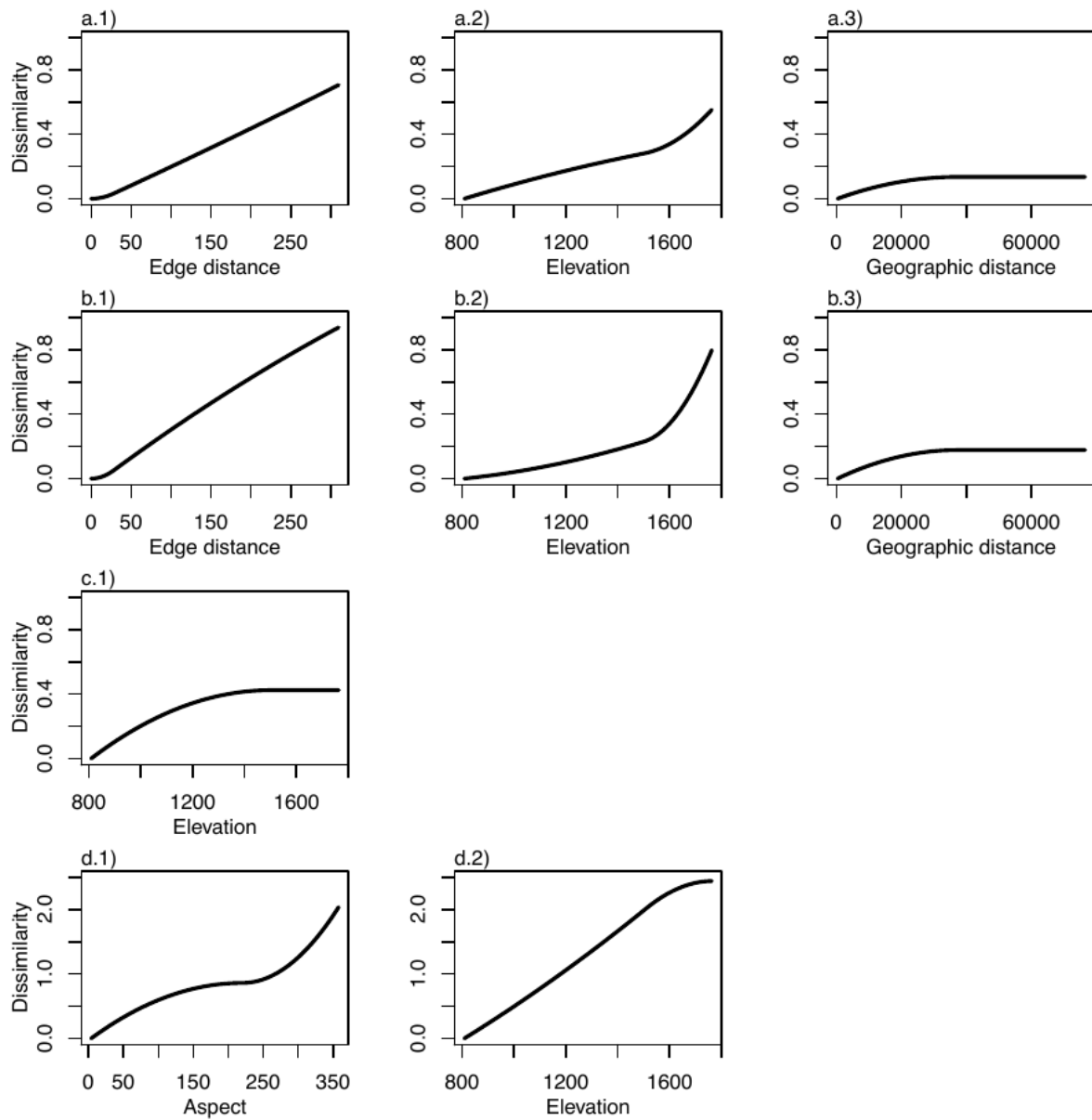


Figure 3.5: Variable importance in predicting species turnover for a) overall assemblage composition, b) low conservation-priority species, c) intermediate conservation-priority species, and d) high conservation-priority species.

Table 3.3: Model-averaged estimates (conditional average) of environmental variables predicting overall grasshopper richness and exponent Shannon diversity as well as for the different conservation-priority species groups (Low - High). Significant variables in bold. RI = relative importance, #models = number of containing models.

Model	Response	Explanatory	beta	se	5%	95%	RI	#models
Overall	Richness	Edge dist	-0.299	0.132	-0.564	-0.033	0.54	1
	exShannon	Edge dist	-0.408	0.136	-0.679	-0.147	NA	1
Low	Richness	Edge dist	-0.307	0.135	-0.579	-0.036	0.45	1
		Aspect	-0.234	0.125	-0.486	0.018	0.19	1
	exShannon	Edge dist	-0.422	0.137	-0.686	-0.157	NA	1
Intermediate	Richness	Drain dist	-0.249	0.134	-0.518	0.02	0.29	1
		maxNBR	0.247	0.15	-0.055	0.548	0.2	1
	exShannon	maxNBR	0.297	0.136	0.023	0.571	0.33	1
		Drain dist	-0.235	0.136	-0.509	0.039	0.2	1
High	Richness	Elevation	0.001	0.0008	-0.0005	0.003	0.46	2
		maxNBR	3.572	2.748	-1.96	9.103	0.19	1
		Aspect	0.002	0.002	-0.003	0.006	0.17	1
	exShannon	Elevation	0.0001	0.0001	-0.0001	0.0003	0.312	1

3.5. Discussion

3.5.1. Grasshopper distribution and turnover

Grassland corridors maintain much high-quality grasshopper habitat, even for species of high conservation-priority, indicating that remnant habitat can support sensitive and range restricted species within production landscapes. This complements previous research, which demonstrated that these corridors, when managed for biodiversity conservation, extend the reaches of neighbouring protected areas (Pryke and Samways 2012b). The distribution of high-quality habitat was driven primarily by vegetation heterogeneity (NDVI and NBR) and topoclimate (cold air drainage and aspect), which was a consistent pattern for low and intermediate conservation-priority species, whereas high-quality habitat for high conservation-priority

species were more influenced by topoclimate than vegetation heterogeneity. Previous work demonstrates that grasshoppers within grassland corridors respond strongly to vegetation structure and bare ground (Bazelet and Samways 2011a), and more recently, that prescribed burning is a major driver modulating vegetation structure (Theron et al. 2021), which further complements my findings on grasshopper distribution patterns.

However, fire through prescribed burning impacts biodiversity in complex ways, due to differences in fire severity, intensity, frequency, and time since last fire. Joubert et al. (2016) studied grasshopper response within grassland corridors to fire frequency and time since last fire, and showed that fire frequency significantly effects grasshopper assemblages, indicating that there is considerable range in preferred habitat. Furthermore, annual burning (high fire frequency) can lead to homogeneous plant communities (Joubert et al. 2014), which negatively impacts some grasshopper species (Poniatowski et al. 2018). This highlights the importance of fire frequency for maintaining high-quality grassland corridors, and my results add to this by demonstrating that fire through prescribed burning has a positive effect on intermediate priority grasshoppers, as well as shaping high-quality grasshopper habitat, but only when fire frequency is somewhat lower (at least once every three years). This corresponds to recent work demonstrating that variation in grassland photosynthetic activity over three years positively influences grasshopper diversity (Theron et al. 2021).

Alongside vegetation structure, topoclimate has a particularly strong impact shaping high-quality grasshopper habitat, especially for more sensitive specialised species. Grassland corridors within the study area cover large areas of complex topography, with large variation in day and night temperatures. This creates opportunities for cold air to form and drain along natural topographic channels, which has major negative impact on grasshopper abundance (Samways 1990). This effect can be even stronger on slopes facing north, which cause grasshoppers to seek refuge on these austral hilltops (Samways 1990). My results add to this by demonstrating the importance of elevation and aspect in predicting grasshopper species turnover, especially for high priority species. Different grasshopper assemblages are supported along an elevation gradient and on different topographic aspects when cold air drainage channels are avoided.

Distance to nearest grassland edge had a clear impact on high-quality grasshopper habitat, where generalists preferred edge habitat, compared to specialists, which preferred the grassland interior. Previous research illustrates the importance of corridor width in determining the strength of edge effects on arthropods

within grassland corridors, where wide corridors are favoured by grassland specialists that inhabit grassland interiors (van Schalkwyk et al. 2020). My results support this, showing that low conservation-priority species (generalists) are more diverse close to grassland edges, and that different grasshopper assemblages occur at greater distances from edge habitat. However, within the study area, the dominant edge effects are created by plantation trees, and more research is needed to assess importance of edge habitat between different contrasting land cover types.

Stacked species distribution modelling used here to study high-quality grasshopper habitat had high sensitivity, but lower specificity, which was a result of using pseudo-absences. This highlights the importance of using accurate absence data for S-SDM. Furthermore, S-SDM generally suffers from relatively high richness prediction error when stacking multiple species (Schmitt et al. 2017), as evident from the overall model and low conservation species model. Other authors have suggested alternative ways of stacking species distribution models (Guisan and Rahbed 2011; Calabrese et al. 2014), but there is not consensus as to which method is best, as it differs for the species mapped, environmental data used, and algorithms selected (Hortal et al. 2012; Benito et al. 2013; D'Amen et al. 2015). Stacking species distribution models has large conservation potential, but more research is needed to further develop this methodology.

3.5.2. Functional connectivity

Grassland corridors between plantation forests greatly contribute to functional connectivity throughout the landscape. The ratio of grassland to plantation compartments had a large influence on functional connectivity, with estate no. 1 and 3 showing the highest amount of functional connectivity due to larger amounts of grassland. These estates also neighbour protected areas, which suggests that these estates will more easily allow biodiversity to spillover (Pryke and Samways 2012b), indicating that high-quality habitat surrounding plantation estates play a key part in sustaining functional connectivity throughout the landscape.

Grassland was the most important land cover for maintaining functional connectivity. However, not all grasslands are the same. Older grasslands have climax grass species with long broad leaves, which are not preferred by most grasshopper species (Bazelet and Samways 2011a). Here, my results provide new insights into how NDVI can be used as a monitoring method for assessing functional connectivity within the wet

summer months, and to help assist spatial planning for prescribed burning. NDVI has previously been used to predict grasshopper diversity, with vegetation structure being the underlying driver explaining this relationship (Theron et al. 2021).

Interestingly, shrubland helped maintain functional connectivity, specifically within timber compartments after trees have been harvested. After the removal of trees, the land is cleared and left fallow, allowing alien vegetation to colonise. After several months, this vegetative layer is removed prior to plantation tree saplings being planted. Vegetation, mostly alien, are once again allowed to colonise, but will eventually die out when tree canopies start to close. Thus, functional connectivity is enhanced during the initial establishment of plantation tree saplings. This suggests that where mature trees are harvested, they have high temporal impact on functional connectivity within the landscape (Pliscoff et al. 2020). Recent research also supports this by showing that rotational harvesting, as opposed to harvesting entire landscapes, can increase vegetation structural diversity, promoting arthropod spillover within the landscape (van Schalkwyk et al. 2021). However, bush encroachment and alien invasion are major threats to grassland ecosystems globally (Stanton et al. 2018, Wang et al. 2019), and can reduce functional connectivity within grasslands (Deák et al. 2020). Thus, alien vegetation should be contained within the timber compartments and prevented from spilling over into grassland corridors.

Within the grassland corridors of the study region, multiple highly important corridors were identified, with only elevation playing an important role in characterising frequently used corridors, even for high priority species. Corridors at higher elevation are key refuges under warming climates (Samways and Pryke 2016), and it is relatively inaccessible to humans and experience less frequent anthropogenic disturbances such as prescribed burning (Gaigher et al. 2019). Thus, corridors at higher elevations should be retained and managed optimally to ensure resilience, especially focussing on larger corridors. Additionally, elevation can help guide the identification of additional high value corridors in other study systems, and to prioritise restoration activities.

In general, I did not find any direct effect of functional connectivity on grasshoppers, supported by other research (Keller et al. 2013; Poniatowski et al. 2016; Löffler and Fartmann 2017). However, functional connectivity for grasshoppers is dependent upon vegetation structure, as shown by my results. This suggests that functional connectivity has an indirect effect on grasshoppers within grassland corridors.

3.5.3. Management recommendations

Here I show that by using S-SDM, functional connectivity analysis, and species turnover calculations, an in-depth understanding of how remnant habitat as the corridors here within production landscapes conserves biodiversity. I recommend use of fire through prescribed burning to maintain high-quality grasshopper habitat and functional connectivity within grassland corridors. Fire frequency should be critically considered, and I recommend burn cycles of 2-3 years, spaced out spatially to enhance heterogeneity in vegetation successional stages. Large corridors with an elevation gradient and north-west facing slope in this austral landscape should be prioritised for grasshopper conservation. In turn, NDVI can be used to assess grasshopper habitat to guide planning for prescribed burning.

Within estates with narrow grassland corridors and low functional connectivity, I recommend that extensive management of some timber compartments be adopted, so that these compartments resemble natural habitat more closely and improve functional connectivity (Betts et al. 2021). Extensive management tries to mimic natural disturbance regimes and vegetation structure that emulates this by retaining some trees and downed wood during harvesting (Betts et al. 2021). Lastly, when timber trees are harvested, and how the land is managed before timber trees mature, should be incorporated into conservation planning. This approach can enhance functional connectivity, even if only in the short-term.

Grassland corridors can conserve biodiversity and maintain ecological resilience within a plantation forest landscape, so long as management ensures functional connectivity and high-quality habitat so that there is long-term conservation of biodiversity in these production landscapes.

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Chapter 4: Mapping an alien invasive shrub within grassland corridors using super-resolution satellite imagery

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4.1. Abstract

Alien invasive plant species are one of the main drivers of global biodiversity loss. Methods for monitoring the spread of alien invasive plants are needed to improve management and mitigate impact on local biodiversity. Recent advances in deep learning and super-resolution image reconstruction holds great potential for mapping and managing alien invasive plants. Within the commercial timber production landscape of KwaZulu-Natal, endangered grassland corridors are threatened by American bramble invasion, impacting plants, birds, arthropods, and soil restoration. Here I aim to improve our understanding of bramble invasion dynamics through using super-resolution satellite mosaics. Super-resolution satellite mosaic classified bramble with very high accuracies (86%) compared to other conventional satellite imagery with different spectral and spatial resolutions. Using landscape analyses, I identified plantation tree harvesting and prescribed burning to be major drivers increasing bramble cover within the landscape. Bramble cover was highest two years after plantation trees have been harvested, whereas continuous prescribed burning positively influenced bramble. Bramble cover was also high close to streams, and under future invasion projections, bramble will severely impact *Ensifera* species alongside high priority grasshopper species habitat. Results also indicate that bramble has a significant negative impact on intermediate priority grasshoppers and plant species richness. For controlling bramble invasion within the commercial timber production landscape, I recommend the adoption of rotational harvesting, as harvesting entire plantation blocks throughout the landscape will dramatically increase invasion potential of bramble. Current bramble removal programmes should prioritise riparian areas and use high priority grasshopper habitat to identify vulnerable terrestrial habitat. Special attention is needed to control bramble two years after harvesting, as this is when bramble cover is highest. I show the benefits of using super-resolution mosaics to gain new insights into alien invasive species dynamics, while further development of this technique will aid in managing alien invasive plant species.

Keywords: Conservation corridors; Plantation forestry; Remote sensing; Deep learning; *Rubus cuneifolius*; Landscape management; Invasion dynamics

4.2. Introduction

Alien invasive plant species are one of the main drivers of global biodiversity loss, which cause the reduction of ecosystem services and human well-being (Pyšek et al. 2020). Alien invasive plants can also have indirect impacts on local biodiversity, through changes in water quality (Le Maitre et al. 2014) and change in soil chemistry (Ruwanza and Shackelton 2016). Removal of alien invasive plants is crucial yet hindered by high costs associated with manual removal and lack of appropriate data on species distributions. There is thus an urgent need to develop methods for monitoring alien invasive plants to optimise removal programmes, and to improve our understanding of the mechanisms driving invasions and their impact on local biodiversity (van Wilgen et al. 2020).

Developing a robust understanding of alien invasive plant dynamics will provide important feedback for optimising management (van Wilgen et al. 2021). This is especially important within production landscapes, as human activity and land use change are important drivers of alien plant invasions (van Rensburg et al. 2018). Furthermore, production landscapes are some of the last frontiers for biodiversity conservation under global change (Samways et al. 2020), as large amounts of natural vegetation still reside within them (Dinerstein et al. 2017). Thus, understanding which operations within production landscapes facilitate the spread of alien invasive plants will provide much needed guidance to design effective conservation programmes within production landscapes (Samways and Pryke 2016).

The endangered grassland biome of South Africa, a biodiversity hotspot, is threatened by commercial timber production, predominately within the KwaZulu-Natal and Mpumalanga provinces. The timber estates protect much remnant habitat of natural vegetation for biodiversity conservation (Samways and Pryke 2016), while providing valuable economic opportunities for the country. However, some operations, such as poor weed control in nurseries, seed dispersal through field machinery, tree felling, logging, planting of plantation tree saplings, and creating new service roads, provide opportunities for alien invasive plants to establish and spread (Le Maitre et al. 2004). These actively managed landscapes have therefore become prime invasion sinks (van Wilgen et al. 2008), and responsibility to manage alien invasive plants has been put onto landowners (van Rensburg et al. 2018).

In South Africa, a total of 559 taxa have been identified as serious alien invasive species that require compulsory control under the Alien and Invasive Species regulations of South Africa (van Wilgen et al. 2020). American bramble (*Rubus cuneifolius*) is one of the most prominent and aggressive alien invasive plants in the grassland biome of South Africa (Henderson 2007). Bramble threatens plant species richness and endemic grassland birds (Reynolds and Symes 2013), dragonflies (Kietzka et al. 2015), pollinating insects (Hansen et al. 2018), soil arthropods and soil recovery (Eckert et al. 2019), as well as large bodied Caelifera grasshoppers (Theron et al. 2021a). Bramble also forms dense stands around newly established sapling plantations, complicating forestry operations (Roberts et al. 2021). Effective tools for monitoring bramble, which prioritises its removal and maximises gains in biodiversity conservation, are needed.

Recent advances in satellite remote sensing and available non-parametric classification algorithms provide much needed tools allowing mapping and predicting of suitable habitat for various alien invasive plants with high accuracy (Royimani et al. 2019). Developing accurate classification models are becoming more affordable, compared to conventional field assessments, especially in remote areas. To date, use of publicly available Sentinel-2 satellite imagery has been reliable in mapping alien invasive trees in the grassland and savanna biomes of South Africa (Rebelo et al. 2021). Furthermore, Rajah et al. (2018a) showed that Sentinel-2 imagery can be used to map bramble within the uKhahlamba Drakensberg Park with an accuracy of 77%.

Mapping alien vegetation requires the ability to effectively differentiate between alien and native vegetation (Royimani et al. 2019). Non-parametric algorithms learning from remote sensing data can accurately differentiate between different land cover classes by identifying differences in their spectral responses (Xie et al. 2008). However, to differentiate between species, and species with similar growth forms, high spectral and spatial resolution imagery is needed. Satellite image pixel size needs to be small enough to discern spatial objects like plant canopies, but also have high enough spectral resolution to help algorithms learn differences in plant species spectral responses. Commercial WorldView-2 satellite imagery with high spectral resolution (8 spectral bands) and high spatial resolution (2 m pixel size), has been used successfully to map *Solanum mauritianum* within a timber estate with accuracies of 91% (Peerbhay et al. 2016). However, such high-quality data comes with a considerable cost and is therefore not widely accessible. Feature level image fusion has been proposed to improve mapping accuracy by combining optical

remote sensing data (Sentinel-2) with active remote sensing data (Sentinel-1). However, this technique failed to improve overall mapping accuracies compared to just using spectral data (Rajah et al. 2018b; Rebelo et al. 2021).

Developments in deep learning has provided new opportunities for image fusion (Palsson et al. 2018; Latte and Lejeune 2020). Image fusion using deep learning involves the joining of imagery with different properties (spectral and spatial) to create a new data product with the desired resolution. This technique is also known as image super-resolution, where the neural network trains to sharpen the resolution of coarse pixels (Dong et al. 2016). Palsson et al. (2018) used this technique to improve all 13 Sentinel-2 bands from 60 m to 10 m. Latte and Lejeune (2020) took this further by fusing the 10 bands of Sentinel-2 (10 and 20 m) with the 4 bands of PlanetScope (3 m) to generate a super-resolution mosaic (10 Sentinel-2 bands at 2.5 m).

Image fusion using deep learning holds great opportunities for monitoring alien invasive plant species at fine scales. Here, I aim to use super-resolution mosaics to map bramble within grassland corridors across a production landscape, to improve our understanding of what makes bramble a successful invader, and to determine the local and landscape impact of bramble. Grasshoppers and plants were specifically selected as study organisms to assess the impact of bramble, as they are effective indicators of high quality grassland habitat (Bazelet and Samways 2011; Joubert et al. 2017). I specifically ask 1) how widespread is bramble, and what is causing higher bramble cover? 2) What is the local impact of bramble on other plants and on grasshoppers? 3) How will uncontrolled bramble invasion impact the landscape? Through answering these questions, I aim to improve our understanding of the influence of image resolution on mapping alien invasive shrubs, mechanisms driving bramble invasion within production landscapes, and impact of bramble on landscape and local biodiversity, as well as provide management recommendations for controlling spread of bramble. I also include discussion on using super-resolution mosaics for mapping alien invasive plants.

4.3. Methods

4.3.1. Study area

The study was conducted within four commercial timber estates across the KwaZulu-Natal Midlands of South Africa (Fig. 4.1). Large grassland remnant patches, covering about 40% of these estates, are set aside for conservation. These remnants form structurally connected corridors which dissect the plantation

compartments and help maintain functional connectivity within the landscape (Theron et al. 2021b), as well as protect some of the last intact grasslands of the highly threatened Maputaland-Pondoland-Albany Hotspot (Dinerstein et al. 2017). Dominant vegetation types include the Mooi River Highland Grassland, Midlands Mistbelt Grassland and Southern KwaZulu-Natal Moist Grassland (Mucina and Rutherford 2011). This temperate region experiences frequent thunderstorms in summer with a mean annual precipitation of 900 mm and mean annual temperature of 15°C (Mucina and Rutherford 2011). The topography is complex, from steep hills with exposed rocks to flat low-lying areas.

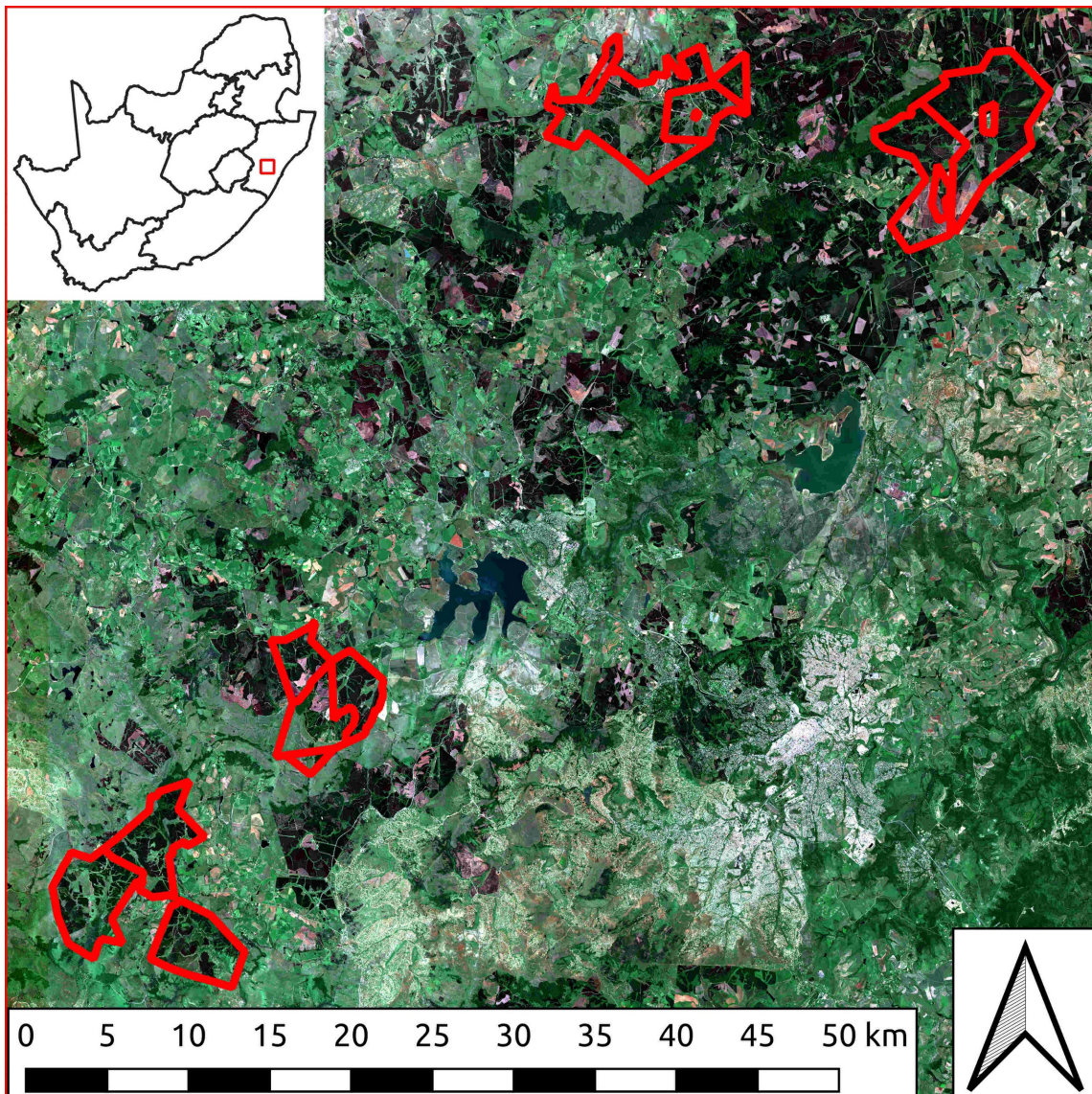


Figure 4.1: Super-resolution mosaic of the study area. Sampling took place within the four timber estates outlined in red.

4.3.2 Field campaigns

4.3.2.1. Bramble ground truthing

Bramble was recorded in the field using a Garmin etrex GPS device to assist with classification of satellite imagery. Waypoint averaging was enabled to improve GPS error to around 1 m. Only locations where bramble cover was $\geq 5\text{m}^2$ was recorded (Fig. 4.2). Locations were captured as close to the centre of bramble patches as possible.



Figure 4.2: Photo showing how dense American bramble (*Rubus cuneifolius*) grows within grasslands.

4.3.2.2. Grasshopper sampling

To determine how bramble impacts grasshoppers, a sweep-net with a diameter of 0.5 m and depth of 0.7 m was used to collect grasshoppers. At every site a total of three parallel 100 m transects were walked separated by 5 m. At every 1 m along the transect, vegetation was swept with a sweep-net, using a 180-degree arc movement. A total of 100 sweeps were performed per transect, with an overall total of 300 sweeps per site. After sweep netting, active searching was employed to capture mobile and elusive species. Two

observers simultaneously searched within the sampling area by flushing out and chasing after large-sized grasshoppers. A total of 40 min of active searching took place per site (20 min per observer). At sites where bramble was abundant, grasshoppers were swept alongside and between bramble bushes.

Sampling occurred in March 2020, the peak season for adult grasshopper activity in this area (Kinvig 2006). Sampling was undertaken between 08h30-16h00 on sunny cloudless days with little to no wind, and took place at the centre of fragments, or > 50 m away from edges (Pryke and Samways 2012). All sampled grasshoppers were transferred to re-sealable bags. They were later placed in a freezer prior to sorting. Immatures were not included owing to identification difficulties, and all adults collected were pooled per site for analysis. See Appendix 4.1: Table S4.1.1 for a species list. A total of 51 sites were sampled within the grassland corridors across the four timber estates. Half of these sites had bramble present. Sites were separated by > 1 km within the estates to ensure independence of sampling, except within estate no. 4, where the minimum distance between sites was 400 m due to smaller grassland fragments. Sites were selected to cover the extent of the corridors, thereby capturing the heterogeneity caused by prescribed burning (Gaigher et al. 2019).

4.3.2.3. Vegetation survey

Vegetation data were collected after grasshopper sampling using 1 m² quadrats, to determine how bramble is impacting local plant species richness. Per site a total of 24 quadrats were randomly placed within the sampling area. Plant richness was then recorded per plant growth form (tree, shrub, succulent, fern, sedges, forb, bulb, grass, and creeper). Additionally, bramble cover was also recorded per plot.

4.3.3. Image classification

4.3.3.1. Image selection and processing

To investigate the influence of image resolution (spectral and spatial) on performing accurate image classification for mapping bramble, I used three different mosaics. Specifically, I used a Sentinel-2 mosaic (10 spectral bands, 20 m pixel), PlanetScope mosaic (4 spectral bands, 3 m pixel), as well as a super-resolution mosaic (10 spectral bands, 2.5 m, see below). Sentinel-2 imagery (ID T36JTN_20200104T074311) was accessed from Copernicus Open Access Hub

(<https://scihub.copernicus.eu/dhus/>) as an atmospherically corrected level-2A bottom of atmosphere reflectance image. Only the 20 m Sentinel-2 data product was used for classification. PlanetScope imagery was accessed from Planet Explorer (<https://www.planet.com/explorer/>) as atmospherically corrected level-3B surface reflectance imagery (Planet Team 2017). All imagery were captured between 4-5 January 2020, contain little or no cloud cover and had an EPSG:32736 projection. Furthermore, these dates were selected to coincide with bramble flowering (Rajah et al. 2018a), to improve class discrimination. Multiple PlanetScope imagery covering the plantation estates were mosaicked, whereas all 20 m Sentinel-2 imagery were stacked into a single mosaic covering the study region. Image processing was done using R version 3.6.3 (R Core Team 2020).

4.3.3.2. Super-resolution mosaic

Latte and Lejeune (2020) developed an image fusion technique using a residual convolutional neural network that combines the fine spatial resolution of PlanetScope imagery with the high spectral resolution of Sentinel-2 imagery into one super-resolution mosaic. The resulting product is a 2.5 m spatial resolution mosaic with the 10 spectral bands of Sentinel-2.

In preparation to train the network, additional PlanetScope imagery between 14 December 2019 and 31 January 2020, were downloaded and mosaicked to cover the full Sentinel-2 image (captured on 4 January 2020), before being co-registered with the Sentinel-2 image using a global linear transformation (Leutner et al. 2019), so all pixels from the different sensors align correctly. The additional imagery allowed the model to train on data outside the study region, to prevent model overfitting. Only high radiometric quality PlanetScope imagery were used. A Gaussian filter was then applied to the registered PlanetScope and Sentinel-2 imagery. This blurring was used to create additional training data and validate that the network can accurately downsample coarse to fine pixels (blurred imagery to normal imagery). Unusable data masks from both PlanetScope and Sentinel-2 were incorporated into the network architecture to mask clouds and aid in radiometric normalisation between the different sensors during training. For more details on this method, see Latte and Lejeune (2020).

Residual convolutional neural networks perform well with image fusion tasks, as this optimised network iteratively learns directly from input data, by extracting features at every (hidden) layer in the

network and using their importance (weights) to make predictions (Dhillon and Verma 2020). The learning occurs during backpropagation, a method where the network updates the importance of features to improve the prediction accuracy.

The neural network architecture used here was set up to enable the network to learn from the 10 m and 20 m Sentinel-2 imagery as well as PlanetScope imagery simultaneously, extracting many features to improve prediction accuracy. See Appendix S4.2: Figure S4.2.1 for network validation plots. The network was trained using a NVIDIA GeForce RTX 2080 graphics card, 2 terabyte solid state drive, 64 gigabyte of random access memory and 20 processor cores. Training took approximately 48 hours to complete and was implemented using the *Keras* R package (Kalinowski et al. 2019).

4.3.3.3. Training data and classification

To classify land cover types within the study area, I used the Random Forest algorithm. Random Forest is used regularly for classification problems and was implemented using the *caret* R package (Kuhn 2020). Only spectral bands were used in classification, and maps were produced separately for Sentinel-2, PlanetScope and super-resolution mosaics. Models were trained to classify the most prominent land cover classes within the study area, specifically, grassland, bare ground, plantation forest, shrubland, thicket, water, woodland, as well as bramble. Alongside the 82 bramble GPS points collected in the field, additional reference data were collected using a 25 cm RGB orthophoto. A total of 1 961 data points were created. To increase the amount of training data, I extracted spectral data within 2.5 m buffers around the data points for the super-resolution (2.5 m) and PlanetScope (3 m) mosaics only. Data were split using 70% for training and 30% for testing. To obtain best performing model hyperparameters, I used a random selection of 10 different hyperparameters combinations. The best combination of hyperparameters was then selected based on the resulting Kappa statistic generated using a bootstrapping procedure. The best performing model, determined from a confusion matrix using testing data, was used to predict land cover classes for entire study region. See Appendix S4.2 for more information on image classification.

4.3.4. Statistical analyses

4.3.4.1. Response variables

To understand the drivers of bramble cover within the landscape, I used bramble from the super-resolution mosaic classification to generate a response variable. First, I created 10 000 random points within the classified bramble pixels before pruning points to exclude those within 500 m of each other to avoid spatial autocorrelation. These points were then clipped into production and conservation areas. This clip was done as bramble might respond differently to the major disturbances within these areas (harvesting in production areas and prescribed burning within conservation areas). Additionally, it was not possible to effectively differentiate between harvesting and burning using remote sensing data products (see below). Bramble cover was then calculated per point using 50 m buffers and used as response variable to regress against other landscape and management variables to identify potential drivers.

Next, to determine how bramble impacts local plant species richness, I calculated plant species richness at the plot level, and used this as response variable to regress against bramble cover within the plots. For determining grasshopper response to bramble, I calculated the average bramble cover across all plots per site. Grasshopper species richness was used as response variable, and was calculated for the overall assemblage, Caelifera species, as well as Ensifera species. I also scored grasshoppers as low, intermediate, and high conservation-priority following guidelines from Matenaar et al. (2015). These scores were based on species rarity, endemism, and mobility. Each parameter had different classes, and the sum of all classes were used to classify grasshoppers (Appendix S3.2: Table S3.2.1). A flightless endemic species which is locally rare will have a high conservation priority, whereas a common widespread species capable of flight will have a low conservation priority.

4.3.4.2. Drivers of bramble invasion

To model drivers of bramble invasion, I used mixed-effect modelling with a negative binomial distribution. Separate models were created for production and conservation areas, fitted with timber estate as random effect to account for spatial autocorrelation. Variables included in the conservation model were distance to stream, distance to woodlands, distance to plantation tree harvesting, Normalised Burn Ration (NBR) index as a proxy for burning, as well as the interaction between distance to streams and burning.

Variables in the production model included distance to stream, distance to woodlands, distance to plantation tree harvesting, as well as the interaction between distance to steam and harvesting.

Distance to streams and woodlands was included in the models as moist areas are highly suitable habitat for bramble (Ndlovu et al. 2018) and frugivorous birds play an important role in bramble seed germination and potential long distance dispersal (Molefe et al. 2020). For harvesting, I used the NBR index over the production area by calculating the minimum NBR index from Landsat 8 imagery per year for five different years (2020 – 2016) in Google Earth Engine (Gorelick et al. 2017). I wanted to determine whether the disturbance from harvesting can have a legacy effect on bramble by creating different models for every year (2020 model, 2019 model etc.). Lastly, minimum NBR was also extracted from Landsat 8 imagery for the five different years within the conservation areas to investigate burn severity and intensity on bramble cover.

I performed variable selection and model averaging to identify most influential variables impacting bramble cover using the *MuMIn* R package (Bartoń 2020). All explanatory variables were first standardised before deriving test statistics. This was repeated for the conservation and production areas separately, as well as per year. All global models used for variable selection and model averaging had variance inflation factor scores < 1.5 .

4.3.4.3. Bramble impact on plants and grasshoppers

To model the response of plants and grasshoppers I also used mixed-effect modelling with timber estate as random effect to account for spatial autocorrelation in both the plant and grasshopper models, but with site identification as an additional random variable for the plant model to account for the nested nature of sampling (i.e., plot data). The plant model was fitted with a Poisson distribution and only contained bramble cover as a fixed effect. Grasshopper models were fitted with a Gaussian distribution, except for high conservation-priority and *Ensifera* response variables, which were fitted with a Poisson distribution. Once again, the grasshopper models were fitted with bramble cover as the only fixed effect variable. Bramble cover was standardised before deriving test statistics. All mixed-effect models were constructed using the *glmmTMB* R package (Brooks et al. 2017).

4.3.5. Stacked species distribution modelling

Stacked species distribution modelling (S-SDM) was used to map local biodiversity hotspots and identify areas, and groups of species, which will be most susceptible to uncontrolled bramble invasion within the landscape. S-SDM were implemented using the SSDM R package (Schmitt et al. 2017). This procedure produces a species richness map using the summed probabilities of suitability maps from individual species distribution models. I used an ensemble approach, averaging the results from Random Forest and Support Vector Machines models. Per species, each algorithm was repeated 10 times and only ensembles with an AUC score of 0.7 or higher were retained for the final stacked model. Furthermore, the final stacked model was evaluated based on a cross-validation procedure using a 70/30 split for training and testing. S-SDM were fitted using presence and pseudo-absence data. Furthermore, only species occurring at > 3 sites were retained for running S-SDM. S-SDM was repeated for all grasshopper response variables.

Only environmentally relevant variables were used during S-SDM. Specifically, I included vegetation structure (Normalised Difference Vegetation Index: NDVI), land cover (super-resolution classification), distance to plantation edge, burning history (minimum NBR over three years), elevation and aspect derived from a digital elevation model, and distance to stream. These variables have previously been used to map local grasshopper hotspots within this region with high accuracy and are significant for predicting species turnover (Theron et al. 2021b). NDVI maps healthy vegetation and can serve as a proxy for vegetation structure, which influences grasshopper diversity in this region (Theron et al. 2021a). Corridor width, or distance to plantation edge, influences the strength of edge effects on arthropods (van Schalkwyk et al. 2020). The minimum NBR index, used as a proxy for burning history, was calculated from Landsat 8 imagery dating back three years from grasshopper sampling, using Google Earth Engine. This index determined whether an area was burned within the last three years, as well as the severity and intensity of the burn (Keeley 2009), which are highly significant for grasshopper diversity (Theron et al. 2021a, 2021b).

Suitable habitat for all grasshopper communities were then filtered to select the top 5% of habitat to calculate the percentage overlap with bramble distribution from the super-resolution classification. A 10 m buffer was then created around bramble pixels to simulate bramble vegetative growth over 10 years when left unchecked, and again percentage overlap with grasshopper suitable habitat was calculated. I estimate that 1 m vegetative spread per year is a conservative rate, as a new daughter plant can form within one season

(Erasmus 1984). All raster variables used in S-SDM were rescaled to 10 m resolution to reduce processing time.

4.4. Results

4.4.1. Image classification

Super-resolution mosaic produced the most accurate land cover classification (Accuracy = 0.95; Kappa = 0.94), followed by Sentinel-2 image (Accuracy = 0.89; Kappa = 0.87) and PlanetScope image (Accuracy = 0.87; Kappa = 0.85). However, Sentinel-2 and PlanetScope imagery failed to accurately classify bramble with 0.56 and 0.65 class accuracies respectively, compared to the super-resolution mosaic with a bramble class accuracy of 0.86 (Table 4.1). All other classes were classified with very high accuracies (Table 4.1; Fig. 4.3).

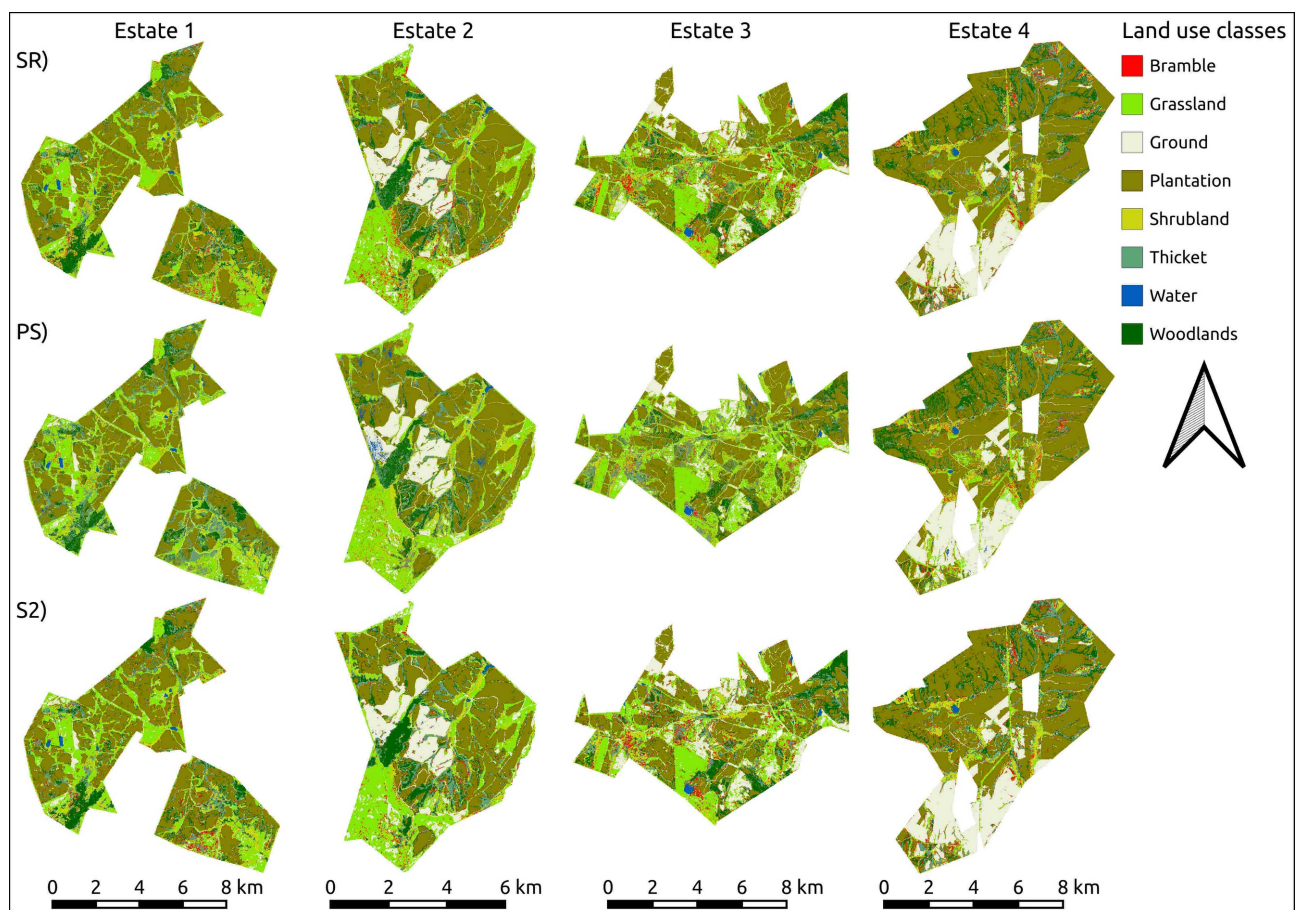


Figure 4.3: Random Forest classification of timber estates for a) Super-resolution mosaic, b) PlanetScope image, and c) Sentinel-2 image.

Table 4.1: Subset of statistics derived from a confusion matrix using the Random Forest algorithm for all imagery classified. SR = super-resolution. PS = PlanetScope. S2 = Sentinel-2. Sensitivity refers to percentage of true positives, whereas Specificity is percentage of true negatives. Accuracy refers to the balanced accuracy of the class.

Image	Statistic	Bramble	Grassland	Ground	Plantation	Shrubland	Thicket	Water	Woodland
SR	Sensitivity	0.716	0.983	1	0.991	0.864	0.928	1	0.924
	Specificity	0.997	0.988	1	0.994	0.988	0.982	1	0.993
	Accuracy	0.856	0.985	1	0.993	0.926	0.955	1	0.958
PS	Sensitivity	0.296	0.919	0.99	0.94	0.797	0.898	0.986	0.73
	Specificity	0.995	0.981	0.999	0.97	0.979	0.953	0.998	0.978
	Accuracy	0.646	0.95	0.994	0.955	0.888	0.926	0.992	0.854
S2	Sensitivity	0.125	0.948	0.954	0.991	0.761	0.874	0.952	0.904
	Specificity	0.995	0.961	0.992	0.992	0.981	0.962	1	0.986
	Accuracy	0.56	0.954	0.973	0.991	0.871	0.918	0.976	0.945

4.4.2. Drivers and impact of bramble invasion

Within the conservation areas, burning had a consistent significant negative impact on bramble cover, where more intense burns (large negative NBR values) resulted in higher bramble cover (Table 4.2). Bramble cover response to burning was most prominent in 2018 (Table 4.2). Furthermore, distance to stream also had a significant negative impact on bramble cover, where bramble cover was highest close to streams (Table 4.2).

In production areas, distance to plantation tree harvesting had a significant negative impact on bramble cover up until 2018, where bramble cover was highest close to areas where trees had been harvested (Table 4.3). Furthermore, distance to woodlands had a consistent significant positive impact on bramble cover, where bramble cover was higher farther away from naturally wooded areas (Table 4.3).

Bramble cover had a significant negative impact on plant species richness as well as intermediate priority grasshopper species richness, where species richness was lower in areas with higher bramble cover (Table 4.4).

Table 4.2: Model-averaged estimates (conditional average) of environmental variables predicting bramble cover within the conservation areas. Significant variables in bold. RI = relative importance, #models = number of containing models. Colon indicates interaction between two variables. Dist = distance to.

Sub model	Variable	beta	se	5%	95%	RI	#models
Bramble 2020	Burning 2020	-0.200	0.049	-0.292	-0.097	1	4
	Dist Stream	-0.108	0.049	-0.199	-0.006	0.83	3
	Burning 2020:Dist Stream	-0.052	0.048	-0.143	0.046	0.24	1
	Dist Harvesting 2020	0.029	0.044	-0.061	0.112	0.17	1
Bramble 2019	Burning 2019	-0.144	0.049	-0.241	-0.046	1	3
	Dist Stream	-0.080	0.048	-0.174	0.014	0.67	2
	Burning 2019:Dist Stream	0.021	0.043	-0.063	0.105	0.19	1
Bramble 2018	Burning 2018	-0.277	0.050	-0.376	-0.178	1	3
	Dist Stream	-0.129	0.049	-0.225	-0.032	1	3
	Dist Harvesting 2018	0.077	0.046	-0.014	0.167	0.67	2
	Dist Woodland	-0.048	0.053	-0.151	0.056	0.23	1
Bramble 2017	Burning 2017	-0.155	0.050	-0.252	-0.057	1	5
	Dist Stream	-0.102	0.051	-0.202	-0.001	0.86	4
	Dist Harvesting 2017	0.085	0.046	-0.006	0.176	0.67	3
	Burning 2017:Dist Stream	0.029	0.053	-0.074	0.133	0.15	1
	Dist Woodland	-0.022	0.057	-0.135	0.091	0.14	1
Bramble 2016	Burning 2016	-0.234	0.050	-0.332	-0.136	1	3
	Dist Stream	-0.128	0.052	-0.231	-0.025	1	3
	Dist Harvesting 2016	0.085	0.046	-0.006	0.177	0.74	2
	Dist Woodland	-0.034	0.055	-0.143	0.075	0.22	1

Table 4.3: Model-averaged estimates (conditional average) of environmental variables predicting bramble cover within the production areas. Significant variables in bold. RI = relative importance, #models = number of containing models. Colon indicates interaction between two variables. Dist = distance to.

Sub model	Variable	beta	se	5%	95%	RI	#models
Bramble 2020	Dist Harvesting 2020	-0.332	0.061	-0.451	-0.212	1	2
	Dist Woodland	0.209	0.071	0.069	0.349	1	2
	Dist Stream	0.053	0.059	-0.063	0.169	0.34	1
Bramble 2019	Dist Harvesting 2019	-0.390	0.049	-0.487	-0.293	1	3
	Dist Woodland	0.210	0.066	0.080	0.341	1	3
	Dist Rivers	0.033	0.056	-0.078	0.144	0.47	2
	Dist Harvesting 2019:Dist Stream	-0.083	0.051	-0.182	0.017	0.26	1
Bramble 2018	Dist Harvesting 2018	-0.302	0.053	-0.406	-0.198	1	2
	Dist Woodland	0.283	0.068	0.148	0.417	1	2
	Dist Stream	0.020	0.059	-0.095	0.136	0.27	1
Bramble 2017	Dist Woodland	0.316	0.074	0.170	0.463	1	3
	Dist Harvesting 2017	-0.107	0.059	-0.223	0.008	0.72	2
	Dist Stream	0.056	0.062	-0.065	0.177	0.25	1
Bramble 2016	Dist Woodland	0.327	0.074	0.181	0.473	1	3
	Dist Stream	0.050	0.062	-0.072	0.172	0.25	1
	Dist Harvesting 2016	0.046	0.063	-0.077	0.170	0.24	1

Table 4.4: Results from mixed-effect models investigating effect of bramble cover on plant and grasshopper species richness. R^2 refers to pseudo R^2 .

Model	Variable	beta	se	R^2	5%	95%
Vegetation Richness	Bramble Cover	-0.072	0.023	0.375	-0.117	-0.027
Overall Grasshopper Richness	Bramble Cover	-0.458	0.57	0.221	-1.574	0.658
Low Priority Grasshoppers	Bramble Cover	0.145	0.395	0.261	-0.63	0.919
Intermediate Priority Grasshoppers	Bramble Cover	-0.59	0.247	0.118	-1.073	-0.106
High Priority Grasshoppers	Bramble Cover	-0.052	0.17	0.061	-0.385	0.281
Caelifera Grasshoppers	Bramble Cover	-0.1	0.492	0.282	-1.064	0.864
Ensifera Grasshoppers	Bramble Cover	-0.16	0.114	0.173	-0.383	0.064

Table 4.5: The percentage bramble overlaps with highly suitable habitat for various grasshopper groupings, under current and projected scenarios. Future projection is based on a 10 m buffer around bramble, simulating 10 years of vegetative spread.

Groups	Current %	Future %	Difference
Overall	5.30	23.81	18.51
Low	6.88	26.57	19.69
Intermediate	4.26	21.22	16.96
High	2.88	23.38	20.50
Caelifera	6.40	25.87	19.48
Ensifera	6.99	29.06	22.07

4.4.3. Stacked species distribution modelling

All models performed well in predicting species richness throughout the landscape and identifying suitable habitat (Appendix S4.3). Richness prediction error was higher for overall and Caelifera grasshoppers, compared to other species groupings containing fewer species (Appendix S4.3 Table S4.3.2).

Distance to stream, elevation, and distance to plantation edge, were highly influential variables in predicting suitable habitat, followed by burning history and vegetation structure (Appendix S4.3 Table S4.3.3).

Bramble overlapped most with Ensifera, low conservation priority, and Caelifera grasshopper suitable habitat, followed by overall, intermediate, and high conservation-priority grasshopper suitable habitat (Table 4.5). Under future bramble vegetative expansion, the Ensifera and high conservation-priority species habitat are most at risk, showing the largest percent increase in bramble overlap (Table 4.5).

All but one estate, show large amounts of vulnerable grasshopper habitat alongside streams and dams as well as at higher elevations, with slight differences between grasshopper groupings (Fig. 4.4).

4.5. Discussion

4.5.1. Mapping bramble in grassland corridors

Here I demonstrate that using deep learning image fusion for mapping alien invasive shrubs is competitive with commercial fine resolution satellite imagery (Peerbhay et al. 2016; Alvarez-Taboada et al. 2017). Super-resolution mosaic was able to effectively discriminate between bramble and other land cover classes (86%), compared to Sentinel-2 (56%) and PlanetScope (65%) imagery, with very high accuracies, highlighting the importance of spatial and spectral resolution in mapping shrubs. Previous research focused on mapping bramble within KwaZulu-Natal, using Sentinel-2 imagery, was only able to achieve up to 77% accuracy for the overall classification (Rajah et al. 2018a). Even conventional image fusion using synthetic aperture radar also fails to improve bramble classification, only obtaining 76% accuracy (Rajah et al. 2018b).

Most research on mapping alien invasive vegetation tend to focus on tree species, as they are more easily identified using remote sensing data (Vaz et al. 2018). Masemola et al. (2020) used Sentinel-2 time series to map *Acacia* species within KwaZulu-Natal with an accuracy of 80%. Furthermore, Rebelo et al. (2021) managed to get over 90% accuracy for discriminating alien vegetation (mostly trees) from other land cover classes within KwaZulu-Natal, using Sentinel-2 imagery. However, as I show here, alien invasive shrubs cannot be accurately mapped at these spatial resolutions (20 m pixels), most likely due to the spectral quality being influenced by the mixing of vegetation captured in larger pixel sizes (Shao and Wu 2008), which limits the use of such imagery for local scale assessments within grassland corridors.

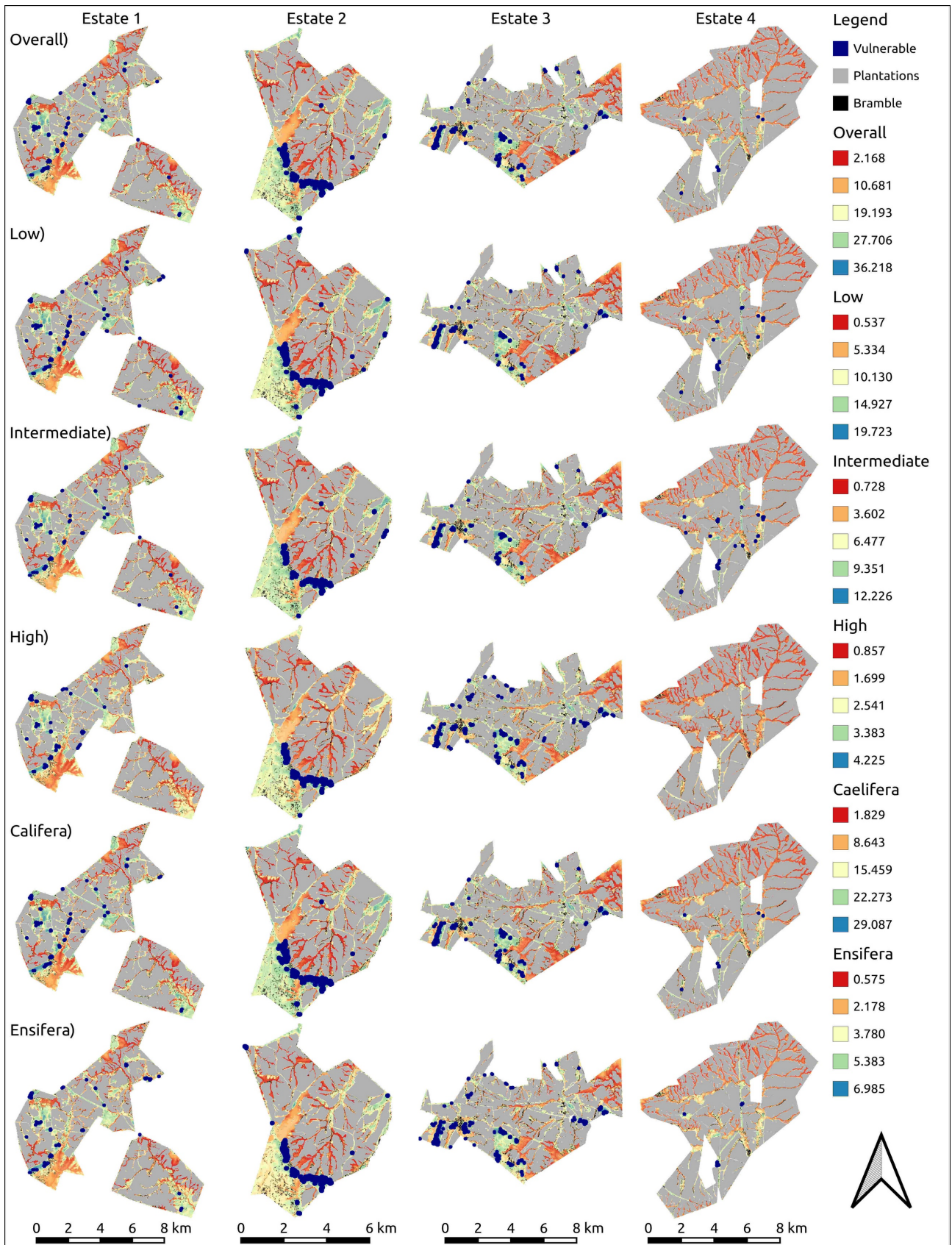


Figure 4.4: Grasshopper suitability maps indicating areas vulnerable to future bramble invasion. The colour gradient (red to light blue) indicates suitability for grasshoppers within grassland corridors, where red is low value habitat and light blue is high value habitat.

Super-resolution image reconstructions have rapidly developed in recent years, improving the ability of convolutional neural networks to learn relationships between low- and high-resolution imagery (Kawulok et al. 2020). Use of this technique shows great potential for earth observations using remote sensing (Kawulok et al. 2020). The further development of this technique will greatly enhance our ability to map alien invasive plant species with great precision and accuracy within grassland corridors, especially when combining this technique with the spectral characteristics of hyperspectral remote sensing data (He et al. 2011). One limitation of this technique is still access to high resolution training data. However, new developments in earth observing satellite constellations (Planet Team 2017), and the push for open access data in biodiversity conservation (Turner et al. 2015), has allowed greater access to high quality data.

4.5.2. Drivers of bramble invasions

Plants only become invasive when they can survive and spread at new locations (Blackburn et al. 2011). Bramble does this remarkably well within the grasslands of South Africa (Henderson 2007), especially at lower elevations on eastern slopes where the air is warm and moist (Ndlovu et al. 2018). However, very little research has focused on the mechanisms and drivers of bramble invasion (Erasmus 1984; Denny 2005). Recently, Molefe et al. (2020) demonstrated the role that frugivorous birds play in bramble seed germination and potential long-distance dispersal. However, I found little evidence to support long distance dispersal, as bramble occurred in higher abundance closer to plantations forests. Fuentes-Lillo et al. (2021) found that anthropogenic disturbances are more important than local biotic and abiotic variables. My results support this by showing the strong relationship between disturbance (harvesting and prescribed burning) and bramble cover.

Prescribed burning has been used successfully to control alien invasive plant species, but in the absence of follow-up treatments, most alien invasive plants (especially larger shrubs) recover after two or three years (Ditomaso et al. 2006). My results support this by demonstrating that continuous prescribed burning significantly increased bramble cover. This could be due to the grassland fires not being hot enough to kill bramble, but rather temporally reducing bramble density (Ditomaso et al. 2006).

On the other hand, harvesting of plantation trees is another large-scale disturbance that greatly alters the landscape. Removal of trees creates new opportunities for plants to establish, which temporarily

improves functional connectivity (Theron et al. 2021b), and supports arthropod diversity (van Schalkwyk et al. 2021). However, this effect is only beneficial when trees are harvested in smaller areas through rotational harvesting (van Schalkwyk et al. 2021). My results show that harvesting an entire plantation as one event leads to increasing bramble cover. This effect is then compounded when trees are harvested across the landscape, which increases the risk of bramble invasion into grassland corridors (Fristoe et al. 2021).

4.5.3. Impact of bramble

Bramble has severe negative impacts on local plant species richness, vegetation structure, endemic birds, and a variety of arthropods (Reynolds and Symes 2013; Kietzka et al. 2015; Hansen et al. 2018; Eckert et al. 2019; Theron et al. 2021a). My results support this by demonstrating the direct impact of bramble on plant species richness. However, I found little support for direct impacts on grasshoppers, as only intermediate priority grasshoppers responded to bramble cover. However, impacts on plant species richness have indirect impacts on grasshoppers by threatening suitable habitat, especially for Ensifera and high conservation-priority species. Furthermore, as bramble cover was greater close to streams, the indirect impact on Ensifera species is expected to be most severe when bramble invasion is not controlled. These indirect effects are also apparent when considering insect flower visitation networks (Hansen et al. 2018) as well as grassland birds searching for nesting sites (Reynolds and Symes 2013).

4.5.4. Control of bramble

Control of bramble within the South African commercial plantations is achieved primarily through using a glyphosate-based product, which comes with a considerable cost (Roberts et al. 2021). Future work investigating alternative control methods is required. The control of invasive plants through prescribed burning could be a potential alternative to using herbicide, especially within grassland corridors, as fire benefits local plant diversity while reducing alien invasive plant cover (Morris et al. 2021; Gordijn and O'Connor 2021). However, follow-up treatments are needed to prevent alien invasive plants from re-establishing in the following years. van Uytvanck and Hoffmann (2009) examined the impact of domestic cattle grazing on bramble cover in Flanders, Belgium, and found that grazing at moderate intensities is successful at reducing bramble cover without negatively impacting local plant diversity. Furthermore,

Masson et al. (2015) also found that herbivory can be used to control bramble invasion in the Mediterranean dry grasslands of La Crau, France. However, more research is needed to investigate the combined effect of prescribed burning and grazing by domestic cattle within grassland corridors as a means of controlling bramble.

4.6. Conclusions

Here I show the benefits of using super-resolution satellite mosaics in mapping an alien invasive shrub, motivating the use of this technique for monitoring alien invasive plants. Through using super-resolution mosaics, I gained new insights into the drivers of bramble invasion, which will help improve our understanding of bramble invasion dynamics. I recommend future work investigate the combined effect of prescribed burning and grazing for controlling bramble. Current control programmes should focus on removing bramble from riparian habitat, alongside using high priority grasshopper habitat to identify vulnerable terrestrial sites. Furthermore, special attention is needed to control bramble two years after a plantation block has been harvested, as this is when bramble cover is highest. Lastly, the implementation of rotational harvesting (as opposed to whole plantation harvesting) can greatly reduce bramble cover within the landscape, and its adoption is highly encouraged.

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Chapter 5: General discussion

Insects are threatened by human action globally (Goulson 2019; Cardoso et al. 2020; Wagner et al. 2021). In this time of rapid anthropogenic change and disruption (Dirzo et al. 2014), satellite remote sensing, in conjunction with integrative modelling, has proven to be a major asset. Satellite data in advanced models improves our understanding of the changing planet, and provides important information to guide conservation management (Pettorelli et al. 2016; Rocchini et al. 2016; Gorelick et al. 2017; Randin et al. 2020). Unfortunately, implementation of satellite remote sensing into biodiversity conservation has been hampered through limited technical knowledge of working with, and extracting information from, satellite data (Turner et al. 2015). However, increased accessibility to open access remote sensing data, provides greater opportunities to address conservation issues (Rose et al. 2015; Zhu et al. 2019). This formed the basis of my dissertation, with the overarching aim of using satellite remote sensing and integrative modelling to perform biodiversity assessments within a dynamic production landscape. I also aimed to provide valuable information to help maintain ecological integrity of natural vegetation between actively managed areas to support biodiversity.

Production landscapes are valuable for biodiversity conservation, as much biodiversity occurs outside formally protected areas (Gray et al. 2016; Dinerstein et al. 2017; Dudley et al. 2018). Within South Africa, remnant natural vegetation within the deciduous fruit growing regions of the Western and Eastern Cape, supports high arthropod and plant diversity (Theron et al. 2020; van Schalkwyk et al. 2020; Galloway et al. 2021), whereas large scale grassland corridors between commercial forestry plantations of KwaZulu-Natal, conserves much biodiversity (Samways and Pryke 2016; Gaigher et al. 2019; van Schalkwyk et al. 2021). Due to the dynamic nature of production landscapes, methods such as satellite remote sensing and integrative modelling are critical for assessing the status of biodiversity, allowing conservation management to adapt under changing conditions. Commercial forestry operations frequently rely on remote sensing data to help with pest outbreak and monitoring tree health to optimise harvesting operations (Xulu et al. 2019; McEwan et al. 2020). However, remote sensing for insect biodiversity conservation is still in its infancy (Rhodes et al. 2021). This dissertation aims to shed light on the value of satellite remote sensing and integrative modelling for better understanding biodiversity response to grassland corridors between commercial forestry plantations, and to guide management for insect biodiversity conservation.

5.1. Synthesis of findings

Overall, I demonstrate how satellite data and integrative modelling can be used to gain deeper insights into biodiversity dynamics within production landscapes (chapter 2, 3 and 4). A major emergent finding from different chapters was the importance of fire within the grassland corridors (chapter 2, 3 and 4). Fire through prescribed burning, is an important natural disturbance and critical for maintaining high-quality grasshopper habitat within grassland corridors (chapter 2 and 3). Grassland plant diversity has evolved in response to fire leading to a wide range of plant adaptations to thrive in fire prone ecosystems, such as resprouting from underground bulbs or the importance of smoke in stimulating seed germination (Mucina and Rutherford 2011). Grassland biodiversity is therefore reliant on fire for completing life cycles and maintaining grassland ecosystem functioning (Yang et al. 2020). Previous work within grassland corridors has demonstrated that prescribed burning is critical for maintaining high plant diversity (Joubert et al. 2014), which promotes grasshopper and butterfly diversity (Joubert et al. 2016; Gaigher et al. 2019). Furthermore, these results are also supported by research from USA, where prescribed burning maintains the host plants for rare grassland butterflies (Adamidis et al. 2019). However, the frequency of fire should be considered carefully.

Prescribed burning seems to have a lasting impact that can continue to affect grasshoppers for up to three years (chapter 2). This corresponds to re-setting of grassland succession as well as grasshopper preference towards more simplistic grassland structure. Frequent burning prevents grasslands from transitioning into thickets (characterised by dominate woody vegetation) (Cadman et al. 2013), which benefits habitat specialist (Fartmann et al. 2012). Fire therefore modulates grassland structure, while also having a significant impact on grasshopper diversity (Bazelet and Samways 2011; Joubert-van der Merwe and Pryke 2018). However, creating optimal prescribed burning regimes that protect timber compartments while maintaining and promoting biodiversity conservation is challenging (Kelly et al. 2015). My results show that the Normalized Difference Vegetation Index (NDVI), derived from satellite imagery, can stand as a proxy for vegetation structure, and can be used to monitor grasshopper habitat and help inform foresters and land managers when and where to burn for maintaining high-quality grasshopper habitat (chapter 2 and 3).

This relationship has also been demonstrated by Klein et al. (2020), further illustrating the effectiveness of NDVI as a widely-applicable monitoring tool for grassland grasshoppers.

The impact of fire on vegetation structure also has implications for functional connectivity within grassland corridors (chapter 3). Fire creates spatio-temporal heterogeneity in vegetation structure, which impacts species in a variety of ways (Koltz et al. 2018; Sitters and Stefano 2020). Most notably, changes in vegetation structure provide varying degrees of resistance to movement, impacting species dispersal and their access to resources (Sitters and Stefano 2020). This change, in turn, affects local population persistence by altering colonisation and extinction dynamics (Jackson and Sax 2010). Furthermore, heterogeneity caused by frequent disturbances such as fire and/or climate warming, can change assemblage composition towards habitat and dietary generalists, and favour species with high dispersal abilities (Koltz et al. 2018). However, my results show that grassland corridors are critical for maintaining functional landscape connectivity, and that heterogeneity throughout these corridors increases grasshopper species turnover, contributing to high landscape diversity and illustrates greater conservation value of grassland corridors (chapter 3), supported by previous work (Pryke and Samways 2015). Additionally, modelling functional connectivity within grassland corridors provides important information on how prescribed burning impacts access to resources (chapter 3), which can help in the management of corridors for biodiversity conservation, so that these corridors extend the effective reaches of neighbouring protected areas (Pryke and Samways 2012a).

Another prominent finding from different chapters is the impact of harvesting timber compartments on biodiversity (chapter 3 and 4). Harvesting of trees and planting of plantation tree saplings, creates opportunities for alien weed species to establish, which temporarily improves functional connectivity (chapter 3). Thus, through selectively harvesting specific timber compartments, changes to functional connectivity can be made to support biodiversity and improve dispersal (Pliscoff et al. 2020). This is also supported by previous research within grassland corridors demonstrating that rotational harvesting can increase vegetation structural diversity, promoting arthropod spillover within the landscape (van Schalkwyk et al. 2021). These findings have implications on how the timber compartments are managed after mature trees have been harvested, which is especially important as timber compartments provide little resources for biodiversity (Pryke and Samways 2012b; Eckert et al. 2019). However, alien vegetation establishing after harvesting poses serious threats to grassland biodiversity (Stanton et al. 2018, Wang et al. 2019) by reducing

functional connectivity within and between grasslands (Deák et al. 2020). There is thus an urgent need to revisit harvesting tools and methodology to help conserve biodiversity and reduce alien species establishment (Betts et al. 2021).

Even though harvesting timber compartments temporarily improves functional connectivity, alien vegetation establishing after removal of trees should be contained within the timber compartments and be prevented from spilling over into grassland corridors. Unfortunately, harvesting has a significant positive effect on American bramble (*Rubus cuneifolius*) cover within the landscape, where bramble cover is highest two years after harvesting (chapter 4). This result is supported by a recent study, which showed that anthropogenic disturbances are more important than local biotic and abiotic variables in predicting plant invasions (Fuentes-Lillo et al. 2021). Harvesting of timber compartments throughout the landscape can therefore have a compound effect on the invasion potential of bramble (Fristoe et al. 2021). In response, adoption of rotational harvesting is highly encouraged to prevent bramble invasion throughout the landscape.

Prescribed burning is frequently used to control the spread of alien invasive plant species while maintaining stable native plant populations (Gordijn and Ward 2014; Gordijn and O'Connor 2021; Morris et al. 2021). However, in the absence of follow-up treatments, most alien invasive plants (especially larger shrubs) recover after two or three years (Ditomaso et al. 2006). My results support this by demonstrating that continuous prescribed burning significantly increases bramble cover (chapter 4). This could be due to the grassland fires not being hot enough to kill bramble, but rather temporally reducing bramble density (Ditomaso et al. 2006). Therefore, for fire to be used effectively in controlling bramble cover, it needs to be combined with additional follow-up treatments. Research has demonstrated the potential of grazing by domestic cattle in controlling bramble cover (van Uytvanck and Hoffmann 2009; Masson et al. 2015). However, more research is needed to investigate the combined effect of prescribed burning and grazing by domestic cattle within grassland corridors as a means of controlling bramble.

Another common finding throughout the dissertation was the negative impact of bramble on biodiversity (chapter 2 and 4). Bramble is an aggressive invader within grasslands of South Africa (Henderson 2007) and has severe negative impacts on local plant species richness, vegetation structure, endemic birds, and a variety of arthropods (Reynolds and Symes 2013; Kietzka et al. 2015; Hansen et al. 2018; Eckert et al. 2019). My results contribute to this by demonstrating that bramble has severe negative

impact on plant species richness, larger-sized grasshopper species (especially Pyrgomorphinae), as well as grasshopper species of conservation concern (mainly Thericleinae) (chapter 2 and 4). Furthermore, my results show that bramble has a large impact on high-quality habitat for high conservation-priority grasshopper species as well as Ensifera grasshoppers (chapter 4). Ensifera grasshoppers are particularly vulnerable, especially if the spread of bramble is not controlled, as bramble occurs in greater cover close to streams (chapter 4), which corresponds with previous work (Ndlovu et al. 2018).

All the results presented in this dissertation provides compelling evidence to motivate the adoption of satellite remote sensing to study patterns in biodiversity within production landscapes. Establishing casual links between local biodiversity and satellite remote sensing will allow us to scale up our local monitoring efforts to better understand global biodiversity response.

5.2. Future research

New methods are urgently needed to rapidly collect data on insect diversity as well as environmental data at a scale relevant to insects. This is crucial for linking local biodiversity with remote sensing data, and then extrapolating this relationship globally. Data on microclimate is particularly important for creating accurate predictive models (Lembrechts et al. 2019), because insects experience climate in their immediate surroundings, which can vary considerably due to changes in vegetation structure and solar radiation (Milling et al. 2018). However, our ability to develop strong and highly accurate predictive models that explain the relationships between remote sensing data (e.g., microclimate) and local biodiversity, is ultimately dependant on the quantify and resolution of available data. Obtaining such data can be challenging, but the rapid development of unmanned aerial vehicles (UAV) over the last several years, has allowed us to monitor biodiversity at fine spatial and temporal resolutions unattainable by satellites (Horning 2018). Structural data can also be obtained by UAV, which is comparable to Light Detection and Ranging (LiDAR) technology (Forsmoos et al. 2018) and can be used to model microclimate. Combining spectral and structural data at very high resolutions (cm) provides opportunities to better study relationship between the local environment and biodiversity response. Unfortunately, local legislation around operating UAV is a significant challenge in many regions, including South Africa, which substantially hampers the adoption of UAV as a remote sensing platform (Dash et al. 2019).

New exciting motion triggered insect camera traps (<https://www.spaia.earth/>) can provide alternative ground truthing platform for collecting data needed to create accurate global predictive models. Leveraging the capabilities of deep learning algorithms and computer vision holds enormous potential to create automated systems for monitoring biodiversity (Christin et al. 2019), especially for insects (Høye et al. 2021). This is important as fieldwork to collect insect samples needed to provide ground truthing for remote sensing data, is extremely time consuming and expensive. Computer vision and deep learning has already been used to create an automated light trap to monitor moths (Bjerger et al. 2021), as well as identify mosquitoes responsible for spreading disease (Pataki et al. 2021).

However, insect camera traps still require substantial taxonomic expertise for identifying insects to create labelled training data. One method to overcome this limitation is through the use of environmental DNA (eDNA) and metabarcoding, which can rapidly and noninvasively collecting large amounts of data on species and community assembly (Thomsen and Willerslev 2015; Seymour 2019; Deiner et al. 2021). Recently, eDNA has been used to study arthropod response to different management regimes in German vineyards (Rasmussen et al. 2021), as well as to monitor flower visiting arthropods in grasslands (Thomsen and Sigsgaard 2019).

Deploying technology that captures data on insect diversity (eDNA) and activity (camera trapping), along with data on the local environment (microclimate), will rapidly enhance our monitoring efforts and their further development is crucial.

5.3. Concluding remarks

Satellite remote sensing and integrative modelling provides greater insight into how biodiversity responds within production landscape, which helps steer management towards considering biodiversity conservation. Here my results illustrate that prescribed burning can have lasting impact on biodiversity, and therefore careful consideration is needed when deciding where, when and how often to burn. To help guide this decision, land managers and foresters can use NDVI to monitor grassland corridor condition, which will also provide insight into how functional connectivity will vary between years. Rotational harvesting is highly recommended, as it will have major benefits on functional connectivity, as well help prevent bramble invasions within the landscape. Special attention is needed to control bramble two years after harvesting, as

this is when bramble cover is highest. This should be done to prevent bramble spillover into grassland corridors, which will impact biodiversity. Current bramble removal programmes should prioritize riparian areas and use high priority grasshopper habitat to identify vulnerable terrestrial habitat.

5.4. Data availability statement

Code and supporting data for chapter 2 are available on Zenodo (<https://doi.org/10.5281/zenodo.5118404>). Land cover classification training data along with grasshopper data and accompanying code for chapter 3 are stored on Github (https://github.com/kjtheron/Functional_Connectivity). Grasshopper and vegetation data with accompanying code for chapter 4 can be found on Github (https://github.com/kjtheron/Invasion_Dynamics). PlanetScope imagery can be ordered from Planet Labs (<https://www.planet.com>). Sentinel 2 image can be downloaded from Copernicus Open Access Hub (<https://scihub.copernicus.eu/dhus>). The 5 m resolution DEM can be ordered from GeoSmart space (<https://geosmart.space/>).

5.5. References

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Appendices

Appendix S2

Table S2.1 Dates for imagery used in *Spectral models*.

Sensor	Area	Date	Image ID
PlanetScope	Estate 1	2019/05/02	20190502_075144_64_105f_3B
		2020/01/24	20200124_080656_10_1057_3B
		2020/03/23	20200323_091450_19_106a_3B
		2020/03/23	20200323_091452_29_106a_3B
	Estate 2	2019/05/02	20190502_075142_57_105f_3B
		2020/01/29	20200129_091654_99_1065_3B
		2020/03/19	20200319_091226_84_106a_3B
	Estate 3	2019/05/03	20190503_093059_13_106a_3B
		2020/01/17	20200117_080646_31_1064_3B
		2020/03/18	20200318_091212_19_106e_3B
	Estate 4	2019/05/10	20190510_075040_15_105a_3B
		2019/05/10	20190510_075042_22_105a_3B
2020/02/15		20200215_080802_12_1057_3B	
2020/03/20		20200320_075746_13_105c_3B	
Sentinel	Estate 1-4	2019/05/24	20190524T073619_20190524T080638_T36JTN
		2020/01/04	20200104T074311_20200104T080039_T36JTN
		2020/03/04	20200304T073801_20200304T080109_T36JTN
Landsat	Estate 1-4	2019/05/24	LC08_168080_20190524
		2020/01/03	LC08_168080_20200103
		2020/03/07	LC08_168080_20200307

Table S2.2 List of grasshopper species sampled during the chapter 2 and 3. GCI = Grasshopper Conservation Index calculated by using scores for species rarity, mobility and endemism.

Family	Subfamily	Species	Abundance	GCI
Acrididae	Acridinae	<i>Acrida acuminata</i> (Stål, 1873)	105	3
		<i>Acrida bicolor</i> (Thunberg, 1815)	17	3
		<i>Acrida propinqua</i> (Burr, 1902)	2	6
		<i>Duronia chloronota chloronota</i> (Stål, 1876)	155	3
		<i>Gymnbothrus carinatus</i> (Uvarov, 1941)	47	4
		<i>Machaeridia conspersa</i> (I. Bolívar, 1889)	54	3
		<i>Duronia chloronota curta</i> (Uvarov, 1953)	140	5
		<i>Rhabdoplea munda</i> (Karsch, 1893)	26	5
	Catantopinae	<i>Anthermus granosus</i> (Stål, 1878)	30	3
		<i>Vitticatantops humeralis</i> (Thunberg, 1815)	195	3
	Coptacrinae	<i>Eucoptacra turneri</i> (Miller, 1932)	11	5
	Cyrtacanthacridinae	<i>Cyrtacanthacris aeruginosa aeruginosa</i> (Stoll, 1813)	3	5
		<i>Ornithacris cyanea cyanea</i> (Stoll, 1813)	3	5
	Eyprepocnemidinae	<i>Eyprepocnemis calceata</i> (Serville, 1838)	29	5
		<i>Heteracris drakensbergensis</i> (Grunshaw, 1991)	6	7
		<i>Rhachitopis melanopus</i> (Burmeister, 1838)	72	4
	Gomphocerinae	<i>Anablepia pilosa</i> (Uvarov, 1953)	87	5
<i>Crucinotacris cruciata</i> (Bolívar, 1912)		60	3	
<i>Diablepia viridis</i> (Kirby, 1902)		3	7	

		<i>Faureia milanjica</i> (Karsch, 1896)	4	5
		<i>Mesopsis abbreviata</i> (Palisot de Beauvois, 1806)	65	4
		<i>Pnorisa angulata</i> (Karny, 1910)	163	3
		<i>Pnorisa squalus</i> (Stål, 1861)	122	3
		<i>Pseudoarcpytera cephalica</i> (Bolívar, 1914)	8	7
		<i>Rhaphotittha levis</i> (Karsch, 1896)	21	4
Hemiacridinae		<i>Acanthoxia gladiator</i> (Westwood, 1842)	1	5
Oedipodinae		<i>Aiolopus meruensis</i> (Sjöstedt, 1909)	37	4
		<i>Gastrimargus africanus africanus</i> (Saussure, 1888)	30	3
		<i>Gastrimargus determinatus determinatus</i> (Walker, 1871)	3	6
		<i>Gastrimargus drakensbergensis</i> (Ritchie, 1982)	20	5
		<i>Morphacris fasciata</i> (Thunberg, 1815)	10	4
		<i>Paracinema tricolor tricolor</i> (Thunberg, 1815)	22	4
		<i>Scintharista magnifica</i> (Uvarov, 1922)	9	6
		<i>Scintharista rosacea</i> (Kirby, 1902)	5	7
		<i>Scintharista saucia</i> (Stål, 1873)	1	6
Oxyinae		<i>Oxya glabra</i> (Ramme, 1929)	81	6
		<i>Oxya hyla</i> (Serville, 1831)	400	3
		<i>Dirshia abbreviata</i> (Brown, 1962)	14	7
Spathosterninae		<i>Spathosternum nigrotaeniatum</i> (Stål, 1876)	58	3
Tropidopolinae		<i>Petamella prosternalis</i> (Karny, 1907)	1	5
Lentulidae	Lentulinae	<i>Betiscoides parva</i> (Key, 1937)	2	7
		<i>Lentula obtusifrons</i> (Stål, 1878)	156	6

Pamphagidae	Porthetinae	<i>Pagopedilum sordidum</i> (Walker, 1870)	1	6
		<i>Pagopedilum subcruciatum</i> (Karsch, 1896)	1	8
Pyrgomorphidae	Pyrgomorphae	<i>Chrotogonus hemipterus</i> (Schaum, 1853)	1	6
		<i>Dictyophorus spumans pulchra</i> (Bolívar, 1904)	1	5
		<i>Phymateus leprosus leprosus</i> (Fabricius, 1793)	1	7
		<i>Phymateus viridipes viridipes</i> (Stål, 1873)	3	5
		<i>Stenoscepa picticeps</i> (Bolívar, 1904)	27	8
		<i>Zonocerus elegans elegans</i> (Thunberg, 1815)	4	5
Tetrigidae	Batrachideinae	<i>Phloeonotus humilis</i> (Gerstaecker, 1869)	78	4
	Cladonotinae	<i>Trachytettix scaberrimus scaberrimus</i> (Stål, 1876)	1	6
	Tetriginae	<i>Dasyleurotettix infaustus</i> (Walker, 1871)	4	6
		<i>Paratettix scaber</i> (Thunberg, 1815)	26	3
		<i>Paratettix subpustulata</i> (Walker, 1871)	12	5
		<i>Tettiella odiosa</i> (Walker, 1871)	57	5
Thericleidae	Thericleinae	<i>Lophothericles marginatus</i> (Descamps, 1977)	1	8
		<i>Thericles miserabilis</i> (Descamps, 1977)	7	6

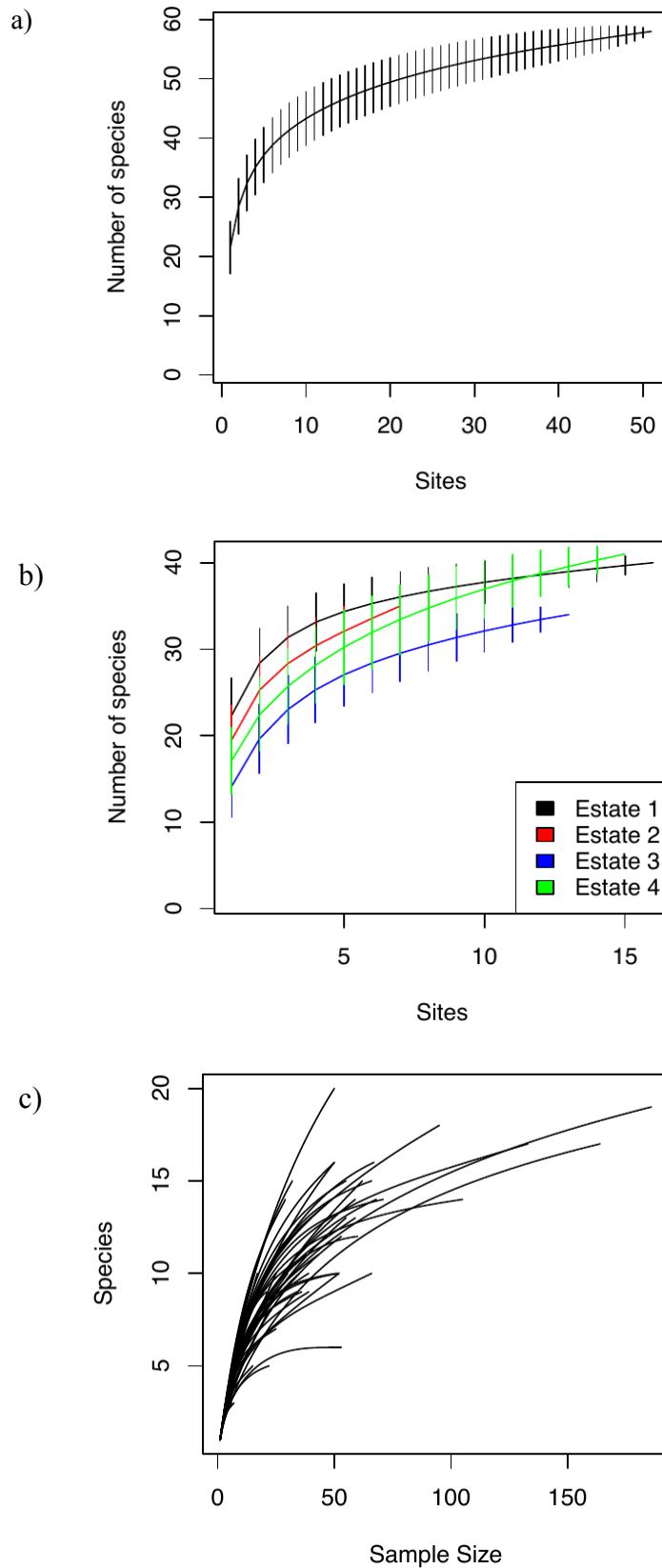


Figure S2.1 Species accumulation curves for a) all sites together, b) grouped per timber estate, and c) for every sampling site separate.

Appendix S3.1

Sampling sites across the timber plantation estates were selected based on a scoring and prioritisation methodology. First, multiple raster variables were selected and used to perform a land cover classification using 5m resolution Rapid Eye satellite imagery. This classification was done in 2019, one year prior to sampling grasshoppers. Using this classification, I scored land cover types based on grasshopper preference (guided by relevant references (e.g. Pryke and Samways 2012)), and summed the scores of the land covers within a larger grid to identify “grasshopper hotspots”. Sampling sites were then selected to cover the extent of the estates (separated by 1 km, except in estate 4 with a minimum distance between sites of 400 m), but to also have high and low habitat value scores to capture a variety of site conditions (almost half low value sites and half high value sites). Figure S3.1.1 provides an illustration of this scoring and prioritisation work-flow.

Furthermore, in preparation to perform stacked species distribution modelling (S-SDM), functional landscape connectivity (FLC) analysis, as well as species turnover calculation, various raster variables were created. Multiple raster data products were sources, and served as the base for deriving further data products (e.g. DEM used to calculate cold air drainage). All raster variables were projected to EPSG:32736, rescaled to 10 m resolution, and clipped to the study extent. Roughly 500 m surrounding the plantation estates were added to the study extent (manually digitised), as high quality grassland habitat surrounds some of these estates, allowing for a better representation of functional connectivity throughout the plantation estates. Processing occurred within QGIS (QGIS Development Team 2019) as well as R (R Core Team 2020). See Table S3.1.1 for specific details pertaining to raster variables.

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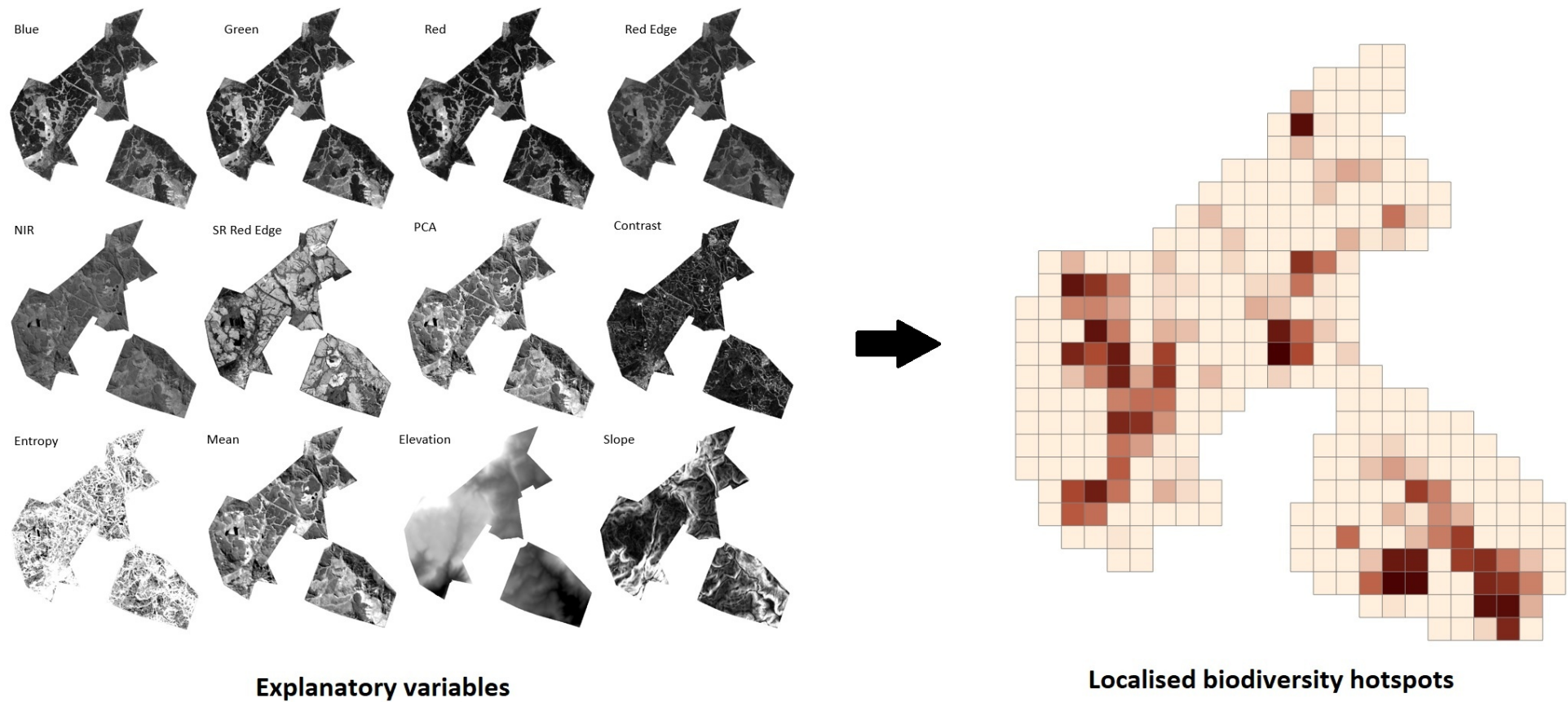


Figure S3.1.1 Variables used for land cover classification. Classified land classes were scored and summed per grid to derive grasshopper hotspots. In the localised biodiversity hotspot figure on the right, dark red indicates high value habitat, whereas lighter colours indicate habitat of lower value. A variety of spectral variables were used (Blue – Red edge), some processed spectral data such as PCA and textural variables (Contrast – Mean), as well as some topographic variables (elevation and slope).

Table S3.1.1 Table illustrating different raster variables used during formal analyses, their source, how they were processed, for what they were used, and the justification of their use. DEM = Digital Elevation Model, Drainage = refers to the water/air drainage channels on a topographic surface such as a DEM, SA_NLC = South African National Land Cover data product, Max_NBR = the maximum pixel value of the Normalised Burn Ration index over 3 years, NDVI = Normalised Difference Vegetation Index, Dist_Drain = distance to water/air drainage channels, Dist_Edge = distance to nearest grassland edge, NIR = near infrared light, SWIR = short-wave infrared light, S-SDM = stacked species distribution modelling, FLC = functional landscape connectivity.

Variable	Source	Processing	Used for	Justification
Sentinel-2	Copernicus Open Access Hub (https://scihub.copernicus.eu/dhus). Image ID 20200129T074049.	Bands were clipped to study extent. Only the Red, Green, Blue and NIR bands were used.	Calculating NDVI.	Sentinel-2 bands with its moderate resolution (10 m) is well suited for land cover classification, S-SDM and FLC. Please see Online Resource 5.
DEM	Stellenbosch University Digital Elevation Model obtained through GeoSmart Space (https://geosmart.space/) (GeoSmart Space 2019).	Projected (EPSG:32736), re-sampled to 10 m, and clipped to study extent.	Calculating aspect, slope, and drainage. Also used in species turnover calculations.	This DEM had a resolution of 5 m and contained more accurate information about the topography compared to NASA's SRTM data product.
Drainage	DEM	Produced using the Fill and Stream QGIS functions on the processed DEM.	Calculating distance to water/air drainage channels.	The GRASS extension to QGIS contains valuable hydrological functions. The stream network (water/air drainage channels) was calculated to include smaller

				channels to simulate cold air drainage along complex topography.
SA_NLC	The Department of Environmental Affairs, Republic of South Africa (https://egis.environment.gov.za/).	Projected (EPSG:32736), re-sampled to 10 m, and clipped to study extent.	Refining land cover type within study extent, by classifying Sentinel-2 data.	This land cover data product produced in 2018 was used to improve the accuracy of the new land cover classification for the current time of the study.
Max_NBR	Landsat imagery on Google Earth Engine (Gorelick et al. 2017).	NBR was calculated within Google Earth Engine using the NIR and SWIR bands from Landsat, selecting the maximum pixel value over 3 years for the study extent. NBR was projected (EPSG:32736), re-sampled to 10 m, and clipped to study extent.	S-SDM, FLC, species turnover calculations.	Google Earth Engine allows users to perform arithmetic per pixel through time and over large spatial scales. NBR is a index used to study fire severity and intensity (Keeley 2009), and ranges from -1 (high burn severity, no vegetation cover) to +1 (no burn, high vegetation cover). Thus, selecting the maximum NBR over 3 years allows me to map the burn history of grassland corridors, were lower NBR values indicate areas of constant burning, whereas higher areas indicate longer burn intervals.
NDVI	Sentinel-2	Calculated in R using the red and NIR bands from the	S-SDM, FLC, species turnover calculations.	NDVI is a popular remote sensing index that stands as a proxy for vegetation greenness. Previous research

		processed Sentinel-2 image captured on the 29 th of January 2020.		showed that grasshoppers within grassland corridors respond to NDVI, and that this relationship is relating to the vegetation structure (Theron et al. 2021).
Slope	DEM	Calculated in R using the processed DEM.	Land cover classification.	Topographic variables, such as slope, aids with land cover classification, as it improves the algorithms ability to accurately discriminate between land cover classes, over just using spectral data (Khalyani et al. 2012).
Aspect	DEM	Calculated in R using the processed DEM.	S-SDM, FLC, species turnover calculations.	Topographic aspect has a significant influence on plant diversity due to varying solar radiation (Moeslund et al. 2013). This in turn effects the microclimatic conditions across the landscape, which has a significant impact on grasshopper diversity (Samways 1990).
Dist_Drain	Drainage	Calculated in R using the Distance function within the Raster package (Hijmans 2020).	S-SDM, FLC, species turnover calculations.	Grasshopper within grassland corridors are impacted by cold air funnelling down topographic depressions, and therefore avoid these cold air drainage channels as it can increase grasshopper mortality (Samways 1990).
Land_Use	Sentinel-2, SA_NLC, DEM	Random Forest classification.	S-SDM, FLC, species turnover	Grasshoppers were only sampled in grasslands. Also,

Dist_Edge Land_Use	<p>Please see Online Resource 3.</p> <p>Selected the grassland class from Land_Use and then calculated the distance to nearest non-grassland pixel using the Distance function in the R Raster package (Hijmans 2020).</p>	<p>calculations.</p> <p>S-SDM, FLC, species turnover calculations.</p>	<p>only grassland species were used. Thus, land cover was therefore included to help improve model performance.</p> <p>The study region consists out of grassland corridors as well as grassland fragments/remnants, which are all of varying shapes and sizes (see study map in main text). Distance to edge was therefore an important variable to stand in as a proxy for grassland corridor/remnant size. Furthermore, arthropods within grassland corridors respond strongly to distance to edge (van Schalkwyk et al. 2020).</p>
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Table S3.1.2. Percentage breakdown of grasslands vs timber compartments within each estate.

Name	Estate ha	Grassland ha	Plantation ha	% Grassland
Estate 1	6003.567	2694.744	3308.823	44.886
Estate 2	3646.103	1694.497	1951.606	46.474
Estate 3	5514.944	2357.941	3157.003	42.755
Estate 4	6213.786	1662.678	4551.108	26.758

Appendix S3.2

Table S3.2.1 Table illustrating different parameters with classes, used to calculate the grasshopper conservation index to classify grasshoppers as low, intermediate, and high conservation value.

Parameter	Score	Description
Endemism	1	Occurring in and outside South Africa
	2	Endemic to South Africa
	3	Local endemic
Dispersal	1	Fully capable of flight
	2	Flight-less
Rarity	1	Common (at > 10 sites)
	2	Intermediate (at ≤ 10 sites)
	3	Rare (at ≤ 5 sites)

Table S3.2.2 Table illustrating number of individuals and species per site within the different plantation estates.

Estate	Site	Individuals	Species
Estate1	Site_10	32	15
Estate1	Site_11	59	13
Estate1	Site_19	50	20
Estate1	Site_20	43	11
Estate1	Site_21	164	17
Estate1	Site_22	66	15
Estate1	Site_23	50	16
Estate1	Site_24	39	9
Estate1	Site_25	95	18
Estate1	Site_26	60	12
Estate1	Site_27	52	10
Estate1	Site_28	186	19
Estate1	Site_29	133	17
Estate1	Site_30	59	14
Estate1	Site_31	34	9
Estate1	Site_32	36	9
Estate2	Site_08	17	10
Estate2	Site_09	50	16
Estate2	Site_33	71	14
Estate2	Site_34	68	14
Estate2	Site_35	67	16
Estate2	Site_36	55	13
Estate2	Site_37	66	10
Estate3	Site_38	6	3
Estate3	Site_39	13	9

Estate3	Site_40	22	5
Estate3	Site_41	24	13
Estate3	Site_42	53	12
Estate3	Site_43	7	3
Estate3	Site_44	15	5
Estate3	Site_45	53	6
Estate3	Site_46	23	8
Estate3	Site_47	40	13
Estate3	Site_48	10	7
Estate3	Site_49	55	15
Estate3	Site_50	25	7
Estate4	Site_00	105	14
Estate4	Site_01	21	9
Estate4	Site_02	51	10
Estate4	Site_03	31	12
Estate4	Site_04	25	10
Estate4	Site_05	49	14
Estate4	Site_06	38	11
Estate4	Site_07	35	10
Estate4	Site_12	22	8
Estate4	Site_13	62	15
Estate4	Site_14	39	10
Estate4	Site_15	29	14
Estate4	Site_16	30	10
Estate4	Site_17	16	6
Estate4	Site_18	52	10

Appendix S3.3

To classify land cover types within the study region, I compared the accuracy of three different algorithms. Specifically, I compared between Random Forest, k-Nearest Neighbours and Classification and Regression Tree. These algorithms are used regularly for classification problems and were implemented using the caret package (Kuhn 2020). Variables selected for classification included the red, green, blue (RGB) and infrared (IR) bands from a Sentinel 2 image, the Principal Component Analysis from these bands, Normalised Difference Vegetation Index (NDVI), slope derived from a DEM, as well as a 2018 land cover data product of South Africa (Thompson 2019).

Models were trained to classify the most prominent land cover classes within the study region, specifically, agricultural land, grassland, bare ground, plantation forest, shrubland, water and woodland. Reference data was collected using a 25cm RGB orthophoto as well as 3m RGB and IR PlanetScope imagery (Planet Team 2017). A total of 1 640 data points were created, and data was split using 70% for training and 30% for testing. To obtain best performing model parameters for all algorithms during training, I used a random selection of 10 different parameter combinations. The best combination of parameters was selected based on the resulting Kappa statistic generated using a bootstrapping procedure. The best performing model, determined from a confusion matrix using testing data, was used to predict land cover classes for entire study region. This land cover data product was smoothed using a modal 3 by 3 moving window to reclassify any small incorrectly classified pixel regions, before being used during stacked species distribution modelling.

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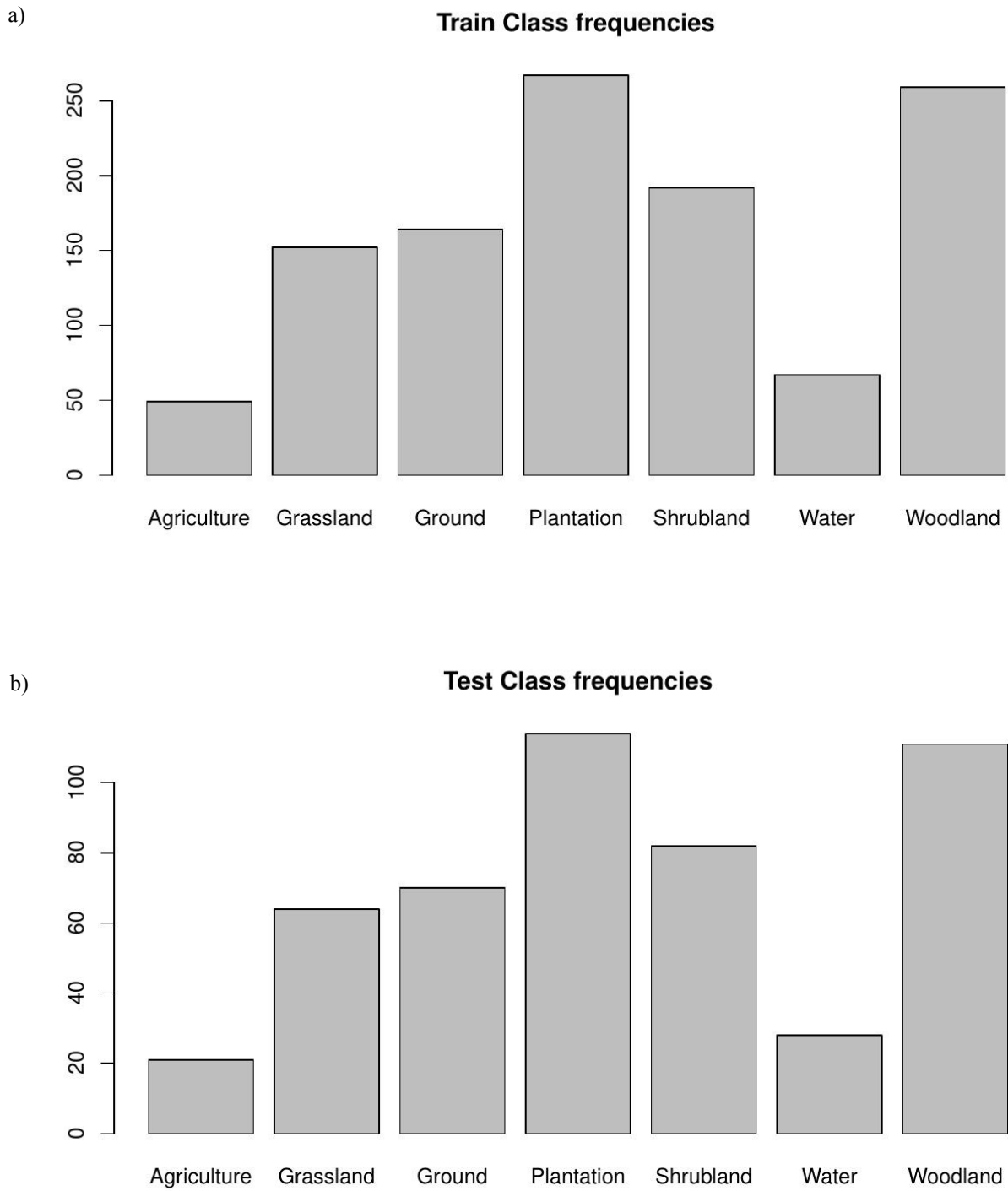


Figure S3.3.1 Reference data collected using 25cm orthophotos and 3m PlanetScope imagery and split, using a 70/30 split, into a) training and b) testing data.

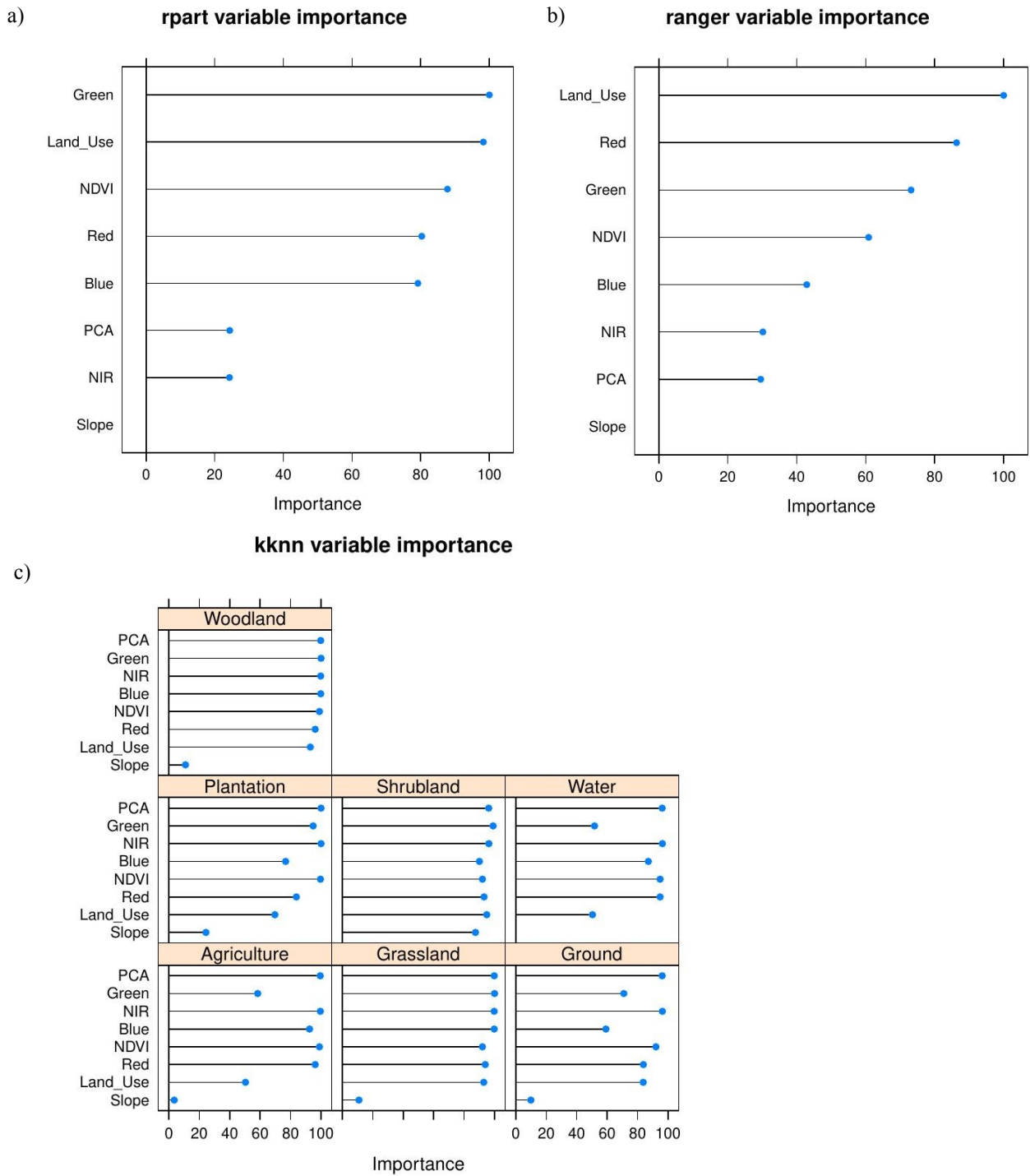


Figure S3.3.2 Variable importance for the a) Classification and Regression Tree algorithm, using the rpart function, b) Random Forest algorithm, using the ranger function, and c) K-Nearest Neighbour algorithm, using kkn function.

Table S3.3.1 Confusion matrix for Classification and Regression Tree with additional accuracy statistics.

Prediction	Reference							
	Agriculture	Grassland	Ground	Plantation	Shrubland	Water	Woodland	
Agriculture	13	0	0	0	2	0	0	
Grassland	4	57	2	0	6	1	0	
Ground	2	0	66	0	0	0	0	
Plantation	0	0	2	109	5	0	5	
Shrubland	2	6	0	3	63	2	10	
Water	0	0	0	0	0	25	0	
Woodland	0	1	0	2	6	0	96	
Overall statistics:								
Accuracy:	0.8755							
95% CI:	(0.843, 0.9034)							
No Information Rate:	0.2327							
P-Value:	<2.2e-16							
Kappa:	0.8485							
Mcnemar's Test P-Value:	NA							
Statistics per land cover class:								
	Agriculture	Grassland	Ground	Plantation	Shrubland	Water	Woodland	
Precision	0.86667	0.8143	0.9706	0.9008	0.7326	1	0.9143	
Recall	0.61905	0.8906	0.9429	0.9561	0.7683	0.89286	0.8649	
F1	0.72222	0.8507	0.9565	0.9277	0.75	0.9434	0.8889	
Prevalence	0.04286	0.1306	0.1429	0.2327	0.1673	0.05714	0.2265	
Detection Rate	0.02653	0.1163	0.1347	0.2224	0.1286	0.05102	0.1959	
Detection Prevalence	0.03061	0.1429	0.1388	0.2469	0.1755	0.05102	0.2143	
Balanced Accuracy	0.80739	0.9301	0.969	0.9621	0.856	0.94643	0.9206	

Table S3.3.2 Confusion matrix for Random Forest with additional accuracy statistics.

Prediction	Reference							
	Agriculture	Grassland	Ground	Plantation	Shrubland	Water	Woodland	
Agriculture	19	0	0	0	0	0	0	
Grassland	0	57	2	0	6	0	0	
Ground	2	1	66	0	0	0	0	
Plantation	0	0	2	110	3	0	2	
Shrubland	0	6	0	4	70	0	6	
Water	0	0	0	0	0	28	0	
Woodland	0	0	0	0	3	0	103	
Overall statistics:								
Accuracy:	0.9245							
95% CI:	(0.8974, 0.9463)							
No Information Rate:	0.2327							
P-Value:	<2.2e-16							
Kappa:	0.9083							
Mcnemar's Test P-Value:	NA							
Statistics per land cover class:								
	Agriculture	Grassland	Ground	Plantation	Shrubland	Water	Woodland	
Precision	1	0.8769	0.9565	0.9402	0.814	1	0.9717	
Recall	0.90476	0.8906	0.9429	0.9649	0.8537	1	0.9279	
F1	0.95	0.8837	0.9496	0.9524	0.8333	1	0.9493	
Prevalence	0.04286	0.1306	0.1429	0.2327	0.1673	0.05714	0.2265	
Detection Rate	0.03878	0.1163	0.1347	0.2245	0.1429	0.05714	0.2102	
Detection Prevalence	0.03878	0.1327	0.1408	0.2388	0.1755	0.05714	0.2163	
Balanced Accuracy	0.95238	0.9359	0.9679	0.9731	0.9072	1	0.96	

Table S3.3.3 Confusion matrix for K-Nearest Neighbour with additional accuracy statistics.

Prediction	Reference							
	Agriculture	Grassland	Ground	Plantation	Shrubland	Water	Woodland	
Agriculture	18	1	0	0	0	0	0	0
Grassland	1	54	2	0	5	0	0	0
Ground	1	0	66	0	0	0	0	0
Plantation	0	0	2	110	4	0	8	
Shrubland	1	9	0	3	63	0	5	
Water	0	0	0	0	0	28	0	
Woodland	0	0	0	1	10	0	98	
Overall statistics:								
Accuracy:	0.8918							
95% CI:	(0.8609, 0.9179)							
No Information Rate:	0.2327							
P-Value:	<2.2e-16							
Kappa:	0.8684							
Mcnemar's Test P-Value:	NA							
Statistics per land cover class:								
	Agriculture	Grassland	Ground	Plantation	Shrubland	Water	Woodland	
Precision	0.94737	0.871	0.9851	0.8871	0.7778	1	0.8991	
Recall	0.85714	0.8438	0.9429	0.9649	0.7683	1	0.8829	
F1	0.9	0.8571	0.9635	0.9244	0.773	1	0.8909	
Prevalence	0.04286	0.1306	0.1429	0.2327	0.1673	0.05714	0.2265	
Detection Rate	0.03673	0.1102	0.1347	0.2245	0.1286	0.05714	0.2	
Detection Prevalence	0.03878	0.1265	0.1367	0.2531	0.1653	0.05714	0.2224	
Balanced Accuracy	0.92751	0.9125	0.9702	0.9638	0.8621	1	0.9269	

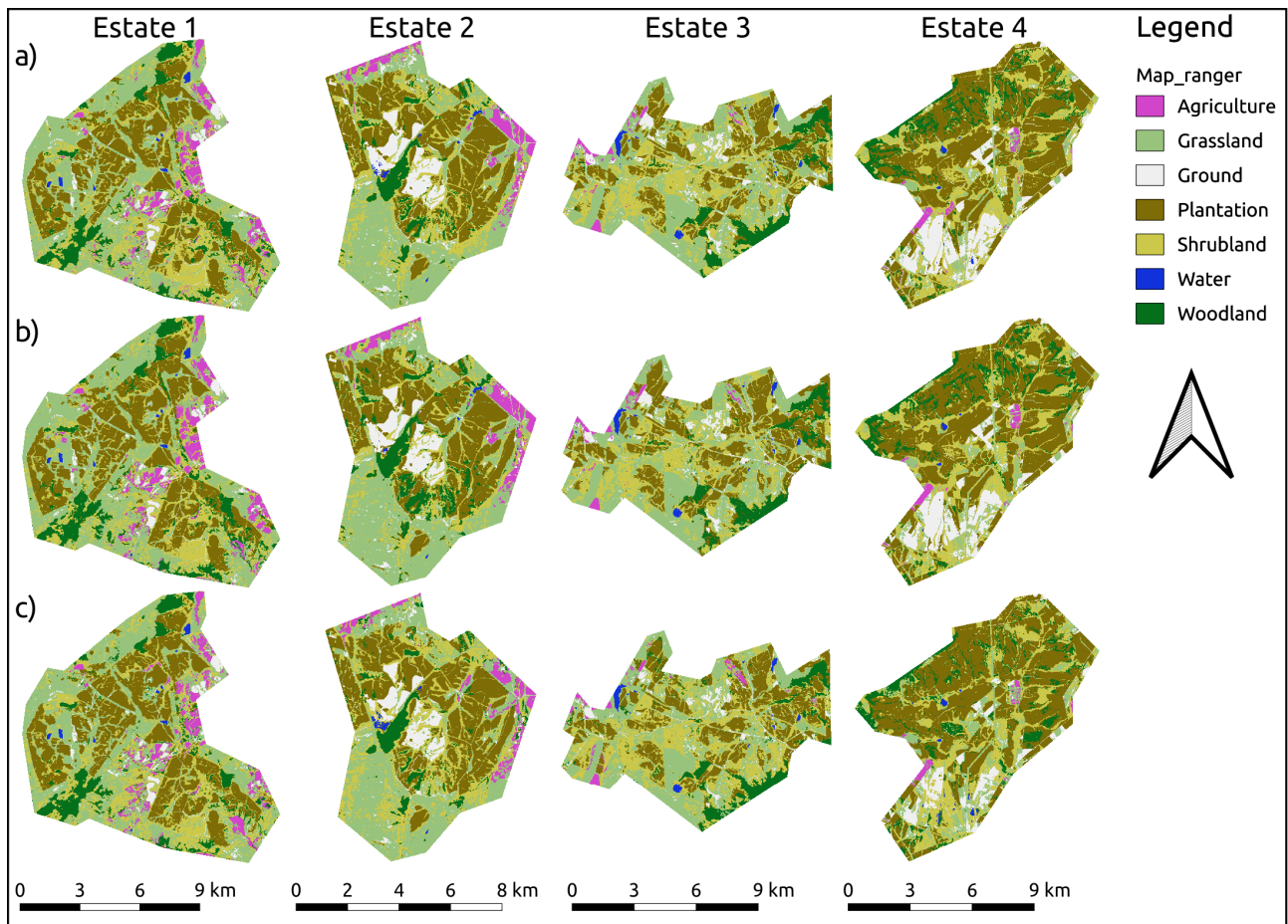


Figure S3.3.3 Land cover classification using a) Random Forest, b) K-Nearest Neighbour, and c) Classification and Regression Tree.

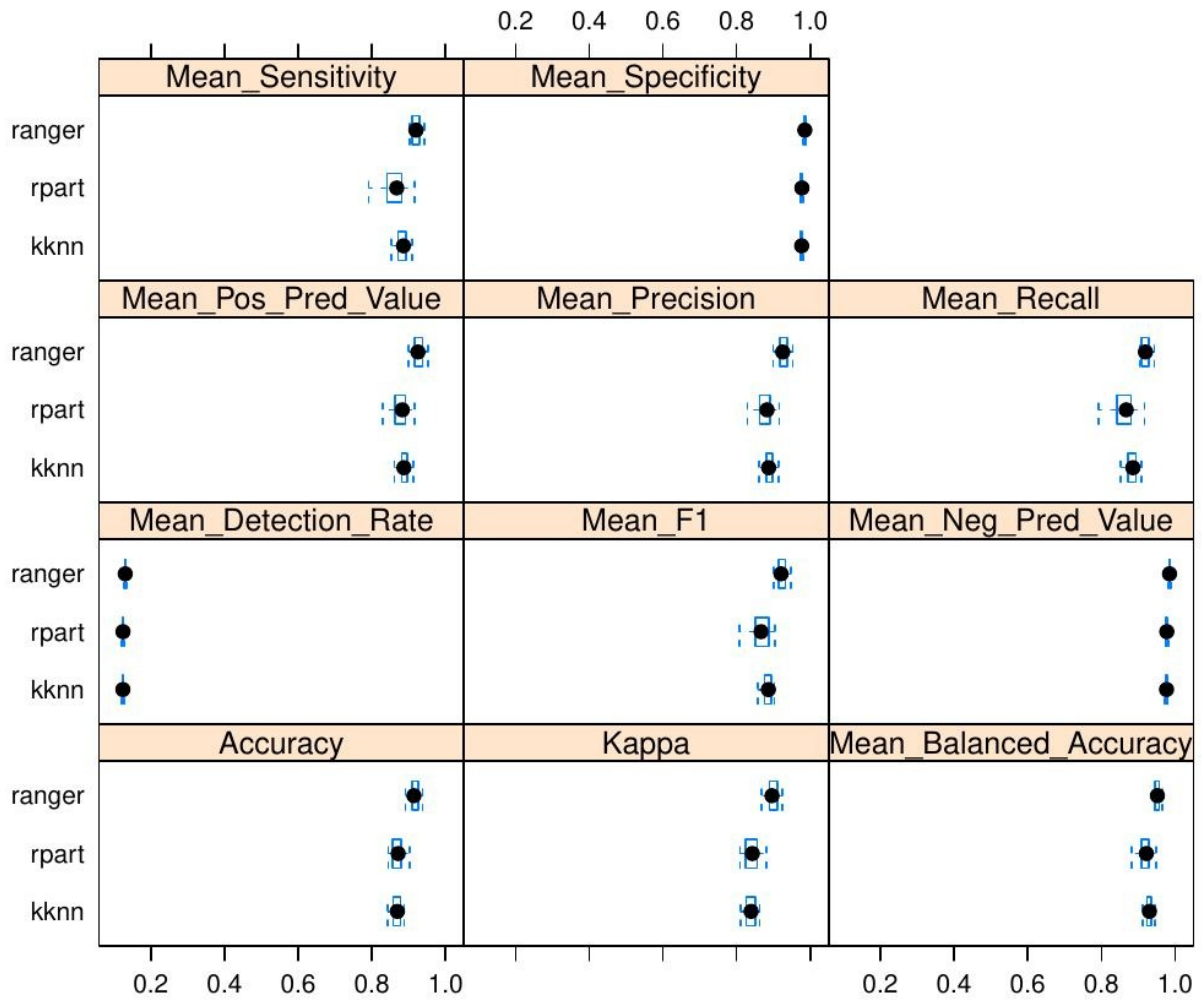


Figure S3.3.4 Comparing model accuracies.

Appendix S3.4

Before running stacked species distribution modelling (S-SDM), I performed preliminary analyses using different raster variables, at different scales (Table S3.4.1-S3.4.2). This was done to refine variable selection and to also identify resolution that best worked for the data and study area. Preliminary S-SDM was performed using the recommended model parameters from the S-SDM R package (Schmitt et al. 2017). Based on these results I identified redundant variables (Slope, Elevation and Surface Temperature) as well as identifying Sentinel-2 resolution (10 m) to be the most accurate compared to Landsat (30 m) and PlanetScope (3 m).

Using the new combination of variables, supported by previous research, I refined the models by tuning the parameters to produce the best models with the data (Figure S3.4.1 and Table S3.4.3). Final model parameters can be found in the main text.

References

Schmitt S, Pouteau R, Justeau D, de Boissieu F, Birnbaum P (2017) SSDM: An R package to predict distribution of species richness and composition based on stacked species distribution models. *Methods Ecol Evol* 8:1795-1803. <https://doi.org/10.1111/2041-210X.12841>

Table S3.4.1 Preliminary testing and variables selection used in S-SDM using the overall grasshopper assemblage. Values represents the relative contribution of environmental variables used in stacked species distribution modelling to predict suitable habitat for grasshoppers. NDVI = Normalised Difference Vegetation Index, Drain dist= distance to nearest cold air drainage line, Elv = elevation, NBR = Normalised Burn Ratio index, Surf Temp = land surface temperature. Mean (\pm SD).

Satellite	Variables						
	NDVI	Land cover	Drain dist	Slope	Elv	NBR	Surf_Temp
Landsat	8.04 (\pm 6.69)	33.95 (\pm 14.63)	9.98 (\pm 11.59)	10.67 (\pm 9.44)	13.98 (\pm 10.89)	16.49 (\pm 8.23)	6.89 (\pm 3.79)
	NDVI	Land cover	Drain dist	Aspect			
PlanetScope_1	22.9 (\pm 13.02)	25.07 (\pm 14.51)	24.61 (\pm 11.22)	27.42 (\pm 18.36)			
	NDVI	Land cover	Drain dist	Aspect	Cor_Width		
PlanetScope_2	20.68 (\pm 11.4)	19.13 (\pm 12.2)	19.37 (\pm 12.02)	19.68 (\pm 10.83)	21.14 (\pm 8.37)		
	NDVI	Land cover	Drain dist	Aspect	Cor_Width	NBR	
PlanetScope_3	13.52 (\pm 7.44)	10.82 (\pm 10.98)	18.05 (\pm 10.15)	15.47 (\pm 9.92)	15.4 (\pm 11.61)	26.74 (\pm 14.05)	
	NDVI	Land cover	Drain dist	Aspect	Cor_Width		
Sentinel_1	20.47 (\pm 9.53)	20.67 (\pm 13.33)	20.48 (\pm 9.9)	15.26 (\pm 7.7)	23.11 (\pm 12.12)		
	NDVI	Land cover	Drain dist	Aspect	Cor_Width	NBR	
Sentinel_2	19.32 (\pm 15.59)	8.39 (\pm 5.52)	16.71 (\pm 7.4)	17.22 (\pm 7.96)	15.75 (\pm 12.3)	22.6 (\pm 11.14)	

Table S3.4.2 Preliminary testing and variables selection used in S-SDM using the overall grasshopper assemblage. Values represents the evaluation statistics for the stacked species distribution modelling that were used to identify drivers of suitable habitat for grasshoppers. Spp rich error = species richness error (difference between predicted and observed species richness), Specificity = assemblage specificity (proportion of true negatives), Sensitivity = assemblage sensitivity (proportion of true positives), and Jaccard = Jaccard index (community similarity). Mean (\pm SD).

Satellite	Evaluation			
	Spp rich error	Specificity	Sensitivity	Jaccard
Landsat	23.41 (\pm 8.53)	0.19 (\pm 0.21)	0.85 (\pm 0.28)	0.28 (\pm 0.14)
PlanetScope_1	15.05 (\pm 8.41)	0.4 (\pm 0.24)	0.66 (\pm 0.28)	0.24 (\pm 0.12)
PlanetScope_2	12.53 (\pm 7.84)	0.34 (\pm 0.27)	0.68 (\pm 0.28)	0.29 (\pm 0.12)
PlanetScope_3	19.31 (\pm 9.11)	0.26 (\pm 0.24)	0.75 (\pm 0.25)	0.26 (\pm 0.12)
Sentinel_1	10.92 (\pm 8.33)	0.38 (\pm 0.29)	0.67 (\pm 0.35)	0.28 (\pm 0.17)
Sentinel_2	12.92 (\pm 7.89)	0.29 (\pm 0.24)	0.72 (\pm 0.33)	0.27 (\pm 0.14)

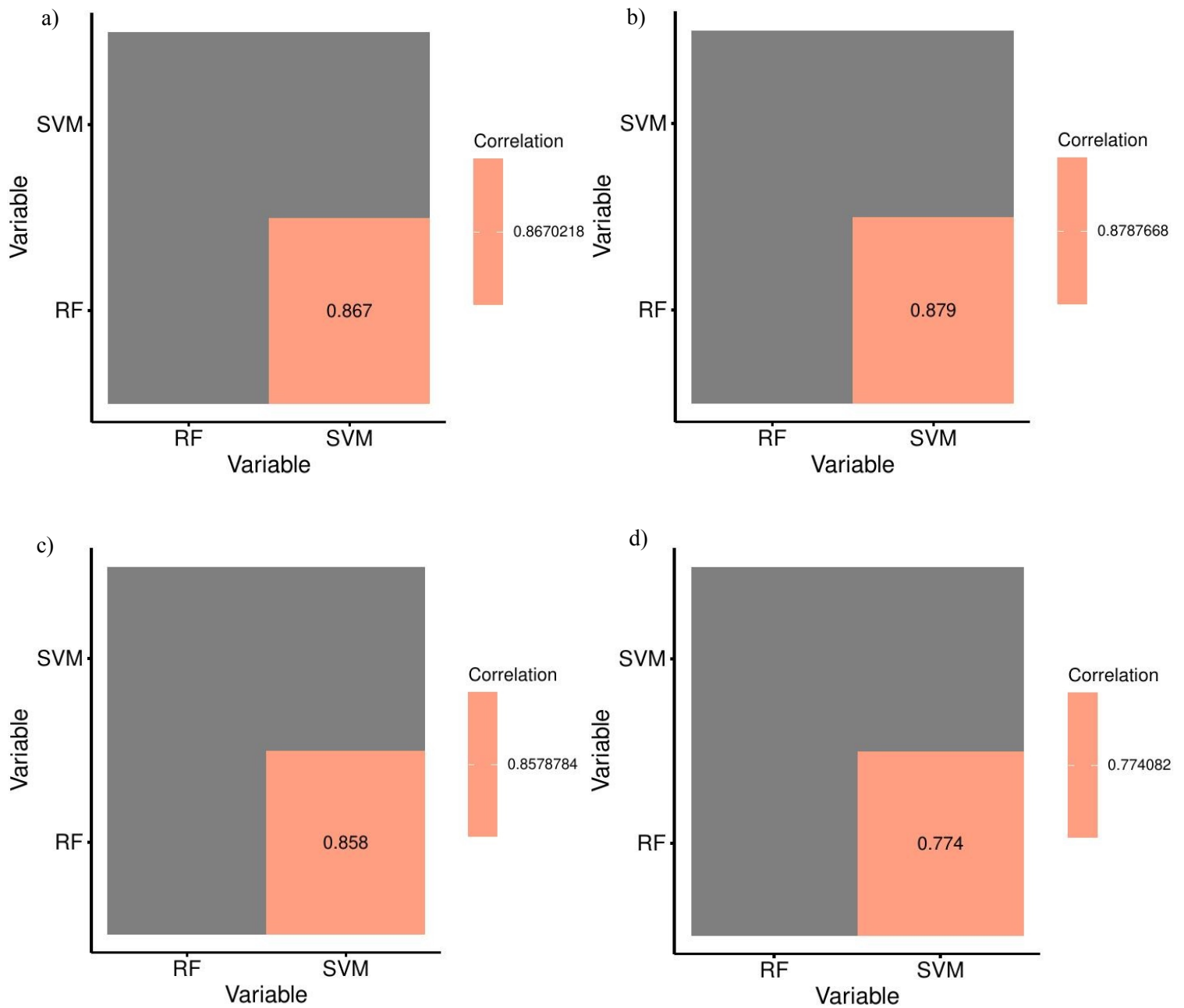


Figure S3.4.1 Algorithm correlations for a) overall assemblage, b) low conservation value assemblage, c) intermediate conservation value assemblage, and d) high conservation value assemblage. RF = Random Forest algorithm, SVM = Support Vector Machines algorithm.

Table S3.4.3 Number of source patches identified using the top 15% of suitable habitat between all plantation estates for all the overall grasshopper assemblage as well as the different conservation-priority species groups (Low - High).

Grouping	Estate 1	Estate 2	Estate 3	Estate 4
Overall	133	43	115	6
Low	141	47	126	6
Intermediate	145	56	135	15
High	92	37	85	6

Appendix S3.5

Performing accurate functional connectivity analysis requires suitable resistance/conductance surfaces (Peterman 2018). As the type of surface can influence the resulting connectivity map, I produced connectivity maps using three different conductive surfaces. Firstly, I used the suitability maps created by the S-SDM. Secondly, I used NDVI as a conductance surface, as previous work demonstrated a relationship between intermediate NDVI values and high grasshopper diversity (Theron et al. 2021). In order to help optimise the the connectivity modelling using NDVI, I applied a reverse Ricker transformation to NDVI using the *Resistance.tran* function within the *ResistanceGA* R package (Peterman 2018) so the transformed values more closely match expected patters in grasshopper diversity (Figure S3.5.2). Lastly, I manually assigned user defined conductance values between 0-100 to every land cover class. These values were based on the vegetation structure and microclimate of land classes, with grasslands having the highest values (conducts current easily) and plantations having the lowest values (restricts current) (Table S3.5.1).

References

- Peterman WE (2018) ResistanceGA: An R package for the optimization of resistance surfaces using genetic algorithms. *Methods Ecol Evol* 9:1638-1647. <https://doi.org/10.1111/2041-210X.12984>
- Theron KJ, Pryke JS, Samways MJ (2021) Identifying managerial legacies within conservation corridors using remote sensing and grasshoppers as bioindicators. *Ecol Appl* 32:e02496. <https://doi.org/10.1002/eap.2496>

Table S3.5.1 Conductivity values assigned to individual land cover classes for functional connectivity modelling.

Land cover	Conductivity value (0-100)
Agriculture	40
Grassland	100
Ground	70
Plantation	10
Shrubland	30
Water	0
Woodland	20

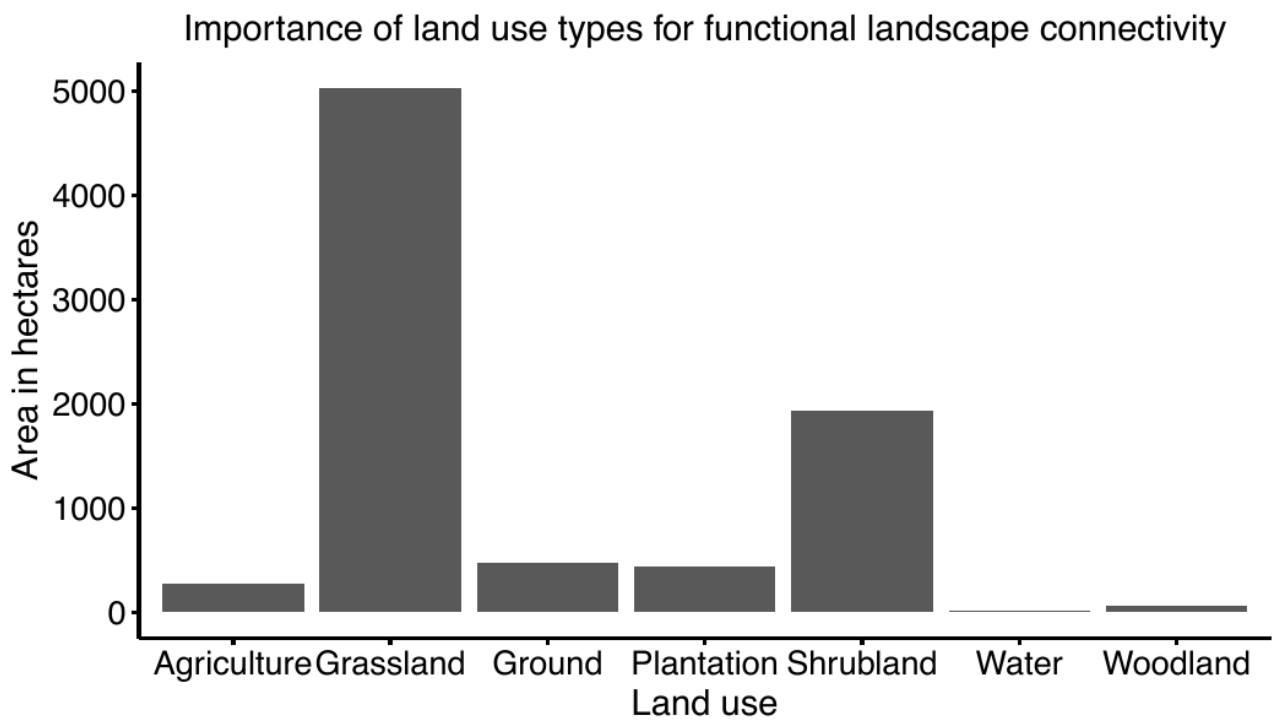


Figure S3.5.1 Land cover types important for maintaining functional connectivity. Area per land cover was calculated using the top 15% of current from the resulting *Circuitscape* maps.

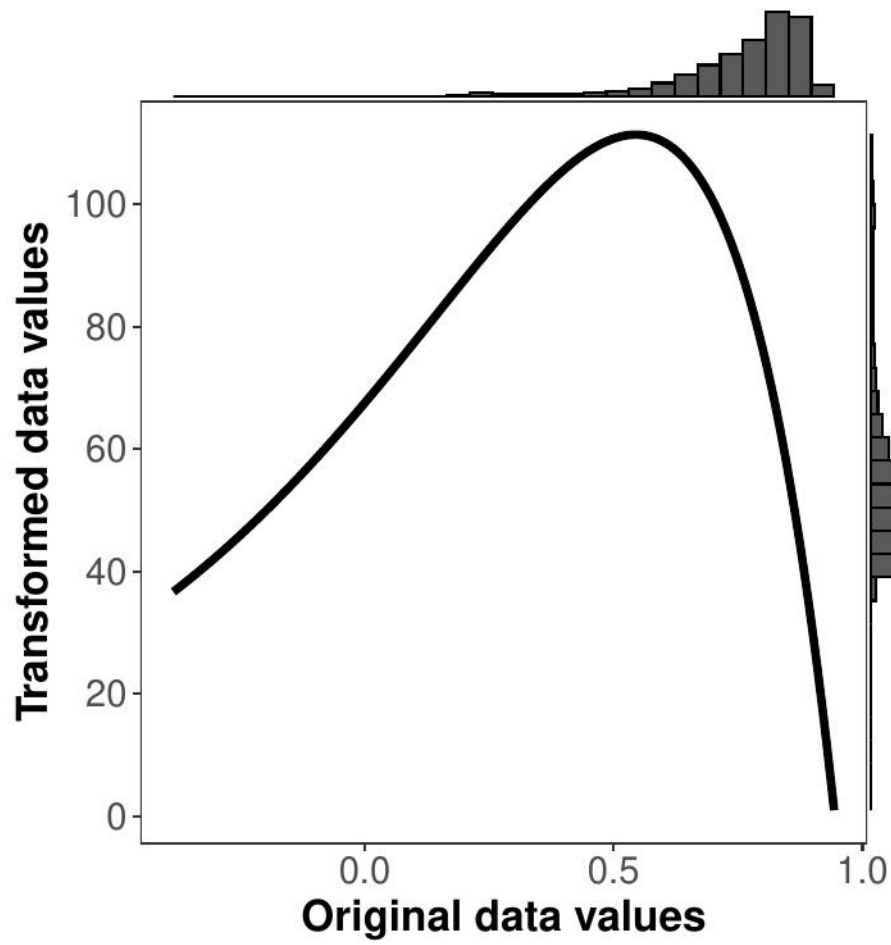


Figure S3.5.2 Distribution of transformed NDVI values using a reverse Ricker transformation.

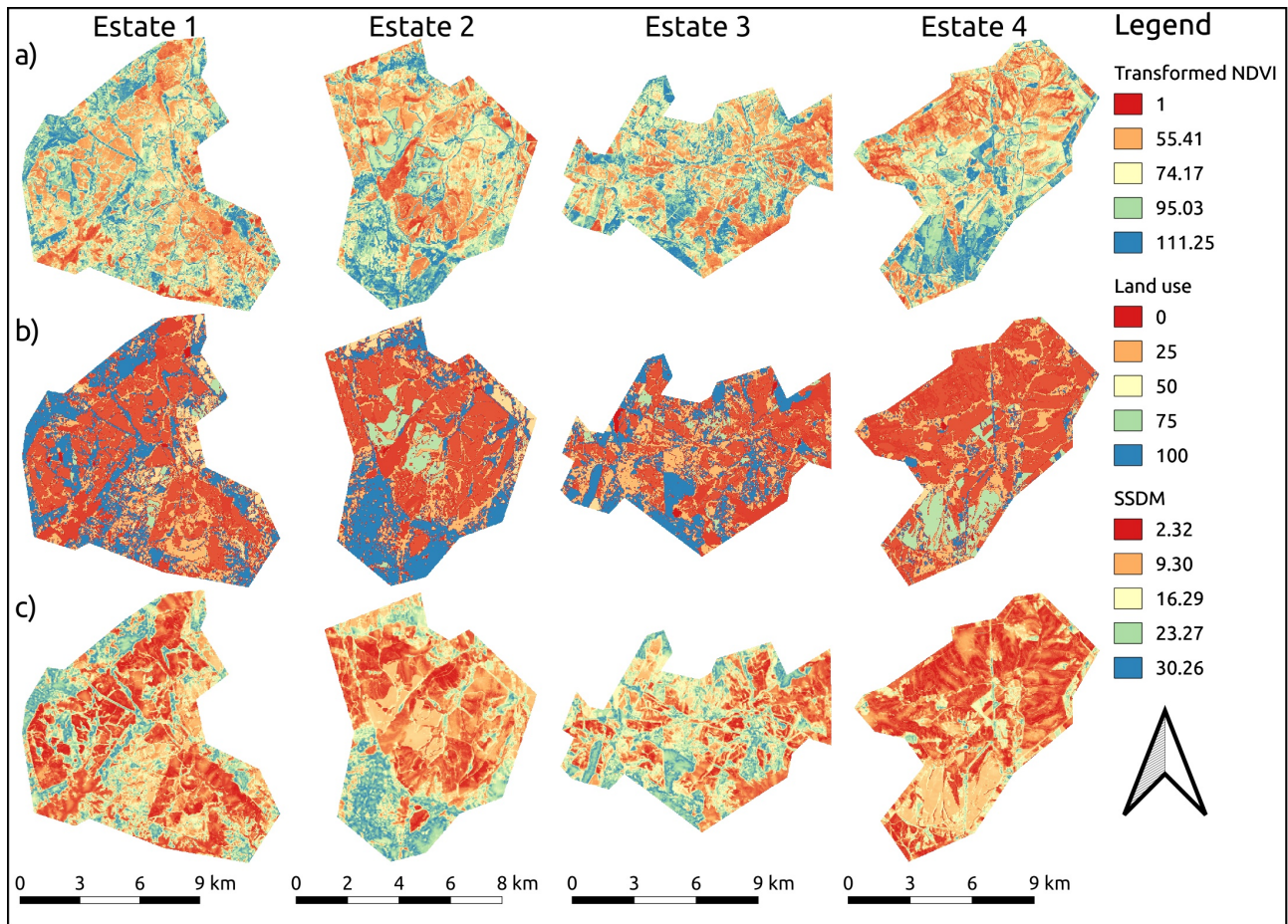


Figure S3.5.3 Conductance surfaces used for functional connectivity analysis in *Circuitscape*. a) Reverse Ricker transformation on NDVI, b) manually edited land cover data product, and c) suitable habitat from stacked species distribution modelling.

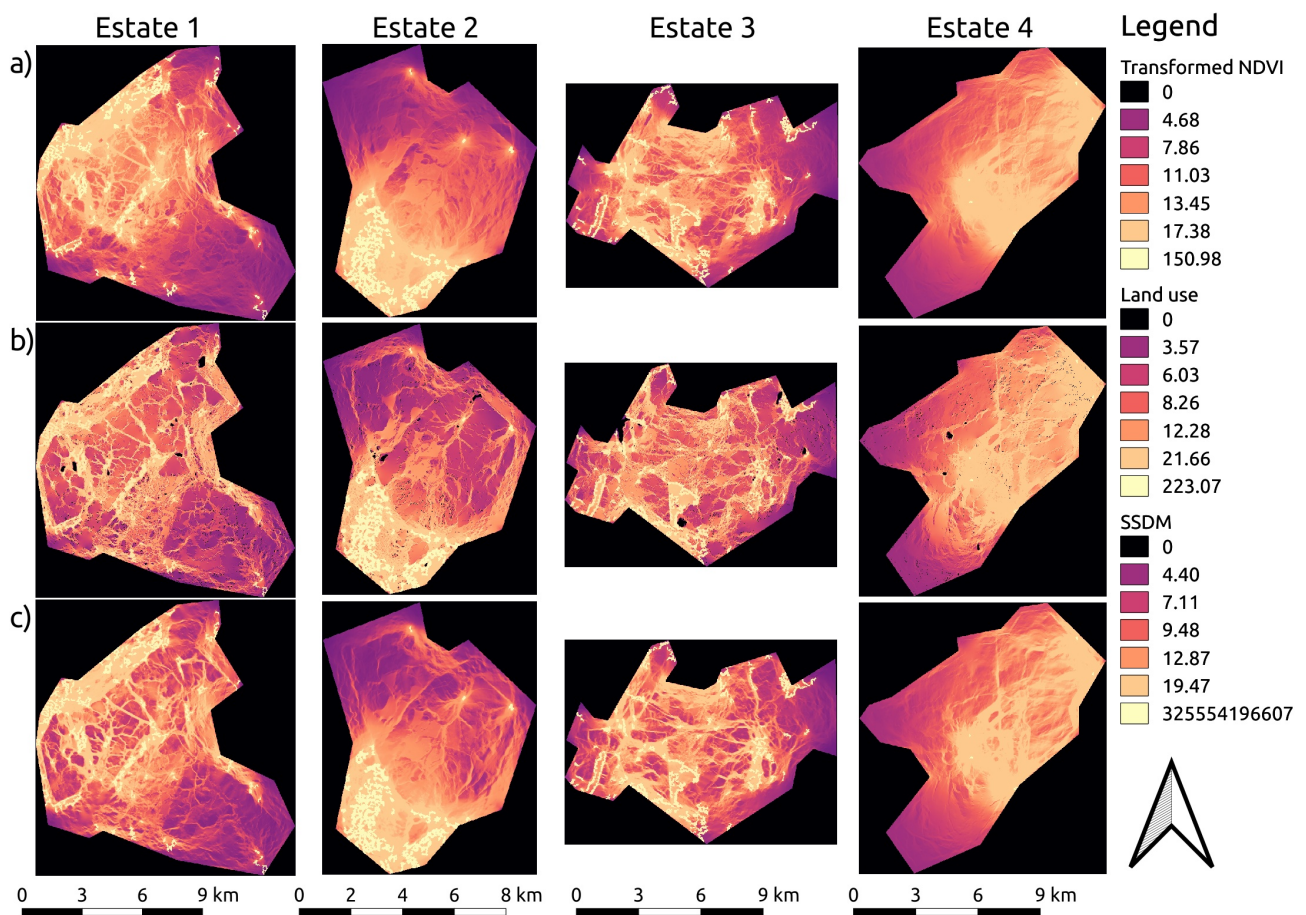


Figure S3.5.4 Connectivity maps produced using a) reverse Ricker transformation on NDVI, b) manually edited land cover data product, and c) suitable habitat from stacked species distribution modelling.

Table S3.5.2 Characteristics of high and low importance corridors for maintaining functional connectivity for overall grasshopper assemblage as well as for different conservation-priority groups (Low - High). Corridor value = high value score corridors and low value score corridors, NDVI = Normalised Difference Vegetation Index, Max NBR = maximum Normalised Burn Ration index, Dist Edge = distance to corridor edge, Elv = elevation, Drain Dist = distance to cold air drainage channels.

Grasshopper	Corridor value	NDVI	Max NBR	Dist Edge	Aspect	Elv	Drain Dist
Overall	High	0.761	0.703	14.142	105.770	1358.635	22.361
Overall	High	0.641	0.611	8.784	69.464	1357.944	27.978
Overall	High	0.732	0.618	54.720	73.456	1363.573	66.302
Overall	High	0.676	0.488	50.000	327.285	1439.992	22.361
Overall	High	0.663	0.606	11.211	199.825	1387.813	43.381
Overall	Low	0.561	0.713	12.873	195.442	935.601	47.292
Overall	Low	0.600	0.630	12.536	165.088	808.128	35.938
Overall	Low	0.650	0.630	11.374	155.197	1026.331	24.694
Overall	Low	0.671	0.694	9.509	178.717	882.984	58.113
Overall	Low	0.673	0.692	9.522	207.552	891.613	56.394
High	High	0.678	0.628	66.376	118.035	1439.897	94.268
High	High	0.749	0.483	58.310	268.104	1532.118	20.000
High	High	0.773	0.666	80.000	109.580	1425.633	53.852
High	High	0.678	0.492	90.554	117.876	1541.384	53.852
High	High	0.646	0.601	63.749	107.255	1518.731	41.220
High	Low	0.675	0.526	54.108	207.541	1642.927	52.048
High	Low	0.689	0.634	12.718	185.767	916.094	47.761
High	Low	0.709	0.724	5.294	251.813	929.958	73.976
High	Low	0.653	0.675	9.296	186.043	869.308	51.299
High	Low	0.620	0.688	9.565	199.906	902.299	61.101
Intermediate	High	0.685	0.592	69.597	46.373	1368.732	56.081

Intermediate	High	0.776	0.711	12.071	108.624	1358.491	18.251
Intermediate	High	0.664	0.611	9.260	66.527	1357.869	28.356
Intermediate	High	0.734	0.627	48.874	87.077	1362.300	68.136
Intermediate	High	0.726	0.597	61.018	45.966	1367.282	65.164
Intermediate	Low	0.658	0.733	31.342	NA	1009.473	76.558
Intermediate	Low	0.673	0.679	10.653	NA	891.246	50.365
Intermediate	Low	0.707	0.729	26.269	NA	1060.095	43.842
Intermediate	Low	0.706	0.686	11.307	165.440	890.006	79.975
Intermediate	Low	0.714	0.734	25.892	NA	1011.359	51.980
Low	High	0.761	0.703	14.142	105.770	1358.635	22.361
Low	High	0.660	0.611	9.045	59.789	1357.891	28.194
Low	High	0.733	0.618	55.190	73.752	1363.600	67.319
Low	High	0.663	0.602	12.031	199.492	1388.629	42.892
Low	High	0.664	0.592	16.251	56.910	1398.975	19.632
Low	Low	0.635	0.625	29.010	198.739	1293.419	53.054
Low	Low	0.603	0.633	11.986	162.366	805.616	35.797
Low	Low	0.613	0.642	9.327	143.185	1026.734	27.520
Low	Low	0.664	0.696	8.876	183.584	883.215	58.415
Low	Low	0.681	0.690	8.091	193.538	888.693	56.876

Appendix S4.1

Table S4.1.1 List of grasshopper species sampled during the study. GCI = Grasshopper Conservation Index calculated by using scores for species rarity, mobility and endemism.

Family	Subfamily	Species	Abundance	GCI	
Acrididae	Acrididae	<i>Acrida acuminata</i> (Stål, 1873)	105	3	
		<i>Acrida bicolor</i> (Thunberg, 1815)	17	3	
		<i>Acrida propinqua</i> (Burr, 1902)	2	6	
		<i>Duronia chloronota chloronota</i> (Stål, 1876)	155	3	
		<i>Duronia chloronota curta</i> (Uvarov, 1953)	140	5	
		<i>Gymnbothrus carinatus</i> (Uvarov, 1941)	47	4	
		<i>Machaeridia conspersa</i> (I. Bolívar, 1889)	54	3	
		<i>Rhabdoplea munda</i> (Karsch, 1893)	26	5	
		Catantopinae	<i>Anthermus granosus</i> (Stål, 1878)	30	3
			<i>Vitticatantops humeralis</i> (Thunberg, 1815)	195	3
	Coptacrinae	<i>Eucoptacra turneri</i> (Miller, 1932)	11	5	
	Cyrtacanthacridinae	<i>Cyrtacanthacris aeruginosa aeruginosa</i> (Stoll, 1813)	3	5	
		<i>Ornithacris cyanea cyanea</i> (Stoll, 1813)	3	5	
	Euryphyminae	<i>Rhachitopis melanopus</i> (Burmeister, 1838)	72	4	
	Eyprepocnemidinae	<i>Eyprepocnemis calceata</i> (Serville, 1838)	29	5	
		<i>Heteracris drakensbergensis</i> (Grunshaw, 1991)	6	7	
	Gomphocerinae	<i>Anablepia pilosa</i> (Uvarov, 1953)	87	5	
		<i>Crucinotacris cruciata</i> (Bolívar, 1912)	60	3	
		<i>Diablepia viridis</i> (Kirby, 1902)	3	7	
		<i>Faureia milanjica</i> (Karsch, 1896)	4	5	
<i>Mesopsis abbreviata</i> (Palisot de Beauvois, 1806)		65	4		
<i>Pnorisa angulata</i> (Karny, 1910)		163	3		
	<i>Pnorisa squalus</i> (Stål, 1861)	122	3		

		<i>Pseudoarcyptera cephalica</i> (Bolívar, 1914)	8	7
		<i>Rhaphotittha levis</i> (Karsch, 1896)	21	4
Hemiacridinae		<i>Acanthoxia gladiator</i> (Westwood, 1842)	1	5
Oedipodinae		<i>Aiolopus meruensis</i> (Sjöstedt, 1909)	37	4
		<i>Gastrimargus africanus africanus</i> (Saussure, 1888)	30	3
		<i>Gastrimargus determinatus determinatus</i> (Walker, 1871)	3	6
		<i>Gastrimargus drakensbergensis</i> (Ritchie, 1982)	20	5
		<i>Morphacris fasciata</i> (Thunberg, 1815)	10	4
		<i>Paracinema tricolor tricolor</i> (Thunberg, 1815)	22	4
		<i>Scintharista magnifica</i> (Uvarov, 1922)	9	6
		<i>Scintharista rosacea</i> (Kirby, 1902)	5	7
		<i>Scintharista saucia</i> (Stål, 1873)	1	6
Oxyinae		<i>Dirshia abbreviata</i> (Brown, 1962)	14	7
		<i>Oxya glabra</i> (Ramme, 1929)	81	6
		<i>Oxya hyla</i> (Serville, 1831)	400	3
Spathosterninae		<i>Spathosternum nigrotaeniatum</i> (Stål, 1876)	58	3
Tropidopolinae		<i>Petamella prosternalis</i> (Karny, 1907)	1	5
Gryllidae	Gryllinae	<i>Acanthogryllus fortipes</i> (Walker, 1869)	31	8
Lentulidae	Lentulinae	<i>Betiscoides parva</i> (Key, 1937)	2	7
		<i>Lentula obtusifrons</i> (Stål, 1878)	156	6
Pamphagidae	Porthetinae	<i>Pagopedilum sordidum</i> (Walker, 1870)	1	6
		<i>Pagopedilum subcruciatum</i> (Karsch, 1896)	1	8
Pyrgomorphidae	Pyrgomorphinae	<i>Chrotogonus hemipterus</i> (Schaum, 1853)	1	6
		<i>Dictyophorus spumans pulchra</i> (Bolívar, 1904)	1	5
		<i>Phymateus leprosus leprosus</i> (Fabricius, 1793)	1	7
		<i>Phymateus viridipes viridipes</i> (Stål, 1873)	3	5
		<i>Stenoscepa picticeps</i> (Bolívar, 1904)	27	8

		<i>Zonocerus elegans elegans</i> (Thunberg, 1815)	4	5
Tetrigidae	Batrachideinae	<i>Phloeonotus humilis</i> (Gerstaecker, 1869)	78	4
	Cladonotinae	<i>Trachytettix scaberrimus scaberrimus</i> (Stål, 1876)	1	6
	Tetriginae	<i>Dasyleurotettix infaustus</i> (Walker, 1871)	4	6
		<i>Paratettix scaber</i> (Thunberg, 1815)	26	3
		<i>Paratettix subpustulata</i> (Walker, 1871)	12	5
		<i>Tettiella odiosa</i> (Walker, 1871)	57	5
Tettigoniidae	Conocephalinae	<i>Conocephalus caudalis</i> (Walker, 1869)	155	6
		<i>Conocephalus conocephalus</i> (Linnaeus, 1767)	217	3
		<i>Conocephalus longiceps</i> (Péringuey, 1916)	31	6
		<i>Conocephalus vaginalis</i> (Karny, 1907)	8	7
		<i>Ruspolia consobrina</i> (Walker, 1869)	26	3
	Phaneropterinae	<i>Phaneroptera sparsa</i> (Stål, 1857)	2	5
	Saginae	<i>Clonia wahlbergi wahlbergi</i> (Stål, 1855)	1	5
	Tettigoniinae	<i>Alfredectes semiaeneus</i> (Serville, 1838)	9	6
Thericleidae	Thericleinae	<i>Lophothericles marginatus</i> (Descamps, 1977)	1	8
		<i>Thericles miserabilis</i> (Descamps, 1977)	7	6
Tridactylidae	Tridactylinae	<i>Trigonidium erythrocephalum</i> (Walker, 1869)	16	6
		<i>Xya</i> sp 1 (Latreille, 1809)	3	8
		<i>Xya</i> sp 2 (Latreille, 1809)	3	8

Appendix S4.2

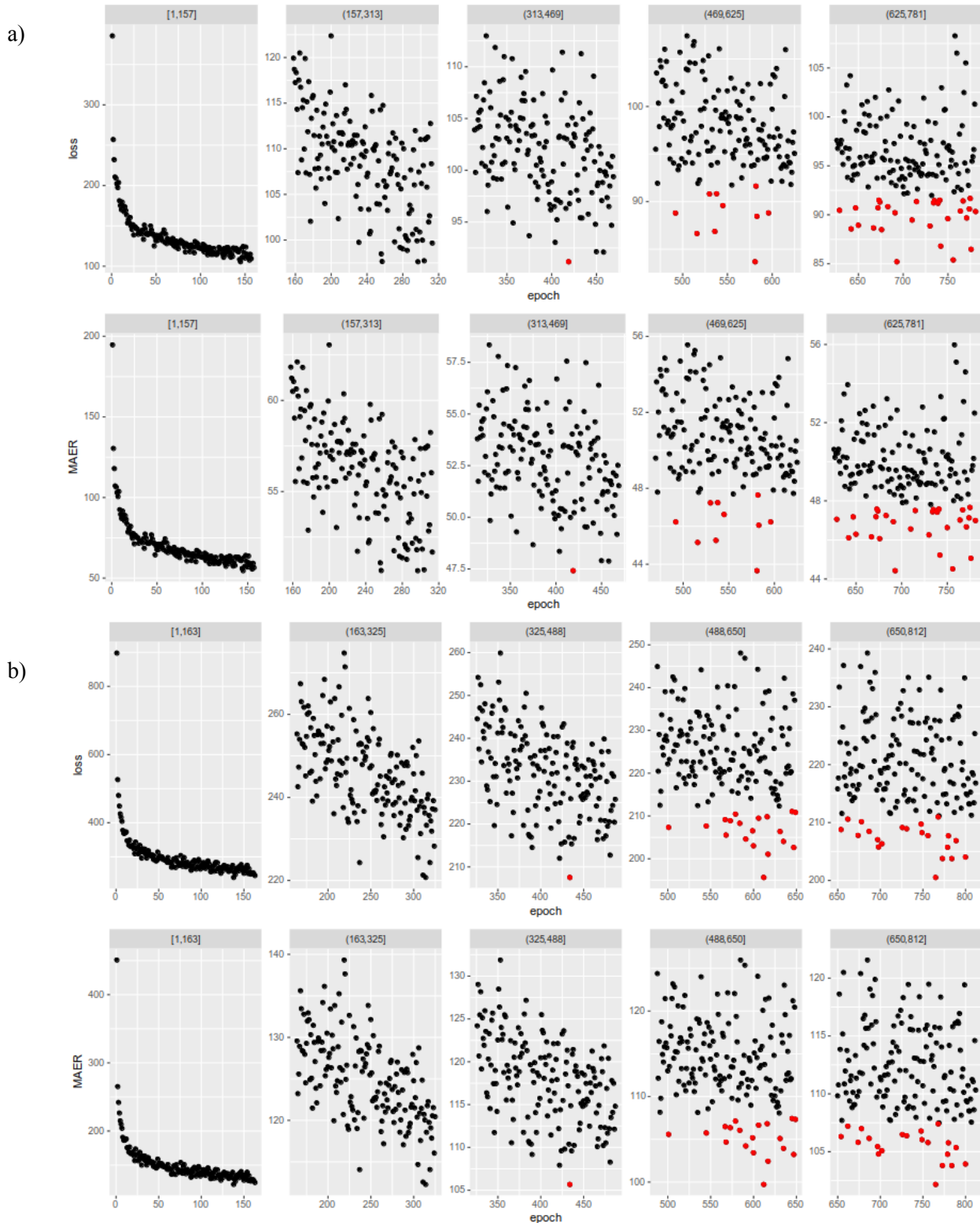
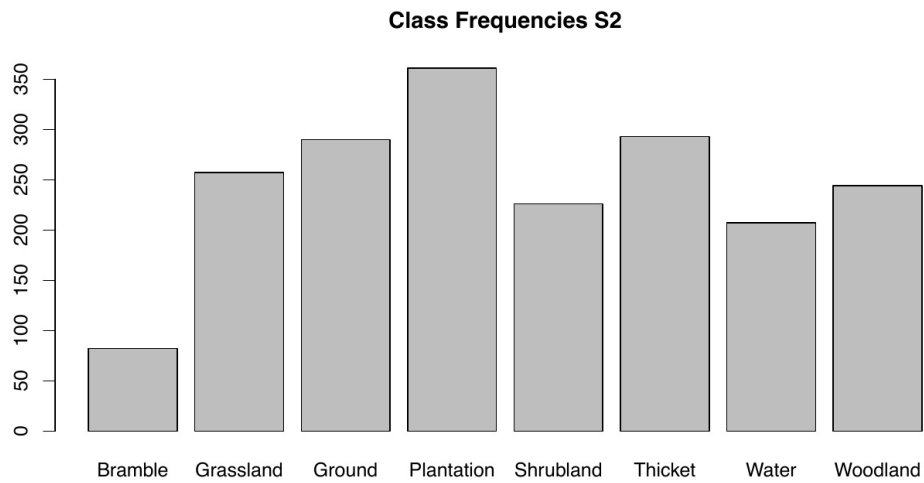
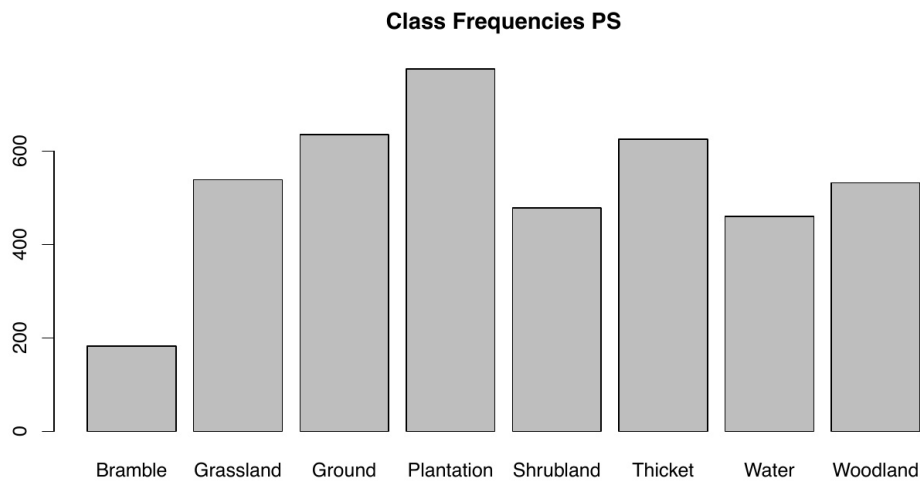


Figure S4.2.1 Network validation plots for a) network training on 10 m data, and b) network training on 20 m data. Loss refers to the amount of error in network predictions, where lower loss values mean more accurate predictions. The Mean Absolute Error (MAER) is another metric used to assess error in network predictions. Red dots show where the loss value is lower than the 5th percentile, indicating sufficient training.

a)



b)



c)

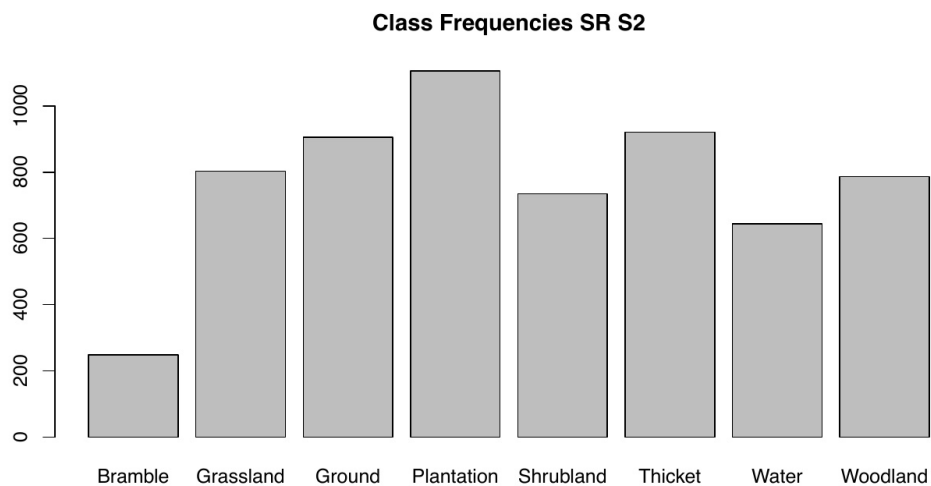


Figure S4.2.2 Class frequencies collected in the field and using 25 cm orthophotos. a) S2 = Sentinel-2, b) PS = PlanetScope, c) SR S2 = super-resolution.

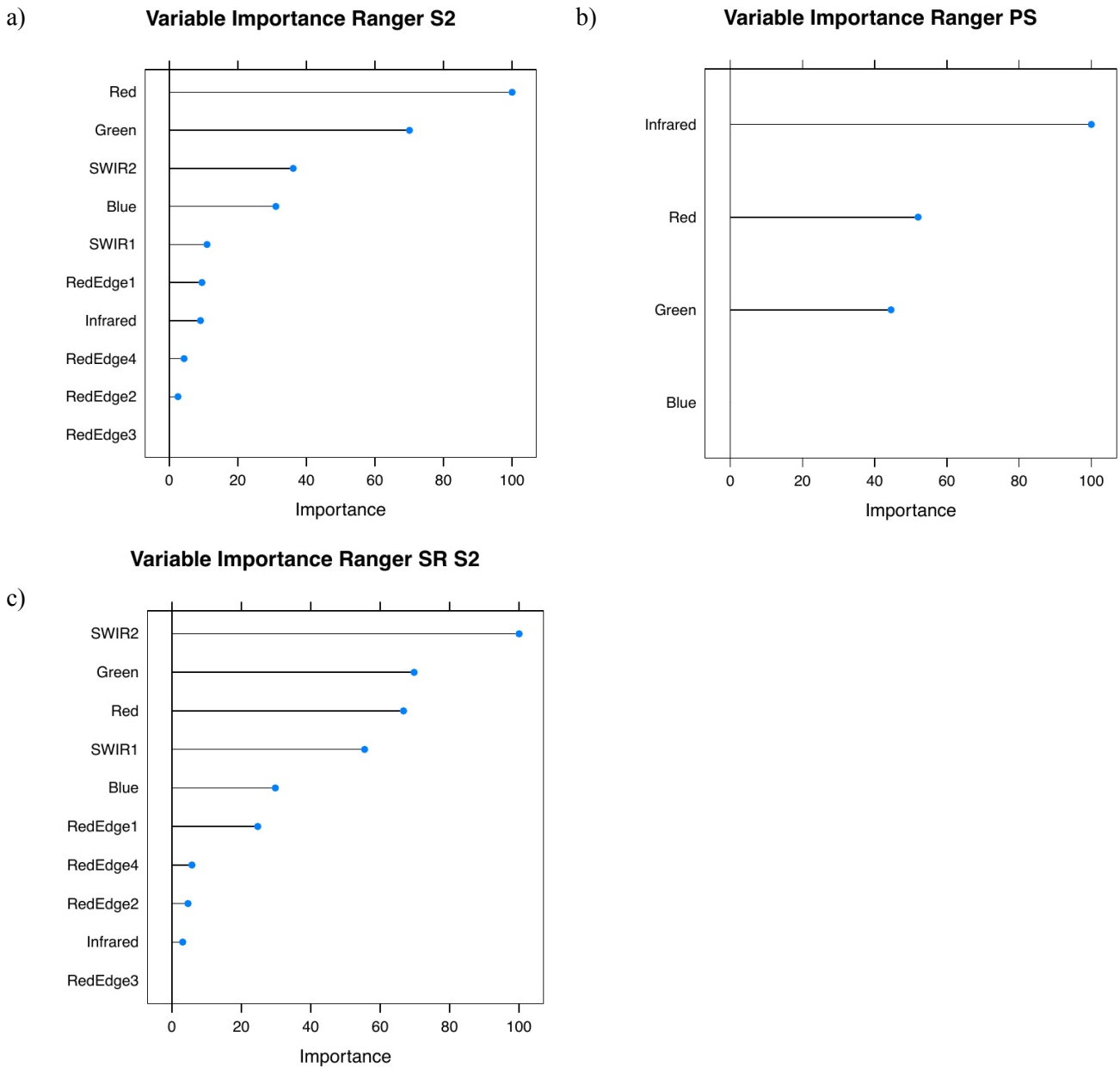


Figure S4.2.3 Variable importance using Random Forest implemented through the *ranger* function in *caret* R package. a) S2 = Sentinel-2, b) PS = PlanetScope, c) SR S2 = super-resolution.

Table S4.2.1 Confusion matrix for Sentinel-2 image with additional accuracy statistics.

Prediction	Reference							
	Bramble	Grassland	Ground	Plantation	Shrubland	Thicket	Water	Woodland
Bramble	3	1	0	0	2	0	0	0
Grassland	12	73	4	0	4	0	0	0
Ground	1	2	83	0	0	0	1	0
Plantation	1	0	0	107	0	0	2	1
Shrubland	4	1	0	0	51	5	0	0
Thicket	3	0	0	0	10	76	0	6
Water	0	0	0	0	0	0	59	0
Woodland	0	0	0	1	0	6	0	66

Overall Statistics:

Accuracy:	0.8855
95% CI:	(0.8568, 0.9101)
No Information Rate:	0.1846
P-Value:	< 2.2e-16
Kappa:	0.8667
McNemar's Test P-Value:	NA

Statistics per land cover class:

	Bramble	Grassland	Ground	Plantation	Shrubland	Thicket	Water	Woodland
Sensitivity	0.125	0.9481	0.954	0.9907	0.76119	0.8736	0.9516	0.9041
Specificity	0.994652	0.9606	0.992	0.9916	0.98069	0.9618	1	0.9863
Pos Pred Value	0.5	0.7849	0.954	0.964	0.83607	0.8	1	0.9041
Neg Pred Value	0.963731	0.9919	0.992	0.9979	0.96947	0.9776	0.9943	0.9863
Prevalence	0.041026	0.1316	0.1487	0.1846	0.11453	0.1487	0.106	0.1248
Detection Rate	0.005128	0.1248	0.1419	0.1829	0.08718	0.1299	0.1009	0.1128
Detection Prevalence	0.010256	0.159	0.1487	0.1897	0.10427	0.1624	0.1009	0.1248
Balanced Accuracy	0.559826	0.9543	0.973	0.9912	0.87094	0.9177	0.9758	0.9452

Table S4.2.2 Confusion matrix for PlanetScope image with additional accuracy statistics.

Prediction	Reference							
	Bramble	Grassland	Ground	Plantation	Shrubland	Thicket	Water	Woodland
Bramble	16	3	0	0	1	2	0	0
Grassland	17	148	1	0	3	0	0	0
Ground	0	1	188	0	0	0	0	0
Plantation	0	0	0	218	0	3	2	26
Shrubland	13	8	0	0	114	3	0	0
Thicket	8	1	0	1	24	168	0	17
Water	0	0	1	1	0	0	136	0
Woodland	0	0	0	12	1	11	0	116

Overall Statistics:

Accuracy:	0.8734
95% CI:	(0.8538, 0.8913)
No Information Rate:	0.1835
P-Value:	< 2.2e-16
Kappa:	0.8528
McNemar's Test P-Value:	NA

Statistics per land cover class:

	Bramble	Grassland	Ground	Plantation	Shrubland	Thicket	Water	Woodland
Sensitivity	0.2963	0.9193	0.9895	0.9397	0.7972	0.8984	0.9855	0.72956
Specificity	0.99504	0.981	0.9991	0.97	0.97859	0.9526	0.9982	0.97828
Pos Pred Value	0.72727	0.8757	0.9947	0.8755	0.82609	0.7671	0.9855	0.82857
Neg Pred Value	0.9694	0.9881	0.9981	0.9862	0.97425	0.9818	0.9982	0.96174
Prevalence	0.04272	0.1274	0.1503	0.1835	0.11313	1.48E-01	0.1092	0.12579
Detection Rate	0.01266	0.1171	0.1487	0.1725	0.09019	0.1329	0.1076	0.09177
Detection Prevalence	0.01741	0.1337	0.1495	0.197	0.10918	0.1733	0.1092	0.11076
Balanced Accuracy	0.64567	0.9501	0.9943	0.9548	0.8879	0.9255	0.9919	0.85392

Table S4.2.3 Confusion matrix for Super-resolution image with additional accuracy statistics.

Prediction	Reference								
	Bramble	Grassland	Ground	Plantation	Shrubland	Thicket	Water	Woodland	
Bramble	53	2	0	0	3	0	0	1	
Grassland	9	236	0	0	11	0	0	0	
Ground	0	0	271	0	0	0	0	0	
Plantation	0	0	0	328	0	0	0	9	
Shrubland	6	2	0	0	190	11	0	1	
Thicket	6	0	0	0	16	256	0	7	
Water	0	0	0	0	0	0	193	0	
Woodland	0	0	0	3	0	9	0	218	

Overall Statistics:

Accuracy:	0.9479
95% CI:	(0.9367, 0.9576)
No Information Rate:	0.1798
P-Value:	< 2.2e-16
Kappa:	0.9395
McNemar's Test P-Value:	NA

Statistics per land cover class:

	Bramble	Grassland	Ground	Plantation	Shrubland	Thicket	Water	Woodland
Sensitivity	0.71622	0.9833	1	0.9909	0.8636	0.9275	1	0.9237
Specificity	0.9966	0.9875	1	0.994	0.9877	0.9815	1	0.9925
Pos Pred Value	0.89831	0.9219	1	0.9733	0.9048	0.8982	1	0.9478
Neg Pred Value	0.98822	0.9975	1	9.98E-01	0.9816	0.9871	1	0.9888
Prevalence	0.0402	0.1304	0.1472	0.1798	0.1195	0.1499	0.1048	0.1282
Detection Rate	0.02879	0.1282	0.1472	0.1782	0.1032	0.1391	0.1048	0.1184
Detection Prevalence	0.03205	0.1391	0.1472	0.1831	0.1141	0.1548	0.1048	0.1249
Balanced Accuracy	0.85641	0.9854	1	0.9925	0.9256	0.9545	1	0.9581

Appendix S4.3

Table S4.3.1 Table showing the strength of spearman rank correlation between the Random Forest (RF) and Support Vector Machines (SVM) algorithms used during stacked species distribution modelling for the overall, Caelifera, and Ensifera grasshopper assemblages, as well as for the different conservation-priority species groups (Low - High).

Model	RF cor SVM
Overall	0.831
Low	0.831
Intermediate	0.829
High	0.796
Caelifera	0.815
Ensifera	0.801

Table S4.3.2 Evaluation metrics for stacked species distribution modelling for the overall, Caelifera, and Ensifera grasshopper assemblages, as well as for the different conservation-priority species groups (Low - High). Spp rich error = species richness error (difference between predicted and observed species richness), Specificity = assemblage specificity (proportion of true negatives), Sensitivity = assemblage sensitivity (proportion of true positives), and Jaccard = Jaccard index (community similarity).

Model	Spp rich error	Specificity	Sensitivity	Jaccard
Overall	18.59 (± 9.33)	0.32 (± 0.20)	0.70 (± 0.22)	0.29 (± 0.11)
Low	8.78 (± 5.78)	0.33 (± 0.23)	0.77 (± 0.21)	0.34 (± 0.13)
Intermediate	5.36 (± 3.58)	0.38 (± 0.22)	0.73 (± 0.25)	0.28 (± 0.12)
High	2.29 (± 1.49)	0.36 (± 0.40)	1 (± 0)	0.46 (± 0.30)
Caelifera	15.53 (± 7.91)	0.28 (± 0.18)	0.73 (± 0.25)	0.29 (± 0.12)
Ensifera	4.31 (± 1.83)	0.31 (± 0.32)	0.92 (± 0.18)	0.42 (± 0.23)

Table S4.3.3 Relative contribution of environmental variables used in stacked species distribution modelling to predict suitable habitat for the overall, Caelifera, and Ensifera grasshopper assemblage, as well as the different conservation-priority species groups (Low - High). NDVI = Normalised Difference Vegetation Index, Dist stream = distance to stream, Dist plan = distance to plantation edge, Fire hist = fire history.

Model	NDVI	Land cover	Dist stream	Aspect	Dist plan	Elevation	Fire hist
Overall	13.15 (±4.84)	10.82 (±5.19)	18.42 (±7.12)	11.16 (±5.72)	14.62 (±4.99)	17.70 (±9.53)	14.13 (±6.33)
Low	12.43 (±5.18)	10.51 (±4.19)	18.50 (±7.09)	10.10 (±3.66)	15.80 (±5.73)	16.17 (±10.00)	16.48 (±6.73)
Intermediate	12.36 (±5.21)	10.91 (6.08)	18.09 (±7.81)	12.78 (±5.39)	14.91 (±7.96)	17.38 (±11.06)	13.57 (±4.69)
High	13.14 (±2.17)	10.75 (±2.84)	18.40 (±6.41)	16.05 (±5.97)	11.96 (±2.11)	18.55 (±5.09)	11.15 (±3.06)
Caelifera	12.85 (±4.40)	11.11 (±4.88)	18.04 (±8.25)	10.54 (±4.94)	14.93 (±5.57)	16.43 (±7.86)	16.09 (±7.23)
Ensifera	10.86 (±2.52)	10.09 (±5.23)	18.27 (±7.48)	10.72 (±4.34)	20.07 (±6.60)	18.48 (±6.58)	11.52 (±3.69)