Patterns of bird community structure in relation to land-use driven habitat changes in the arid grasslands of Thar Desert

Dissertation submitted to Saurashtra University, Rajkot
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Master’s Degree in Wildlife Science

By

Varun S Kher

Supervisors

Sutirtha Dutta, PhD

Navendu Page, PhD

Malvika Onial, PhD

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भारतीय वन्यजीव संस्थान
Wildlife Institute of India

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CERTIFICATE

This is to certify that **Mr. Varun Kher** has carried out an original piece of research in partial fulfilment of Master's Degree in Wildlife Science from the Saurashtra University, Rajkot, Gujarat. The topic of his dissertation is **"Patterns of bird community structure in relation to land-use driven habitat changes in the arid grasslands of Thar Desert"**. The study was carried out under our supervision from December 2018 to June 2019. We hereby certify that this work has not been submitted for any degree to any university

Sutirtha Dutta, PhD
(Supervisor)
Scientist 'D',
Wildlife Institute of India,
Chandrabani, Dehradun-01.

Navendu Page, PhD
(Co-supervisor)
Scientist 'C',
Wildlife Institute of India,
Chandrabani, Dehradun-01

Malvika Onial

Malvika Onial, PhD
(Co-supervisor)
Scientist 'D',
Wildlife Institute of India,
Chandrabani, Dehradun-01

Date: 30th June, 2019
Place: Dehradun

पत्रपेटी सं० 18, चन्द्रबनी, देहरादून – 248 001, उत्तराखण्ड, भारत
Post Box No. 18, Chandrabani, Dehradun - 248 001, Uttarakhand, INDIA
ई.पी.ए.बी.एक्स : +91-135-2640114, 2640115, 2646100 फैक्स : 0135-2640117
EPABX : +91-135-2640114, 2640115, 2646100 Fax : 0135-2640117
ई-मेल/E-mail : wii@wii.gov.in वेब/Website : www.wii.gov.in

1. Executive Summary

1. The Indian Thar desert has seen a massive loss of grassland habitat in the last few decades. The main driver of this habitat loss has been the large-scale change in land-use from pastoralism to agriculture, leading to expansion of cultivated land over grasslands. This expansion, further compounded by a simultaneous rise in livestock population has drastically increased grazing pressure on the remaining rangelands. To complicate things further, irrigation schemes (notably the Indira Gandhi Canal) have led to intensification of agriculture in many areas. Protected area network in this landscape is minimal and ineffective, making the multiple-use agro-pastoral landscapes very important for conservation of wildlife. The largest protected area in the landscape – the "DNP WLS" – is also a multiple-use landscape and home to more than 50k people whose livelihood is tied to the federal mandate of conservation in the sanctuary. Understanding the impact of land use change on native biodiversity is thus very important for conservation of biodiversity in this critical habitat. In this context, my study tries to find effects of land-use change on community structure of birds in the arid grassland of Jaisalmer district in the Thar Desert.
2. Understanding ecology or distribution and abundance of species is incomplete without holistically understanding the patterns and processes occurring at the community level. To this end, I explored the patterns of bird community structure in the Thar Desert and tried to understand how these properties change with land-use driven habitat change, by comparing fundamental properties of biological communities like species richness, abundance and composition. Additionally, I tried to find out potential habitat correlates of these properties, so as to shed some light on the processes that might be driving community assembly in response to land-use change.
3. Bird community structure: My results indicate that local-scale species richness, abundance and composition did not differ significantly between protected grasslands, rangelands and extensive rain-fed croplands, during either of the seasons. However, intensive irrigated croplands had a notably different community structure with higher species richness and abundance, during both winter and summer. The change is community structure of intensive croplands was influenced

by the change in native species along with ingression of newly colonised species. Most of the newly colonised species were restricted to areas with intensive agriculture where their survival was potentially facilitated by the new microhabitats created by irrigation and associated changes (Rahmani & Soni, 1997).

4. Regional species pool: Intensive agriculture increased the overall species of birds in the region by sustaining newly colonised bird species; while the number of native species in this pool was only marginally lower than protected grasslands and comparable to all the other land-uses in both the seasons. Considering both the seasons together, protected grasslands had the highest naïve and estimated number of native species while the naïve and estimated number of native species in other three land-uses – Rangelands, extensive croplands and intensive croplands – was only marginally lower. This signifies that most species found in the region can use the entire gradient of land-use types at their current levels of intensification. Although this result by itself does not indicate that, all land-use types can sustain all the native species.
5. Seasonality of patterns: In winter, protected grasslands, rangelands and extensive croplands had similar bird communities, which together were significantly different from the communities in intensive croplands. The same pattern repeated in summer, but the magnitude of difference between bird communities in intensive agriculture and other land-uses was much lower. This pattern was correlated to the pattern shown by vegetation structure of intensive agriculture, which also became more similar to other land-uses after harvesting of crops in the summer. This potentially suggests that bird communities are influenced by vegetation structure and areas with similar vegetation structure would have similar bird communities.
6. Habitat correlates of species richness and bird community composition: In both the seasons, species richness was positively associated with the foliar volume of woody vegetation and negatively associated with forb volume (which in turn was negatively correlated with grass volume). During winter, species richness was positively related to crop volume and during summer, with compositional diversity of vegetation. Community composition like richness was influenced significantly by woody plant foliar biomass in both the seasons. Crop volume also had a significant influence on

bird communities during both winter and summer, whereas grass volume was significantly influential only in winters.

7. Conservation implications: This study corroborates many others in indicating that low-impact land-uses are important secondary habitats for conservation of grassland species (Dutta & Jhala, 2014; Wright, Lake, & Dolman, 2012). The inferences further support the commonly advocated approach of conserving grasslands at a landscape scale by strategically placing them as mosaics of low-impact agro pastoral land-use with small protected areas embedded within them (Dutta & Jhala, 2014; Dutta, Rahmani, & Jhala, 2011; Singh et al., 2006).

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2. Introduction

2.1 Community ecology as a conceptual framework to assess effects of land use change on biodiversity

Understanding the effects of anthropogenic land use on the distribution and abundance of species at different scales of organisation is an important aspect of modern ecological research (Gaston, Blackburn, & Klein Goldewijk, 2003; Laurance, Sayer, & Cassman, 2014; Newbold et al., 2015). Achieving this understanding by studying species individually is an arduous undertaking, which is further complicated by the fact that species do not live in isolation, and are influenced both by their abiotic environment and by biotic interactions (Krebs, 1972; Vellend, 2010). Thus, understanding patterns, processes and mechanisms at the scale of "biological communities" is ubiquitous to holistically understand the impacts of anthropogenic activities on biodiversity (Green, Cornell, Scharlemann, & Balmford, 2005; Lima, Dallimer, Atkinson, & Barlow, 2013; McGill, Dornelas, Gotelli, & Magurran, 2015). The body of science dealing with this subject - community ecology - aims to gain integrative understanding of how biotic and abiotic factors mould local species pools at different spatiotemporal scales (Vellend, 2010). This involves scientific enquiry on two fronts viz. a) Descriptive – involving exploration and analysis of patterns and b) Functional – dealing with the deterministic and stochastic processes that lead to a particular pattern.

The field of community ecology has often been termed a "mess" due to its overwhelming complexity and fine-scale contingency of patterns (Lawton, 2007). Moreover, the functional component of community ecology has lacked a generalised universal theory to explain how community assembly takes place (Lawton, 2007; Vellend, 2010). However, with recent progress in empirical and experimental investigations, advancements in theoretical underpinnings and modern statistical methods, community ecologists have converged on a synthesis that acknowledges the role of both deterministic and stochastic processes in driving community assembly (Vellend, 2010). These processes include deterministic processes of speciation, dispersal and selection, which occur due to abiotic environmental filtering and biotic interactions; along with stochastic processes like ecological drift and neutrality. All these forces working at different scales, interact at different hierarchical levels to give rise to individual local communities.

As proposed by Zobel (1997) and explained by Ovaskainen (2017), “the assembly processes can be envisaged as ‘filters’ operating at different scales. In this scheme, the ‘global species pool consists of all existing species, the ‘regional pool’ of all species able to colonise a given area, and the ‘local species pool’ of the set of species found at the finest scale considered (Cornell & Harrison 2014). Clearly, the species pools found at finer scales are filtered also by assembly processes acting at broader scales (Cornell & Lawton 1992). Of these hierarchical sieves, ‘environmental filters’ correspond to those abiotic factors which prevent the establishment or persistence of species in local communities (Kraft et al. 2015) and thus outline the fundamental niche of a species. ‘Biotic filters’ refer to interspecific and intraspecific competitive and facilitative interactions that determine the set of species in local communities (Wisz et al. 2013; Garnier et al. 2016) and thus determine their realised niches. These two types of forces may interact, as environmental filters may modify biotic interactions (e.g. Callaway & Walker 1997). Beyond the deterministic processes selecting species from regional to local scales, stochastic processes create additional variation in the local communities. These processes – related to colonisation, extinction, ecological drift and environmental stochasticity – generate divergence among communities occupying identical environments (Chase & Myers 2011). The responses of the species to abiotic and biotic filters vary depending on species-specific characteristics known as the response traits, including e.g. their dispersal propensity and competitive abilities (Lavorel & Garnier 2002) (Figure 1). Thus, they will determine what species reach and colonise given areas, and what species succeed in securing adequate resources (McGill et al. 2006; Bolnick et al. 2011).” This elaborate process of community assembly finally results in discrete groups of organisms that we call biological communities - defined as ‘a group of organisms representing multiple species living in a specified place and time’ and characterised by the number, identity, traits and abundances of species.

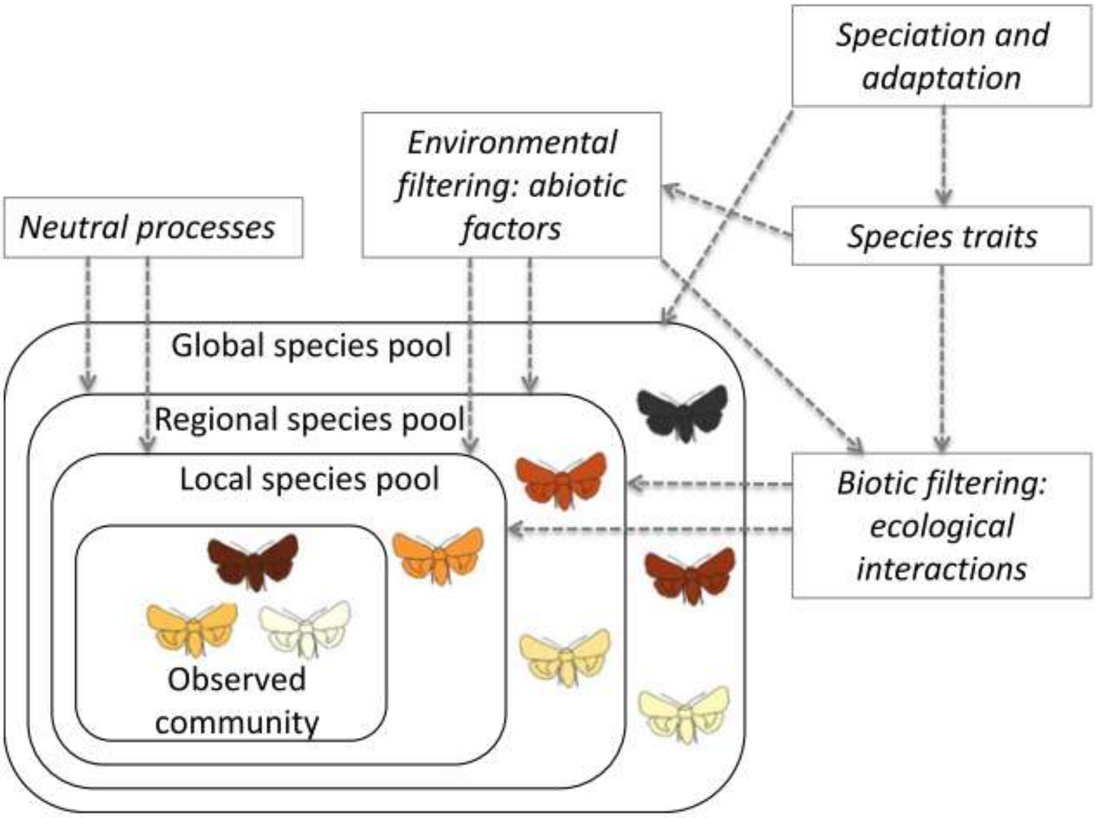


Figure 1: Conceptual synthesis of community ecology as published in Ovaskainen, Roy, Fox, & Anderson (2016*)*

The primary (biotic) filter driving the process of community assembly in animals is the local-scale habitat. The habitat can be visualised as an n-dimensional niche space with every axis being a particular resource. This niche space is then divided into realised niches of many animal species and individuals, in proportions decided by various deterministic (eg. Competition) and stochastic (eg. Ecological drift) processes, which are further influenced by response traits of the potentially interacting organisms. Thus, any change in the niche space or habitat results in a change in the process of community assembly and changes various parameters of the community. Different land-use types alter the primary habitat in different ways, thus changing the niche space in a contingent manner. Considering this, the realised magnitude of impact caused by a land-use change on functioning of a particular ecosystem can be measured by assessing the effects of it on various biological communities.

Bird communities are perfectly suited for assessing the magnitude of impact caused by different types and intensities of land-use as they are sensitive to subtle changes in habitat and show a perceivable difference with change in habitat components (Newbold et al., 2015). Additionally, bird communities contain numerous species having unique ecological traits and exhibit diverse response traits when exposed to a particular change (Newbold et al., 2012). Bird communities are hence one of the best-studied groups among all animal communities and have been commonly used as a model groups to understand impacts of land use change on biodiversity (Gaston et al., 2003; Green et al., 2005; López-Ricaurte, Edwards, Romero-Rodríguez, & Gilroy, 2017; Phalan, Onial, Balmford, & Green, 2011).

2.2 Two land-uses that changed the world

Domestication of plants and animals for producing food marks a remarkable step in human history, as it gave man the ability to engineer natural ecosystems (Ellis & Ramankutty, 2008). Today, anthropomorphically engineered ecosystems cover more than 50% of the terrestrial surface and are constantly expanding (Ellis, 2011; Ellis & Ramankutty, 2008). A vast majority of these human-dominated systems are under croplands and rangelands, with a smaller portion coming from pastures, settlements and miscellaneous land-uses (Ellis, 2011; Jeuken, van den Berg, Alkemade, de Leeuw, & Reid, 2012; Laurance, 2007). With the expected populations rise, the expansion and intensification of production land-uses for food production are considered inevitable (Laurance et al., 2014; Tilman, Cassman, Matson, Naylor, & Polasky, 2002). The expansion is expected to be the highest in developing countries, which are expected to hold half of the globe's population by 2050 (Laurance et al., 2014). Further, developing countries of the tropics hold a disproportional 78% of the world's biodiversity, while feeding more than half of the world's hungry population (Barlow et al., 2018; Laurance et al., 2014).

Contemporary food security concerns have led to rapid conversion of primary habitats into agriculture over the last few decades. Grasslands and savannahs which cover around 20% of the world's terrestrial surface have been the frontiers of this crisis due to their fertility and relative ease of clearing. Conversion to croplands changes the habitat drastically, first due to frontier clearing and then by changing the microhabitat through various means (DeFries et al., 2005). Further intensification of croplands causes more frontier clearing and large-scale homogenization of habitat. Farming practices associated with agricultural intensification such as pesticide usage deplete food for birds, thereby degrading the habitat quality. Similar to croplands, livestock grazing also has a massive footprint on natural habitats and affects more than 25% of the globe. Unnatural levels of grazing degrade the habitat by causing changes in productivity, biomass, stand structure and community composition.

In India, grasslands and savannahs have been the largest recipients of land-use change since the green revolution of the 1970s and their extent has drastically reduced since then (Tian, Banger, Bo, & Dadhwal, 2014). Most grasslands have been converted to croplands during this time and an ever-increasing number of domestic cattle now heavily grazes the remaining few (Singh et al., 2006). Semi-arid and arid grasslands now remain only in certain pockets of India, with the largest expanse being in the arid zone of Thar Desert and Kutch (Rawat, Adhikari, & (Eds.), 2015). Agriculture expansion and intensification, compounded by grazing intensification are progressively threatening these grasslands as well (Dutta et al., 2017; Singh et al., 2006). However, quantification of the impact of such agricultural expansion and intensification on bird communities is scanty in India.

2.3 Reconciling wildlife conservation with human livelihoods

Biodiversity conservation and food production are generally considered contradictory mandates. Efficient food production through intensive agriculture is often very detrimental to wildlife whereas low-intensity and wildlife-friendly agriculture don’t always produce enough food (DeFries et al., 2005). From the wildlife perspective, protected areas hold significantly more wildlife but are inadequate in their expanse whereas the more expansive human-dominated areas are mostly not suitable for a bulk of wildlife. These mutual contradictions often invoke the academic debate on how to sustainably reconcile biodiversity conservation with adequate food production (Fischer et al., 2008; Green et al., 2005).

In India, 86% of farmers are marginal land-owners with less than 2ha of land and more than 60% live on rain-fed farming. This extensive form of agriculture produces bulk of India’s food and also sustains a large number of domestic livestock. In the drier regions, livestock forms the backbone of the rural economy and pastoralism on rangelands and community-owned grasslands is a major livelihood. This human-dominated rural countryside is also the interface where wildlife and humans often co-occur. On the other hand, protected areas cover only 4% of India’s terrestrial area and are considered the considered sentinels of wildlife conservation. Most of them are less than 100 sq.km and inadequate to conserve biodiversity by themselves. In Western India, where most of India's last remaining dry grasslands occur, these social and ecological statistics are much grimmer. Landscape-scale conservation is thus the widely advocated strategy for these systems (Dutta et al., 2011). Such a strategy must invariably assess the effects of land-uses on biological communities, and find solutions to reconcile food production and biodiversity conservation concerns.

2.4 The newly tame desert

The Thar Desert lying towards the north-western border of India is an important biogeographic region of India and contains large stretches of arid grasslands home to variety open-habitat flora and fauna. The region is especially important for birdlife as it marks the eastern range limit of many arid zone species while also marking the western range limit of many semi-arid species of the Indian subcontinent. At the same time, it is an important wintering ground for many Palearctic migrants and falls on two migratory flyways. Grasslands of Jaisalmer district in Thar Desert are the last remaining stronghold of critically endangered Great Indian Bustard and many other threatened and range-restricted species. The largest protected area in the region encompassing ~3000 sqkm area – Desert National Park WLS - is listed as an Important Bird Area by Birdlife International.

Till recently, these harsh grasslands of Thar Desert were sparsely populated and nomadic pastoralism was the most dominant land-use. But from 1980s, lifestyle of people took a sedentary shift and agriculture started expanding on the vast rangelands. Simultaneously human and livestock populations rose rapidly, thus increasing the pressure on land that was amply available earlier. The reduction in area available for grazing due to expansion of croplands and the simultaneous rise of livestock populations drastically increased the grazing pressure on the remaining rangelands of the region. At the same time, various irrigation schemes, notably the Indira Gandhi Canal removed the primary limiting factor on intensive agriculture, and caused large-scale intensification of croplands in the irrigated zone. Irrigation canal has also brought in forestry and agroforestry plantations for combating desertification and this has created new microhabitats in irrigated agricultural landscape.

As of today, majority of the landscape is under extensive rain-fed agriculture which is left fallow in the dry season and in drought years. The remaining area is primarily used as rangelands and is grazed intensively by domestic livestock, which includes cattle, goat, sheep and free-ranging camel. The irrigated zones of the Indira Gandhi Canal and some low-lying areas are under intensive year-round cultivation. Hunting, agriculture expansion and intensification, overgrazing along with expansion of surface water, energy/power and mining projects are considered the largest threat to the wildlife of the region (Dutta et al., 2017). However, very little scientific enquiry has gone into assessing the effects of these threats on native wildlife.

2.5 Studying bird communities in the contemporary land use scenario of the Thar Desert

Like all grasslands ecosystems of India, Thar Desert is human-dominated and largely unprotected landscape. Even the largest protected area in the region, the Desert National Park Wildlife Sanctuary, is home to more than 50 thousand people and has only ~200 sq.km under strict control of the Forest Department. Thus, to effectively conserve biodiversity in the larger landscape, it is essential to find out sustainable thresholds of anthropogenic land-use that can sustain wildlife while achieving other mandates of the greater multiple-use landscape (Dutta & Jhala, 2014). To do so, it is necessary to understand the impact caused by each land-use on native biodiversity. It is also necessary to scientifically investigate both traditional and recently introduced land-use regimes for their ecological value and understand the trade-offs between livelihoods and conservation holistically. Information on these lines will potentially aide policymakers to manage land uses in the area sustainably with the help of strategies that achieve sustainability through optimisation of food security, social equity and ecological protection.

In this context, my study looks at how bird communities change with the intensifying progression of land-use in Thar Desert. To understand this, I compared different parameters of bird community structure like species richness, abundance and composition across different land-use types of the region and assessed the relative impact that progression of land-use has on native bird communities. I further looked at the potential drivers of these community patterns with the perspective of finding potential management solutions to maximise native bird diversity in the human-dominated landscape.

2.6 Aims and objectives:

2.6.1 Objectives:

1. To compare bird community parameters between different land-use types of the region.
2. To find potential habitat drivers of local-scale species richness, abundance and community composition.

2.6.2 Questions:

1. How does local species richness, abundance and community composition vary across different land-use types?
2. What effect does land use have on regional species pool of birds?
3. What are the habitat correlates of bird community parameters like species richness, abundance and composition?

3. Literature Review

3.1 Birds in croplands and rangelands

Conversion of natural habitats by crop-based farming and livestock grazing is considered the most voluminous land-use change on the globe (Laurance et al., 2014). Croplands cover more than 25% of global terrestrial area today and are constantly expanding all around the world, resulting in tremendous change of primary habitats (Defries, Foley, & Asner, 2004). In line with the magnitude of change, a lot of research has gone into documenting the effects of agricultural expansion and intensification on native biodiversity. Studies dealing with this subject have focused on a variety of taxa including birds (Kamp et al., 2015; Mendenhall, Sekercioglu, Brenes, Ehrlich, & Daily, 2011; Phalan et al., 2011), plants (Egan & Mortensen, 2012; Kleijn et al., 2012; Phalan et al., 2011), mammals (Decarre, 2015; MacDonald, Tattersall, Service, Firbank, & Feber, 2007) and insects (Hodgson, Kunin, Thomas, Benton, & Gabriel, 2010). In this spectrum, effects of land-use on birds have been assessed in most detail and these studies have been synthesized in numerous reviews and meta-analyses at both regional (Chamberlain, Fuller, Bunce, Duckworth, & Shrubb, 2000; Donald, Green, & Heath, 2001) and global scales (Gaston et al., 2003; Newbold et al., 2012). The literature in this field is mainly dominated by studies conducted in European or North-America, where agricultural land-use change has caused precipitous declines of birds in the last few years (Chamberlain et al., 2000). Barring a few recent studies, systematic research from other regions of the world is largely lacking (Decarre, 2015; Elsen, Kalyanaraman, Ramesh, & Wilcove, 2017; Kamp, Urazaliev, Donald, & Hölzel, 2011; Karanth et al., 2016; Mendenhall et al., 2011; Phalan et al., 2011).

A meta-analysis by Newbold et al. (2012) showed that intensification of land-use change reduces the species richness, probability of occurrence and abundance of forest birds all across the world (Newbold et al., 2012). Another study estimates that global bird populations have declined by 20-25% due to the conversion of primary habitats to other land-uses, mainly agriculture (Gaston et al., 2003). A global synthesis also suggests that different ecological groups respond differently to land-use change, and in forests, species that are large, long-lived, non-migratory, insectivorous, frugivorous or habitat specialist show the highest declines (Newbold et al., 2012). While most studies have reported negative effects of agriculture land use on bird communities and populations, a few studies have also documented positive impacts of these changes on a select set of species (Kamp et al., 2011; Wolff, Paul, Martin, & Bretagnolle, 2001).

While the importance of primary habitats for conservation of bird diversity has been rarely questioned, recent studies have shown that low-intensity land-uses like sustainably grazed pastures, agroforests, extensive organic croplands etc. can also support substantial biodiversity (Chang, Karanth, & Robbins, 2018; Karanth et al., 2016; Mendenhall et al., 2011; Wright et al., 2012). Many studies from the forested tropics have examined the conservation value of these low-impact/sustainable land-uses and have found them to be important habitats for bird conservation (M. O. Anand, Krishnaswamy, Kumar, & Bali, 2010; Bhagwat, Willis, Birks, & Whittaker, 2008; Daily, Ehrlich, & Sánchez-Azofeifa, 2001; Elsen, Ramesh, & Wilcove, 2016; Ranganathan, Daniels, Chandran, Ehrlich, & Daily, 2008). Some other studies have focused on finding the drivers of abundance and richness in production landscapes and have found that heterogeneous landscapes mimicking natural habitat structure are used extensively by many bird species (Mandyam Osuri Anand, Krishnaswamy, & Das, 2008; Benton, Vickery, & Wilson, 2003; Ranganathan et al., 2008; Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005).

Production landscapes and human-dominated agro-ecosystems have globally attracted a lot of academic attention but multiple gaps have remained in terms of regions and habitats surveyed. In the tropics, most of the studies have assessed impacts of agricultural land-use change on forested ecosystems (Chang et al., 2018; Elsen et al., 2016; Karanth et al., 2016; Mendenhall et al., 2011). Tropical grassy biomes (Parr, Gray, & Bond, 2012), which are equally threatened by land-use changes, have been sparsely surveyed so far. The intimate linkages of grassy biomes with human livelihoods, food security and biodiversity conservation necessitate studying impacts of land-use change on these underappreciated systems in greater detail (Murphy, Andersen, & Parr, 2016; Parr et al., 2012).

In India, most studies have investigated the effects of agriculture on the forested landscapes of the Western Ghats and North-east India, which are global biodiversity hotspots (Myers, Mittermeier, Mittermeier, Fonseca, & Kent, 2000). In Western Ghats, number of studies have primarily focused on assessing conservation value of landscapes modified into commodity agriculture like tea (Sreekar, Mohan, Das, Agarwal, & Vivek, 2013; Sreekar et al., 2015) and coffee plantations (M. O. Anand et al., 2010; Mandyam Osuri Anand et al., 2008; Bali, Kumar, & Krishnaswamy, 2007; Chang et al., 2018; Karanth et al., 2016). Impacts of shifting cultivation (jhum) and palm oil plantation on native biodiversity has been studied in Mizoram (Mandal & Shankar Raman, 2016; Raman, 2001). Some recent work on agroecosystems has been reported from the Greater Himalaya (Elsen et al., 2017, 2016) and the Terai belt of North India (Phalan et al., 2011). Few others have studied the biodiversity of agricultural landscapes in different contexts like man-animal conflict (Athreya, Odden, Linnell, Krishnaswamy, & Karanth, 2013; Kshettry, Vaidyanathan, & Athreya, 2017) and sustainable development (Bawa, Joseph, & Setty, 2007).

Similar to the trend across the globe, most studies have focused on birds as a model taxon followed by mammals and plants (M. O. Anand et al., 2010; Elsen et al., 2017; Mandal & Shankar Raman, 2016; Sreekar et al., 2015). There is a great disparity of research when it comes to the spatial coverage of investigation, with nearly all the systematic studies restricted to the biodiversity-rich Western-Ghats, North-Eastern forests and Himalaya. There exist no systematic studies which evaluate the impact of agricultural land-use changes on the bird communities of arid and semi-arid regions of the country. Even in the forested landscapes, most studied have focused on commodity agriculture which accounts for relatively little in terms of area under cultivation.

Like croplands, rangelands also cover over about 25% of global landmass, and in variety of forms including secondary grasslands, savannahs, woodlands, scrublands etc.(Ellis, 2011; Jeuken et al., 2012) But in contrast to agriculture, studies investigating effects of livestock grazing on biodiversity have been fewer and have mostly focused on plants (Jeuken et al., 2012; Rutherford & Powrie, 2013; Song et al., 2016; Yan & Lu, 2015) and mammals (Eccard, Walther, & Milton, 2000; Song et al., 2016), with relatively fewer studies on birds (Kamp et al., 2011). With regards to birds, available scant evidence suggests that rangelands grazed at sustainable intensities can sustain avifaunal diversity and are important habitats for grassland birds (Dutta & Jhala, 2014; Kamp et al., 2011). In spite of the large extent in which rangelands are found, studies looking at effect of livestock grazing intensification on native biodiversity (especially birds) are exceptionally few.

4. Study Area and Study Species

4.1 Location

The study was conducted over an extensive study area of 2016 sq.km, spread across an arid landscape of ca7000 sq.km (27.42 to 26.56 N, 70.89 to 70.14 E) in Thar desert of Jaisalmer district (Rajasthan) in north-western India. Jaisalmer district is located at the northwestern boundary of India and is flanked by Barmer district on the southeast and Bikaner district on the northeast. The extent of the study area was bound by two towns on its edges – 'Jaisalmer' in the West and 'Ramgarh' to the North. The southern part of the study area comprised of the Desert National Park Wildlife Sanctuary (DNP WLS henceforth). Large parts of the study area fell under the extent two proposed Thar Ecozone and Thar Biosphere Reserve. Parts of the Indira Gandhi Canal, a flagship irrigation scheme were situated towards the northwest of the study area. Close to the western edge was the sub-divisional administrative headquarter of 'Sam'. Other important villages in the study area included Bandha, Habur, Jamra, Kanoi, Mokla, Neemba, Kuchhri, Sanu, and Siambar.

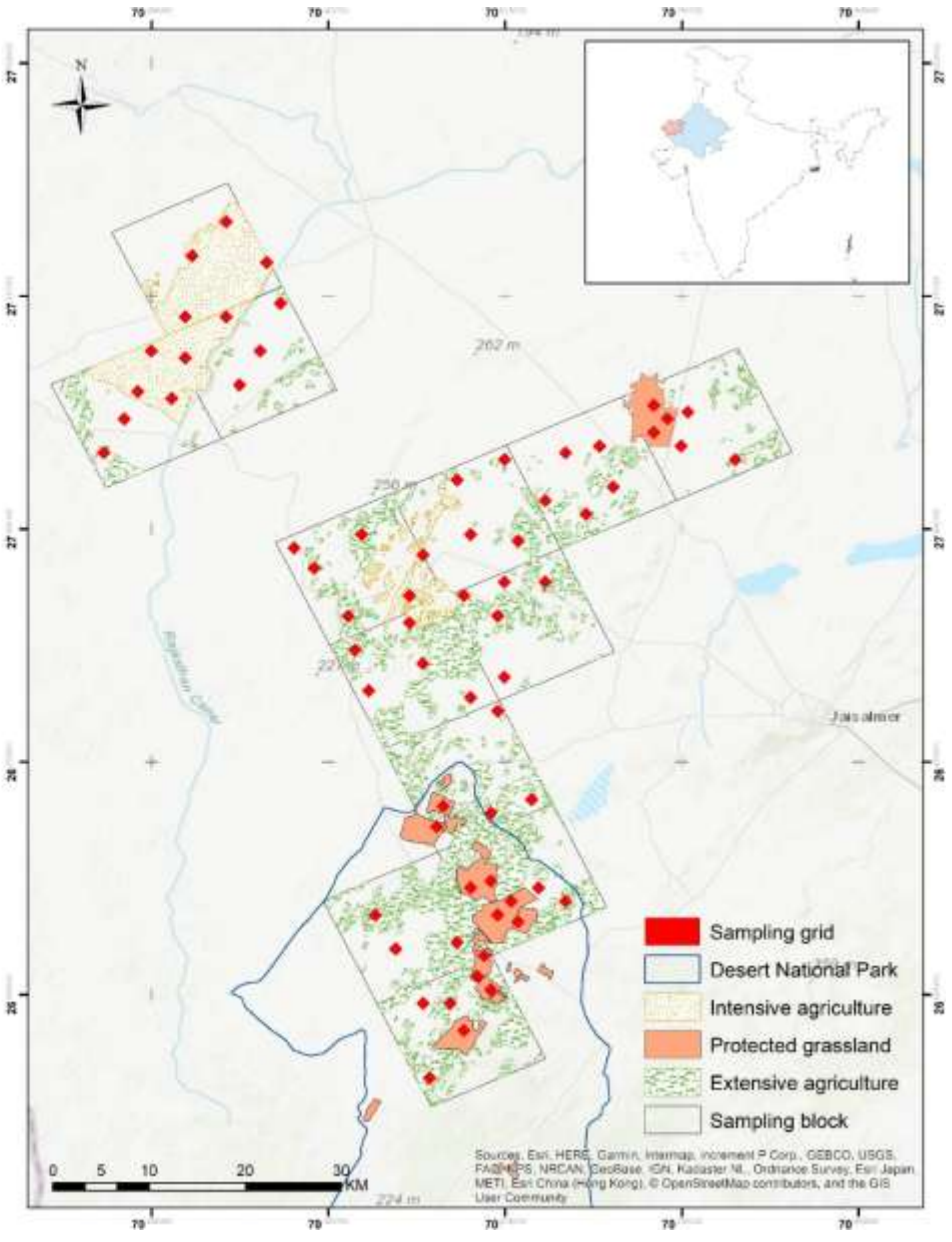
4.2 Distal features of the study area

4.2.1 Physical features

The entire desert consists of level to gently sloping plains broken by sand dunes and low barren hills. The blown sand, due to aerodynamic processes and biotic interferences, forms shifting sand dunes i.e. with the progress of time they change positions or shift from one place to another. The inter-dunal depressions are formed by wind depletion of surface soils and by dried-up beds of desert streams. Seasonal streams, locally called *'Nalas'* flow for a few days immediately after the rains. The rainwater is collected and held up in low-lying areas called *'Khadeens'* and *'Nadis'* and is then used for drinking and also for cultivation in the moist water catchments. Rocky outcrops (Locally called "Magra) are seen in a few locations.

4.2.2 Climate

The regions of Thar desert falling in the Jaisalmer district are typically characterised by an arid climate. The summers are hot and dry with temperatures reaching up to 50C, whereas winters are cold and windy with temperatures reaching as low as 0C. The daily temperature fluctuations are considerably high during all seasons with nights and early mornings being cold throughout the year. Rainfall is erratic and largely ranges between 100 and 350 mm in the Jaisalmer district. Most of the rainfall occurs during the passage of southwestern monsoon in the months of July and August. Rainfall during other times of the year is negligible. Hot winds and dust storms are a common occurrence during the summers.



Map 1: Map of study area in Jaisalmer district of Western Rajasthan, India. The map depicts the dominant land-use types in the area along with important boundaries. Please note the Rajasthan Canal running along the Western edge of the map. The uncoloured area inside the sampling blocks is a mix of rangelands, sand dunes and rocky/gravely outcrops.

4.3 Habitats and wildlife

4.3.1 Natural habitats

The natural habitat in the region is arid grasslands and savannahs mainly dominated by the grass *Lasiurus scindicus* and the tree Capparis decidua. Stabilised sand-dunes have a typical habitat dominated by *Panicum turgidum* grass and with interspersion of shrubs like *Crotalaria buhria* and *Leptadenia pyrotechnica.* Some stabilised are covered with prostrate woody forbs *Calligonum polynoides* and *Haloxylon salichornium.* The short grass layer consists of *Dactyloctenium scindicum* and *Cenchrus biflorus*. *Zizypus nummularia* is also common in many places, especially the community protected grasslands or sacred groves. The iconic *Prosopis cineraria* is found in low lying areas and inter-dunal valleys which have largely been converted to agriculture. *Calotropis procera* is another common tree which mainly grows in disturbed area. *Salvadora persica, Salvadora olenoides* and *Euphorbia sp.* are found in some rocky areas. The riverine vegetation consists of all the aforementioned trees along with some specialists like *Tamarix sp.*

The neo-biota in the desert includes the invasive *Aerva javanica* and the weedy *Dipterigyium glaucum, which* mostly grow on regenerating croplands and overgrazed areas. Additionally, forestry plantations of Acacia tortoilis and Tecomella undulata have naturalised in many places. *Prosopis juliflora*, commonly planted as a firewood tree, is seen around villages but has not invaded other areas in the desert. Other weeds like *Tephrosia purpurea* and *Cassia senna* are also potentially introduced to the area by the nomadic livestock that moves through the area.

4.3.2 Anthropogenic habitats

As large parts of the Thar Desert have been converted to croplands, there is a wide array of anthropogenic habitats available for the wildlife. This includes the croplands itself which in the low-intensity form are structurally very similar to the grasslands but devoid of grassy understory. Large trees of Prosopis cineraria and Zizypus nummularia are often seen in these extensive agricultural fields. On the other hand, intensive agriculture has brought in agro-forestry tress like *Acacia nilotica, Acacia senegal, Acacia tortilis* and *Prosopis juliflora* which create new habitat due to their dissimilarity with the native trees of the region. Forestry plantations carried out through the Desert Development program are also new anthropogenic habitats that have been created very recently.

4.3.3 Wildlife

Thar desert harbours a variety of wildlife which is important from ecological and conservation perspective. The flagship species of the landscape is the critically endangered Great Indian Bustard (Ardeotis nigriceps), whose 90% global population is restricted to the arid grasslands of Jaisalmer district. Notable mammal species in the region include rodent Indian desert jird *Meriones hurrianae*, ungulates like chinkara *Gazella bennettii*, nilgai *Boselaphus tragocamelus* and wild pig *Sus scrofa*, and carnivores like the Desert fox *Vulpes vulpes pusilla*, Indian fox *Vulpes bengalensis*, desert cat *Felis sylvestris ornata.* The herpetofauna is represented by a wide range of arid species, notably the Desert Monitor *Varanus griesius,* Persian Dwarf-Gecko *Microgecko persicus,* Saw-scaled viper *Echis carinatus sochureki,* Spiny-tailed lizard *Saara hardwickei etc.*

4.4 Study species

The Indian Thar desert is the eastern boundary of the extensive arid tract comprising the Sahara-Sindian Desert complex of Northern Africa and Western Asia. Unsurprisingly, the resident avifauna of the Indian Thar desert is very similar to the avifauna of these Afro-Asian deserts. It is also the easternmost range limit for many of these desert species from the extensive Afro-Asian arid region (eg. Black-crowned Sparrow-lark, White-eared bulbul etc.). At the same time, it forms the penultimate western range limit of some birds from the semi-arid regions of the Indian subcontinent (Eg. Great-Indian Bustard, Rufous-fronted Prinia etc.). This area is also an important wintering ground for large number of migratory grassland species (eg. Desert Wheatear, Desert Warbler etc.) especially from Eurasia; and also a critical stopover site for passage migrants using the Central Asian and East Asia-East Africa flyway (eg. Rufous-tailed scrub robin, Black-headed bunting etc.). It is an important nesting ground for many raptors such as Tawny Eagle *Aquilla rapax,* Red-headed vulture *S*arcogyps calvus, Laggar Falcon *Falco jugger etc.*

With the advent of Indira Gandhi Canal or the Rajasthan Canal, new species from neighbouring regions have colonised into the erstwhile inhospitable desert (Rahmani & Soni, 1997). These species include forest/woodland generalists like Jungle Babbler *Turdoides striatus*, White-browed Fantail *Rhipidura aureola*, Asian Paradise Flycatcher *Terpsiphone paradise* etc. and wetland birds like White-throated Kingfisher *Halcyon smyrnensis,* Common Sandpiper Actitis hypoleucos etc.

5. Methods

This study was aimed at understanding the patterns of bird community structure in the Thar Desert, with special emphasis on effects of increasing land use change. To achieve this, community structure was explored on three dimensions - species richness, abundance and composition. Further, to understand what factors led to the observed patterns, bird community parameters were tested against various ecologically meaningful environmental variables. Data on environmental variables was collected by vegetation sampling. All this information was analysed using appropriate analytical techniques to understand the patterns of and factors affecting community assembly of local bird species.

5.1 Selection of study area and reconnaissance

To understand the effects of land-use on dry grasslands, it was necessary to select a study area which had a gradient of land-use in close proximity to a federally regulated near-natural control area. After a thorough review of literature to find such sites, the following sites were shortlisted: 1. Naliya Grasslands and 2. Banni Grasslands of Gujrat, 3. Bustard sanctuaries of Nannaj, Rehekuri, Karmala in Maharashtra, 4. Desert National Park and environs, Rajasthan. Among these Nannaj, Rehekuri and Karmala were discarded due to absence of near-natural environments in the form of relatively large enclosures which were critical for the study. Banni grasslands were discarded as they are sea inundated and have little agricultural intensification, thus reducing the land-use-gradient that could be examined. Between Desert National Park and Naliya grasslands, the former was selected as it had larger homogenous area with a well-defined gradient of land-use. Moreover, DNP had many regulated enclosures which could provide the study with near-natural control plots. All this coupled with logistic feasibility owing to ongoing research projects in Desert National Park and its environs in Jaisalmer district rendered it to be selected as the Study Area.

5.1.1 Reconnaissance

A reconnaissance survey was carried out in September 2019 to ascertain the suitability of the study area to meet the objectives. Certain changes were made to the original objectives based on observations during this survey. Bird species and abundances were recorded to decide suitable sampling method and design. Discrete land-use strata were visually determined and then compared with remotely sensed data, to get a better picture of the extensive study area. The extent of the study area was roughly decided after the reconnaissance survey.

5.2 Study Design

5.2.1 Delineation of sampling strata

The 7000 sq.km extent of the study area was divided into 50 blocks of 144 sq. km. each, of which 14 blocks amounting to an area of 2206 sq.km were further selected as the extensive study area. The selection criteria for these blocks was mainly based on logistic feasibility and accessibility, but conscious effort was made to choose blocks that broadly cover different habitats so that maximum heterogeneity of the landscape is covered in the sampling. The chosen blocks covered all the habitat and land-use types of the region and were a good representation of the study area as well as much of the Thar desert Landscape.

The selected extensive study area was further divided into 1 sq. km. cells, the scale at which further sampling was done. The habitat and land-use types in the study area were largely homogenous at this scale and the smallest homogenous patches were also of approximately this size. From this set, cells containing non-arable land – settlements, forestry plantations, rocky/gravely barren land and shifting dunes - were removed. Additionally, cells with roads and canals were also excluded to reduce confounding factors. After these exclusions, the remaining suitable sampling area was stratified based on dominant land-use type at the at 1 sq.km scale. Boundaries of the protected areas and irrigated lands were obtained from government records. The remaining area was classified using remotely sensed land cover data and visual inspection of satellite imagery. The resultant classified imagery was further validated by inspection of satellite imagery. This elaborate process of classification resulted in delineation of four dominant land-use categories in the study area, which are mentioned below along with brief descriptions –

1. Protected grasslands: Protected grasslands in the study area were confined to the graze-proof enclosures built up by the Desert National Park and Desert Development Program of the Forest Department. Grazing was ‘regulated’ inside these areas and agriculture was strictly prohibited. The grazing pressure in these areas was much lower than the rangelands even during prevalent drought conditions. Additionally, no lopping was allowed inside these areas and illegal hunting was unlikely due to

strict protection. These enclosures were built at different times and had different histories of management. Many of these enclosures were reseeded with perennial grass *Lasiurus scindicus* to aid recovery of grassland after enclosing.

2. Non-irrigated croplands: Most parts of the Thar desert are not irrigated and receive erratic rainfall, thus limiting farming to the monsoon or the 'Kharif' cropping season, that too in years of good rainfall. The land is left fallow after cropping and allowed to regenerate through the dry months. Grazing is also allowed on these lands after harvest and during the fallow period. Most fields lie fallow during the years of erratic and low rainfall which is a common occurrence in this region. All the non-intensive croplands in the study area were fallow at the time of sampling. In majority of cases, the last crop cultivated on these non-irrigated farmlands was Guar (*Cyamopsis tetragonoloba)*, which is a cash crop that has been recently introduced to this region. Some fields were tilled for the upcoming monsoon whereas some other were regenerating after remaining fallow for more than a year.
3. Rangelands or Grazing Lands: Rangelands were primarily used for grazing domestic livestock –goat, sheep, cattle and camel and for collection of firewood and timber for household needs. They did not have any recent history of farming and were not subjected to any management intervention concerning the habitat. These areas differed from the conserved grasslands due to their much high grazing pressure and human disturbance. Most of these areas were highly stocked with domestic livestock and were often grazed to the ground. Goat, sheep, cow and camel were the major livestock animals with the first two being more numerous. These areas were also used for grazing by wild herbivores – Chinkara (*Gazzella bennetti*), Nilgai (*Boselaphus tragocamelus*) and Desert Jird (*Meriones hurrianae*).
4. Irrigated croplands: This category included croplands irrigated either by canal water or through tube-wells. Most of this land was under cultivation during the winter, and the dominant crops were Bengal gram (*Cicer arietinum*), jeera (*Cuminum cyminum)* and mustard (*Brassica sp.)*. A distinct feature of irrigated croplands was presence of hedges with introduced trees like *Acacia nilotica*, *Acacia senegal*, *Prosopis juliflora* and *Dalbergia sisoo*. In most cases, native vegetation was completely cleared or left only on the hedges. A majority of these areas were fallow during the summer, after the harvest of 'rabi' crops in April.

5.2.2 Transect placement

Seventy line transects of 1km length were placed across the study area to conduct bird and vegetation surveys. A total of 5 (±1) transects were laid randomly in each of the 14 blocks (144 sq.km), with proportional coverage given to each land-use type within the block. This approach of proportional randomization within the block resulted in placing 26 transects in rain-fed croplands, 18 in rangelands, 15 in protected grasslands and 9 in irrigated croplands. All transects were oriented in a North-South direction and were placed at least 3km apart from each other (1 km in case of protected grasslands) to maintain spatial independence.

Bird transects were conducted in two seasons – winter (December 25 to February 20), when the migrants were present and summer (21 March to 21 April), when many resident species started breeding. All transects were repeated three times in every season to achieve adequate temporal replication. Habitat sampling for trees and shrubs was conducted only once for all transects whereas the understory was surveyed twice – once in every season since the latter underwent significant seasonal variation.

5.3 Field methods

5.3.1 Bird Surveys

All perched birds present along the 1km line transects and following readings of each sighting were recorded - species, count of individuals, distance of bird from the observer, angle of the bird with respect to the transect and position of observer. All the positions were realised using a handheld GPS device (Garmin etrex 30), while distances were calculated using a laser rangefinder (Yukon HRS300). Angles were measured using a handheld Sunnto compass or a compass enabled mobile handset. Bird surveys were conducted from dawn until four hours after sunrise in the morning and during last two hours before sunset in the evening. These sampling times coincided with the time when the birds were most active. Predefined line transects were walked at a uniform slow speed of approximately 2km/hr (30-40 minutes per 1km transect), and all birds were recognized on field using a binocular (Nikon Monarch 8x42). The birds that could not be identified on field were photographed and identified later with the help of field guides – Birds of Indian subcontinent, Handbook of the birds of the world, BNHS Salim Ali. Clements Checklist was followed for names and taxonomy. Detection covariates like weather conditions, time of transect and name of observer(s) were noted during each replicate.

5.3.3 Vegetation Surveys

Vegetation sampling was carried out on all 70 line transects to assess the structural and floristic composition of vegetation that might have an influence on the avifauna. Five rectangular belt transect were laid perpendicular to the main line, starting at 100m and then at an interval of every 200 m. The belt-transect had dimensions of 100 × 25 m on either side of the line making it a rectangular plot of 1 ha (200 × 10 m). This plot was used for recording trees, which were defined as plants with GBH greater than 30cm and height more than 2m. All the trees were identified and recorded along with their GBH, height, diameter of the crown and canopy start height (Sutherland, 2006). The GBH was rounded off to the closest multiple of 5cm for every stem, while tree height, diameter of crown and canopy start height was rounded off to the closest multiple of 10cm. Shrubs and forbs were counted on a nested 200 x 10 m plot located at the centre of aforementioned 200 x 50 m tree plot. For every shrub, the highest diameter and dominant height were recorded along with the name of the species. Grasses were sampled by laying 1 x 1 m transect at four predefined locations on the central axis of the tree plot. To surrogate grass biomass, I recorded the height and percentage cover of grass inside the 1x1m quadrat. Some grasses were identified only till the genus level due to absence of distinct identification features in the phonological stage prevalent during sampling. Other habitat variables like type of substrate, availability of surface water and anthropogenic disturbance were noted down for every transect. In total, an effective area of 350 hectares was sampled during the entire study.

Table 1: Habitat variables collected during field sampling and the rationale of collecting them.

Plant form	**Variables Collected**	**Field sampling**	**Rationale**
Trees			
1	Girth at breast height (GBH)	GBH was collected separately for every (stem of a) tree by measuring the circumference	GBH further converted to Basal area is a fundamental property of vegetation and also surrogates the age of the stand and size of the tree.
2	Diameter of the crown	As the GBH was not found to be a good surrogate for foliar biomass, diameter of the crown was measured to then calculate the foliar volume of the tree	As foliar biomass and GBH were superficially uncorrelated in the study system, foliar volume was calculated for each plant. To obtain this the dominant diameter length of each tree was measured.
3	Height of the tree	The height of the tree measured with rangefinder at the start and estimated occularly after familiarisation	Height was a parameter used for measuring foliar volume and even to understand the structure of the habitat.
4	Canopy start height	Height at which the canopy started	The canopy start height, often defined by the browse line was also a parameter associated with the foliar volume
Shrubs & Forbs			
1	Diameter of the plant	Measured as the diametric length of the plant	Similar to foliar biomass, foliar volume of shrubs and forbs were calculated separately using the diameter data. The diameter was also used to get cover of forbs
2	Height of the tree	Height of the plant.	To calculate foliar biomass
Grasses			
1	% cover	Percentage cover in 1x1 m quadrat	To calculate grass biomass
2	Grass Height	Height of grass measured as ordinal variable in distinct classes (0-5,5-10,10-30,30-60, >90)	To calculate grass biomass

5.4 Analytical Methods

Different techniques of comparison, modelling and ordination were used to answer specific questions relating to species richness, abundance and composition of bird communities. All the procedures were conducted on a dataset with all the recorded species and then with a dataset having only the originally native species. I used the 'species recorded in Protected grasslands' as a yardstick to differentiate originally present species from the newly colonised ones. The analyses were done separately for each season and for the overall year-long data.

All the analyses were conducted on two nested datasets – 1. Dataset with all the recorded species and 2. Dataset having only the originally native species. Native species were defined as species recorded in the protected grasslands and mentioned in literature as originally present before advent of Indira Gandhi canal (Rahmani & Soni, 1997).

Table 2: List of native and non-native species as classified by empirical data from current study and Rahmani & Soni (1997)

Native species		
1	Greater Hoopoe-lark	*Alaemon alaudipes*
2	Desert Lark	*Ammomanes deserti*
3	Tawny Pipit	*Anthus campestris*
4	Long-billed Pipit	*Anthus similis*
5	Great Indian Bustard	*Ardeotis nigriceps*
6	Trumpeter Finch	*Bucanetes githagineus*
7	Greater Short-toed Lark	*Calandrella brachydactyla*
8	Houbara Bustard	*Chlamydotis undulata*
9	Rock Pigeon	*Columba livia*
10	House Crow	*Corvus splendens*
11	Cream-coloured courser	*Cursorius cursor*
12	Black Drongo	*Dicrurus macrocercus*
13	Black-crowned Sparrow-lark	*Eremopterix nigriceps*
14	Gray Francolin	*Francolinus pondicerianus*
15	Southern Grey Shrike	*Lanius meridionalis*
16	Indian Silverbill	*Lonchura malabarica*
17	Bimaculated Lark	*Melanocorypha bimaculata*
18	Little Green Bee-eater	*Merops orientalis*
19	Purple sunbird	*Nectarinia asiatica*
20	Desert Wheatear	*Oenanthe deserti*
21	Isabelline Wheatear	*Oenanthe isabellina*
22	Variable Wheatear	*Oenanthe picata*
23	Red-tailed Wheatear	*Oenanthe xanthoprymna*
24	House sparrow	*Passer domesticus*
25	Chestnut-shouldered Petronia	*Petronia xanthocollis*
26	Rufous-fronted Prinia	*Prinia buchanani*
27	Chestnut-bellied sandgrouse	*Pterocles exustus*
28	Red-vented Bulbul	*Pycnonotus cafer*
29	White-eared Bulbul	*Pycnonotus leucotis*
30	Common stonechat	*Saxicola torquatus*
31	Laughing dove	*Stigmatopelia senegalensis*
32	Eurasian Collared-Dove	*Streptopelia decaocto*
33	Rosy starling	*Sturnus roseus*

34	Lesser Whitethroat	*Sylvia curruca*
35	Desert Warbler	*Sylvia nana*
36	Common Babbler	*Turdoides caudata*
Newly colonised/Non native/Neobiota		
37	Richard's Pipit	*Anthus richardi*
38	Cattle Egret	*Bubulcus ibis*
39	Common Rosefinch	*Carpodacus erythrinus*
40	Pied Kingfisher	*Ceryle rudis*
41	Indian Roller	*Coracias benghalensis*
42	Rufous Treepie	*Dendrocitta vagabunda*
43	Black-headed Bunting	*Emberiza melanocephala*
44	Crested Lark	*Galerida cristata*
45	Demoiselle Crane	*Grus virgo*
46	White-throated Kingfisher	*Halcyon smyrnensis*
47	Booted Warbler	*Hippolais caligata*
48	Sykes's Warbler	*Hippolais rama*
49	Eurasian Wryneck	*Jynx torquilla*
50	White Wagtail	*Motacilla alba*
51	Citrine Wagtail	*Motacilla citreola*
52	Yellow Wagtail	*Motacilla flava*
53	Indian Peafowl	*Pavo cristatus*
54	Black Redstart	*Phoenicurus ochruros*
55	Common Chiffchaff	*Phylloscopus collybita*
56	Dusky Warbler	*Phylloscopus fuscatus*
57	Greenish Warbler	*Phylloscopus trochiloides*
58	Plain Prinia	*Prinia inornata*
59	Red-naped Ibis	*Pseudibis papillosa*
60	Rose-ringed Parakeet	*Psittacula krameri*
61	White-browed Fantail	*Rhipidura aureola*
62	Pied Bushchat	*Saxicola caprata*
63	Brahminy Starling	*Sturnus pagodarum*
64	Orphean Warbler	*Sylvia hortensis*
65	Common Greenshank	*Tringa nebularia*
66	Green Sandpiper	*Tringa ochropus*
67	Large Grey Babbler	*Turdoides malcolmi*
68	Eurasian Hoopoe	*Upupa epops*
69	Red-wattled Lapwing	*Vanellus indicus*

5.4.1 Comparison of vegetation composition and structure

Vegetation composition of sites was visualised using Non-metric multidimensional scaling (NMDS) carried out on a site vs species matrix having volume of the plant as the abundance value. A bray Curtis index of similarity was used to plot the NMDS ordination. The differences in composition of sites from each land-use type were statistically checked using multi-response permutation procedure (MRPP). The habitat difference was inferred to be significant at 95% C.I. if the p-value was less than 0.0125, taking into account a Bonferroni correction. The magnitude of difference between cluster was inferred by looking at the A-value which increased with difference from 0 to 1. Additionally, some other vegetation composition parameters like vegetation diversity or woody plant diversity were calculated to relate vegetation composition to bird community parameters. Compositional diversity was calculated by the Shannon-weinner index of diversity used on the vegetation dataset.

Similar to composition, structure of vegetation was compared between land-use types using NMDS and then statistically tested using ANOSIM. The following structural variables were calculated for every site:

1. Foliar volume of woody plant: Foliar volume for each individual plant was calculated as the product of canopy cover and canopy height. Canopy cover was derived by multiplying the maximum canopy diameter by 2π. Canopy height was calculated by subtracting canopy start height from the total tree height. Finally, foliar volume of each plant was added up and standardised to 1ha, to get this index which surrogated foliar biomass of woody plants.
2. Woody plant stem density: The GBH for each stem was converted into area and then added up, to get woody plant density for a hectare. The woody plant density was a surrogate for productivity and age of the habitat.
3. Average GBH: As larger GBH indicated presence of larger trees, the average GBH informed about the stand structure of vegetation in the area.
4. Herbaceous volume: The volume of each forb was calculated by multiplying height by cover and then added up to get Herbaceous volume per hectare.
5. Grass volume: Similar to herbaceous volume, grass cover was multiplied by height to get volume which surrogated biomass.
6. Crop volume: Similar to grass and herbaceous volume.
7. Average height for each plant-form: The average height of each phenotypic form was calculated for each transect.

5.4.2 Bird species richness analysis

To compare local bird species richness across different land-use types, Analysis of Variance (ANOVA) was conducted. This was followed by a post-hoc multiple comparisons by Tukey’s HSD to check for pairwise differences in species richness. Seasonal differences in species richness were compared using a paired Wilcoxon sign-ranked test on species richness of every site.

A species accumulation curve was used to check whether species richness has reached asymptote at a landscape scale. Since the asymptote was not reached for some land-uses, landscape-scale richness of bird communities was estimated using sample-based rarefaction with bootstrap method on site-level data. This data was analysed separately for both the seasons and for the overall data.

5.4.3 Bird community composition

To visualise the differences in community composition of sites with individual land use types, ordination of the data was performed using non-metric multidimensional scaling NMDS. Bray-Curtis index of similarity was used estimate the ecological distance between the communities of two sites. The differences were then statistically tested using non-parametric multivariate analysis of variance (npMANOVA) or permutation multivariate analysis of variance (perMANOVA) with each community as the response variable and land use type as the explanatory variable. To ensure that the perMANOVA results were robust and not affected by heterogeneous multivariate dispersion between different groups, a permutational multivariate test of dispersion was conducted using the betadisper function in vegan package of R. The results of this test were subjected to multiple comparisons using Bonferroni correction of p-values and also by Tukey HSD. After performing the perMANOVA analysis, the results were compared for pairwise differences after Bonferroni correction of p-values.

5.4.4 Habitat correlates of species richness and community composition

To understand the relation of species richness with underlying habitat factors, Generalised Linear Models were used on richness data with preselected habitat factors as predictor covariates. The predictor covariates tested were foliar biomass of woody plants, forb biomass, overall vegetation diversity and grass biomass. Quadratic functions of some of the variables were also tested as predictors, to check whether there was any peaking at intermediate levels. The predictors were scaled prior to performing the analysis so that the output represented relative importance of each predictor variable.

Table 3: Hypothesized relationship of predictor variables with species richness.
Note: Forb volume was inversely correlated with grass biomass.

Variables	**Hypothesized relationship**	**Rationale**
Foliar biomass of woody vegetation	+	Higher foliar biomass would represent higher productivity and was expected to increase species richness (Sekercioglu, 2002)
Crop volume	-	Increasing crop volume represented increasing gradient of agriculture intensification and was expected to negatively influence bird richness (Flynn et al., 2009)
Forb volume	Quadratic	To a certain threshold, forb intensity was expected to be beneficial for bird richness. Forb volume increase beyond a certain threshold would potentially indicate a biome switch and was expected to negatively influence species richness. Additionally, the forb species in the study area were unpalatable and either weedy or invasive. (Sirami, Seymour, Midgley, & Barnard, 2009)
Compositional diversity	+	Compositionally more diverse habitats were expected to be associated with more bird species. (Terborgh, 2015)
Grass biomass	+	Grass biomass was expected to be associated with higher species richness.

Model selection was based on the information theoretic approach and was performed in the following way: a) A global model with all covariates was created and all simpler combinations of this model were produced using the dredge function in MuMIN package of R. b) Ecologically sensible models with delta-AIC less than 2, when compared to the best model, were selected for multimodal selection. C) The variables that potentially affect the species richness were identified using a step-wise backward selection of models.

To understand habitat correlates of community composition, a Canonical Correspondence analysis was conducted. Structural attributes of vegetation used for checking relation with species richness were again used as predictor variables for this analysis. A global model with all the variables was run and visualized as a biplot. Multi-collinearity between variables was then tested by calculating variance inflation factor with the “vif.cca” function in vegan package on R statistical Platform. If correlation was found, one of the collinear variables was dropped. The remaining were tested for significance by performing permutational MANOVA using the “cca.anova” function in vegan package. A simple model was then created with only the significantly influencing variables. A CCA biplot was used to understand the influence on specific variables on different bird species.

6. Results

6.1 Comparison of vegetation across land-use types

A total of 19 woody plant, 18 forb, 10 grass and seven crops species were recorded in the study area during vegetation sampling. Most transects were very homogenous with very few species of plants occurring within them. The mean species richness (species / sq.km) of all plant forms together was largely similar across all land uses (Table 4). A peculiar difference between land use types was in terms of Forb species, which were higher in extensive croplands. Intensive agriculture was devoid of grass but had higher number of tree species.

Table 4 Mean(SE) Species Richness (per sq.km) of each plant form grouped according to the land-use type.

Plant Form	Intensive Croplands	Extensive Croplands	Protected Grasslands	Rangelands
Crop	2.77 (0.43)	NA	NA	NA
Forb	3.75 (0.36)	4.68 (0.29)	3.07 (0.44)	3.2 (0.42)
Short_Grass	NA	1.86 (0.19)	1.66 (0.15)	1.44 (0.16)
Shrub	2.22 (0.36)	3.08 (0.24)	2.83 (0.54)	2.22 (0.23)
Tall_Grass	NA	1.05 (0.05)	1.4 (0.13)	1.38 (0.14)
Tree	5.33 (0.62)	3.03 (0.25)	2.73 (0.26)	2.94 (0.20)

There were stark differences in different land-use types when volumes (surrogate of biomass) of plant forms were compared against each other. Mean foliar biomass of woody plants was much higher in intensive agriculture as compared to other land uses whereas forb biomass was highest in rangelands. However, none of these means was significantly different from each other at α=0.05. Grass biomass was notably higher in protected grasslands as compared to other land uses (Table 5).

Table 5: Mean(SE) volume in cu.m per ha for each plant form (column) in every land use type (rows), during winter (Top) and summer (bottom)

Winter					
Type	**Crop**	**Diversity**	**Forb**	**Grass**	**Woody Plant**
Extensive_croplands	13846.15 (10153.85)	1.05 (0.09)	342.68 (114.59)	44.67 (15.91)	427.54 (131.15)
Intensive_croplands	1146666.67 (242926.4)	0.59 (0.13)	4.9 (2.81)	0 (0)	1497.02 (1004.45)
Protected_Grasslands	0 (0)	1.19 (0.06)	294.8 (96.36)	1107.38 (317.16)	512.8 (163.34)

Rangelands	0 (0)	0.99 (0.13)	738.5 (454.98)	337.14 (164.65)	637.48 (360.28)
Summer					
Type	**Crop**	**Diversity**	**Forb**	**Grass**	**Woody Plant**
Extensive_croplands	0 (0)	1.14 (0.07)	342.68 (114.59)	44.67 (15.91)	427.54 (131.15)
Intensive_croplands	779.17 (540.25)	1.38 (0.11)	38.22 (10.84)	170.83 (158.48)	1497.02 (1004.45)
Protected_Grasslands	0 (0)	1.19 (0.06)	294.8 (96.36)	1107.38 (317.16)	512.8 (163.34)
Rangelands	0 (0)	0.99 (0.13)	738.5 (454.98)	337.14 (164.65)	637.48 (360.28)

6.1.1 Vegetation composition and structure

Vegetation composition of different land uses was compared visually using NMDS and statistically using perMANOVA and ANOSIM. The results showed clear segregation between plant community compositions of intensive agriculture as compared to all the other land-uses (perMANOVA: $p_{summer} < 0.001$, $p_{winter} <0.001$). Protected grasslands and rangelands had very similar local community composition of plants whereas composition in non-intensive agriculture was significantly different. The magnitude of compositional difference between intensive agriculture and other land-uses was much higher during winter and reduced notably during the summer (Figure 2).

Vegetation structure showed a similar pattern across land-uses. Intensive agriculture had distinct vegetation structure compared to other land-uses during winter (perMANOVA: $p_{winter} < 0.001$). Protected grasslands also had unique structure, which was different from rangelands and non-intensive croplands during both seasons (Figure 2). The structure of rangelands and extensive croplands was very similar. In summer, the vegetation structure of intensive agriculture was similar to rangelands and extensive agriculture but remained different from that of protected grasslands and other land uses (perMANOVA: $p_{summer} < 0.001$).

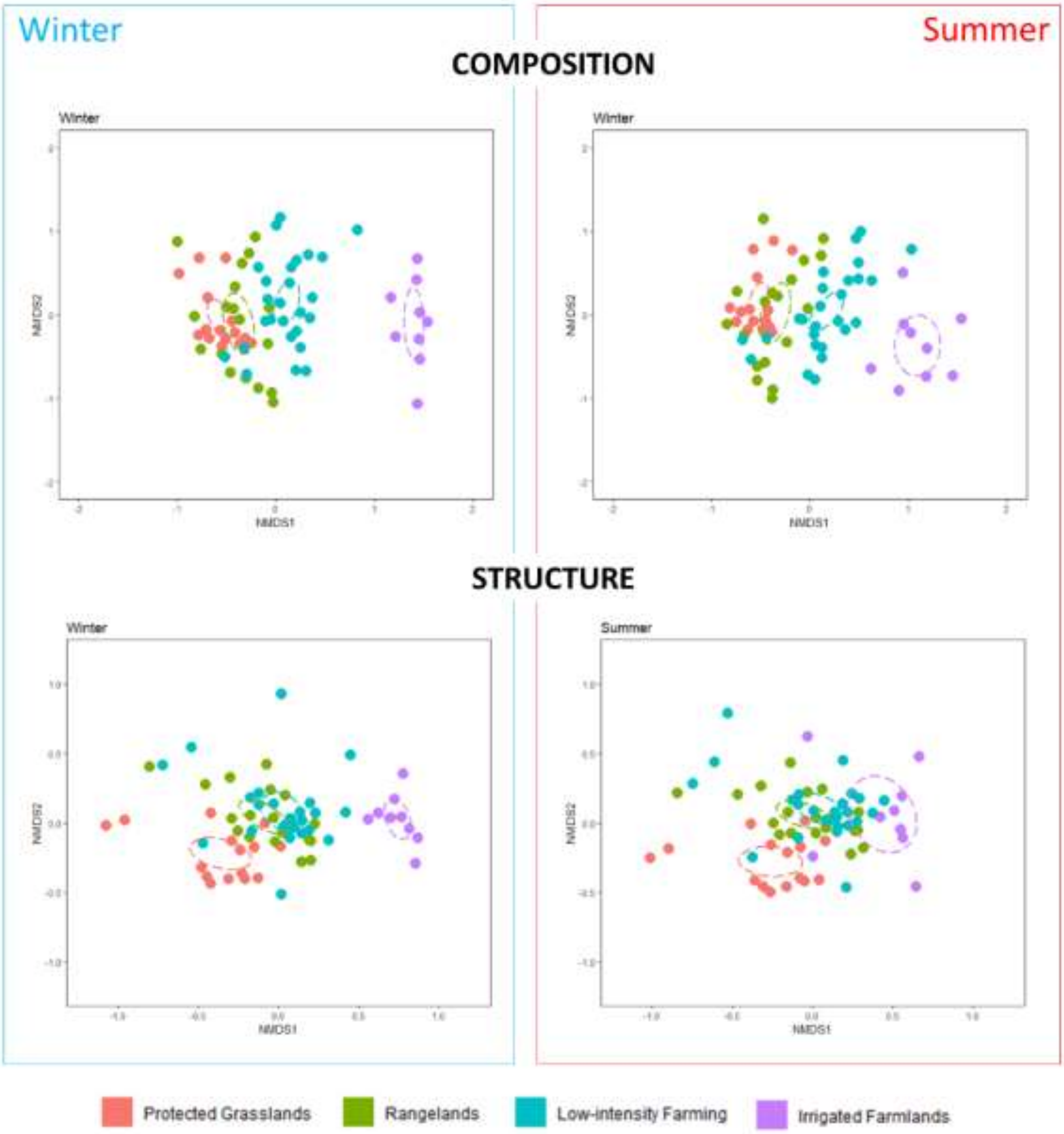


Figure 2: NMDS ordination showing differences in composition (above) and structure (below) of vegetation in different land-use types during winter (left) and summer (right). The ellipsoids are centred at mean MDS value of both axis and the radius is determined by the standard error of mean at 95% C.I. Stress values of all plots were less than 0.25 and the non-metric fit was more than 90%.

6.2 Bird Species Richness

A total of 1521 individuals belonging to 51 species were recorded during winter sampling (January 2019 to March 2019), while 1834 individuals belonging to 52 species were recorded during summer sampling (March 2018 – May 2019). Overall, 3555 individuals belonging to 72 species were recorded during the entire study period (December 2018 to May 2019). Thirty-three species out of the overall 72 were recorded in both seasons.

6.2.1 Local bird richness

Result of paired Wilcoxon Sign Test on sample species richness during winter and summer showed that median of local-scale species richness was different between seasons (V = 1145.5, df = 67, p = 0.0045), and the mean richness was slightly higher during winter (9.47 ± 0.51 SE) than summer (8.353 ± 0.532). Considering this seasonal difference in species richness, further comparisons were conducted separately for seasons.

Mean species richness was different between land-use types during both seasons (Winter: F = 10.97, df = 67 , $p < 0.05$; Summer: F = 11.27, df = 67, $p< 0.05$). Tukey's HSD post-hoc test indicated that mean bird species richness was significantly higher in irrigated high-intensity agriculture as compared to other land uses (Table 6, Figure 3). There was no significant difference in mean species richness between other land use types. Year round, the pattern of local scale mean species richness was similar to the one observed during individual seasons.

However, these patterns changed after controlling for non-native species. In winter, mean species richness of irrigated croplands was not different from protected grasslands whereas extensive agriculture and rangelands had lower species richness than protected grasslands and irrigated croplands (Figure 3, Table 6). In summers, only rangelands and irrigated croplands had significantly different mean species richness. The year-round patterns were similar to that in summer. In both seasons, mean richness of native species richness in high-intensity croplands reduced drastically when non-native species were not included, but the same was not true for any other land-use; indicating that intensive agriculture attracted non-native species in particular (Figure 3, Table 6).

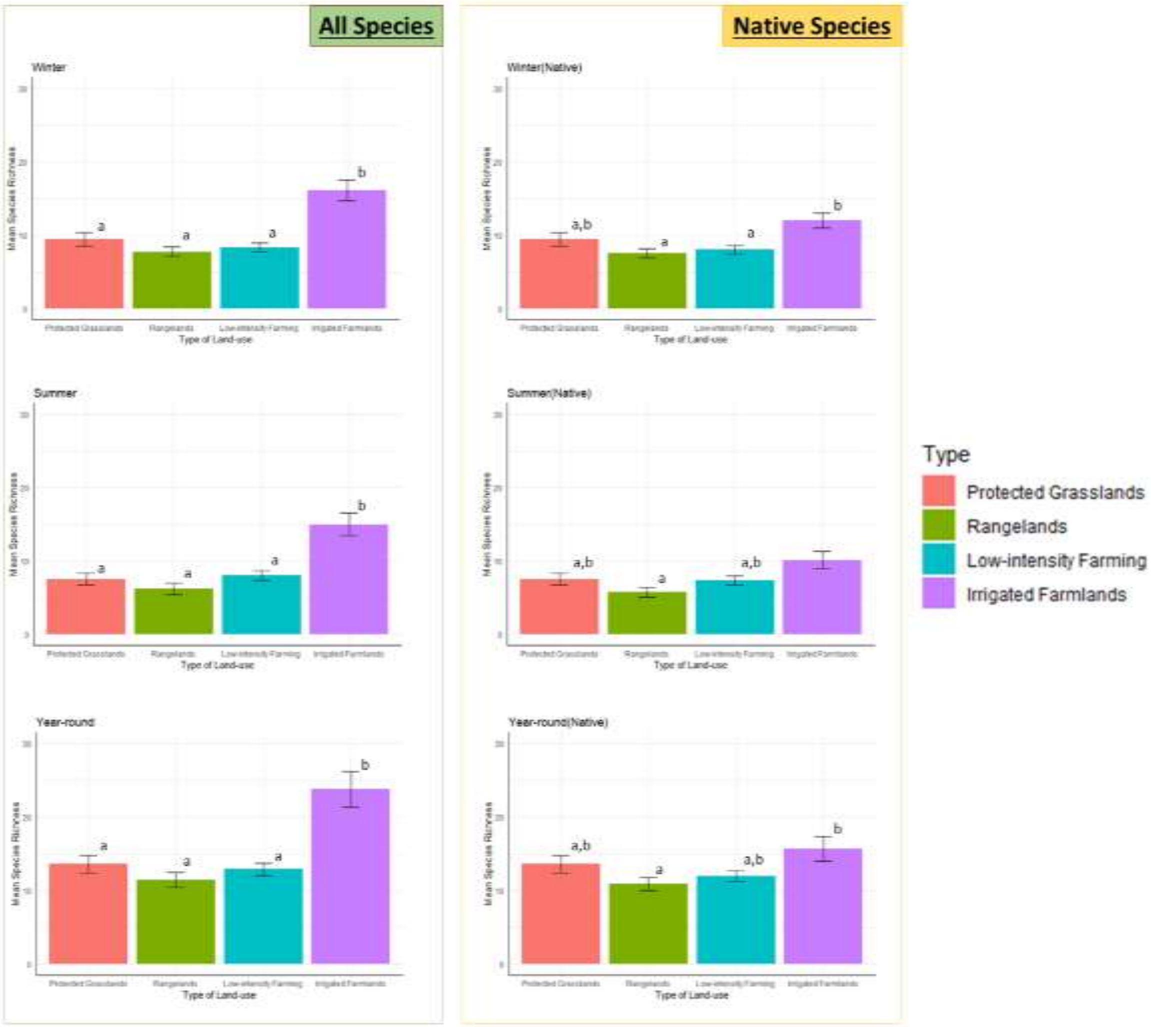


Figure 3: Bar plot representing the mean species richness of all species (left) and native species (right) across land-use types during winter (top), summer (middle) and both seasons together (bottom). The error bars represent the standard error on them

Type	Parameter	Protected Grasslands	Rangelands	Low-intensity agriculture	Intensive agriculture	ANOVA pvalue
Winter	Mean(SE) Overall	9.46 (0.92)^{a}	7.72 (0.67)^{a}	8.3 (0.60)^{a}	16.11 (1.45)^{b}	<0.001
	Mean(SE) Native	9.46 (0.92)^{a,b}	7.56 (0.62)^{a}	8.03 (0.55)^{a}	12 (1.02)^{b}	0.003
Summer	Mean (SE) Overall	7.53 (0.76)^{a}	6.16 (0.8)	8.88 (0.68)^{a}	15 (1.53)^{b}	<0.001
	Mean (SE) Native	7.53 (0.76)^{a,b}	5.72 (0.66)	7.34 (0.58)^{a,b}	10.11 (1.18)^{b}	0.008
Year Round	Mean (SE) Overall	13.6 (1.17)^{a}	11.44 (1.04)	12.88 (0.82)^{a}	23.78 (2.40)^{b}	<0.001
	Mean (SE) Native	13.6 (1.17)^{a,b}	10.88 (0.89)	11.92 (0.7)^{a,b}	15.67 (1.67)^{b}	0.026

Table 6: Mean (SE) species richness of all bird species and native bird species in different land-use types during winter and summer. Subscripts along the means indicate grouping according to Tukey's post-hoc test at 95% significance level.

6.2.2 Landscape-scale bird richness

Visual examination of species accumulation curves suggested that sampling could not capture the entire set of species for all land-use types. During winter, the naïve and bootstrapped estimated species richness was significantly higher in intensive agriculture as compared to all other land-uses. Protected grasslands and rangelands had similar estimated and naïve species richness, whereas non-intensive agriculture had slightly higher species richness. In summer, the naïve and estimated species richness was highest in intensive agriculture followed closely by low-intensity agriculture. Protected grasslands and rangelands had much lower species richness than two agricultural land-uses (Figure 4).

After controlling for newly colonised species, protected grasslands had the highest species richness in all seasons, indicating loss of certain native species in other land-use types. The estimated species richness among the three non-protected land-uses was largely similar. The drastic reduction in species richness of intensive croplands after controlling for native species shows that nearly half the species seen in this land-use are newly colonised. Similarly, the species richness in non-intensive croplands during summer reduced sharply when non-native species were excluded.

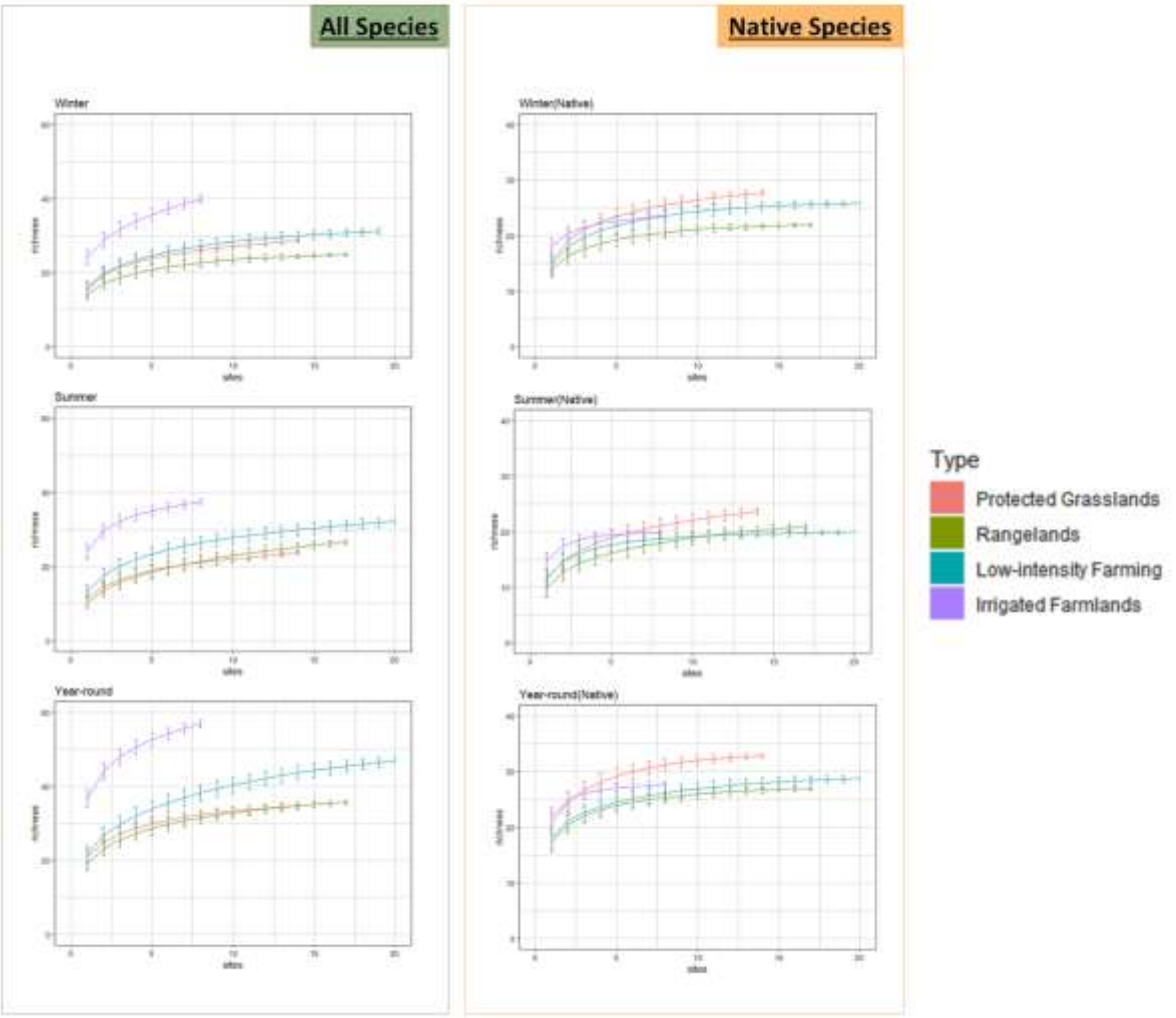


Figure 4: Species accumulation curve with sites in the x-axis and accumulated landscape-scale species richness on the y-axis. The plots represent landscape-scale species richness of all species (left) and native species (right) in winter (above), summer (middle) and across both seasons (bottom). The error bars represent the standard error on the mean at every position.

Season	Species richness	Protected Grasslands	Rangelands	Low-intensity agriculture	Intensive agriculture
Winter	Naïve Overall	28	25	32	41
	Mean (SE) Overall	31.24 (1.80)	27.71 (1.56)	35.88 (1.93)	46.35 (2.93)
	Naïve Native	28	22	26	24
	Mean (SE) Native	31.24 (1.80)	23.64 (1.09)	27.95 (1.18)	25.54 (1.35)
Summer	Naïve Overall	24	27	34	38
	Mean (SE)	27.33 (1.95)	31.13 (2.48)	38.96 (2.82)	42.26 (2.59)
	Naïve Native	24	21	20	20
	Mean (SE)	27.33 (1.95)	23.46(1.83)	20.70 (0.74)	21.05 (1.29)
Overall	Naïve Overall	34	36	49	58
	Mean (SE)	36.98 (1.53)	40.07 (2.69)	56.52 (3.45)	64.53 (3.39)
	Naïve Native	34	28	30	29
	Mean (SE)	36.98 (1.55)	29.68 (1.28)	31.93 (1.13)	30.26 (1.34)

Table 7: Naive and estimated species richness of different land-use types at a regional scale. The estimated richness was calculated using bootstrap methods for sample-based rarefaction.

6.3 Overall Bird Abundance

Average bird abundance was higher in intensive agriculture as compared to other land uses during both seasons (Table). The difference between intensive agriculture and protected grasslands was marginally non-significant at $\alpha = 0.05$ in winter but was significant during the summers (Range $_{\text{intensive agriculture}}$ = [333.8,616.5]; Range $_{\text{Protected Grasslands}}$ = [177.5,396.4]). Rangelands and non-intensive croplands had notably low average abundance during both the seasons (Figure 5, Table 8).

After controlling for non-native species, the average abundance in different land-uses was only marginally different during winter (ANOVA: F-value=2.07, p-value=0.053), but was significantly higher in intensive croplands during summer (ANOVA: F-value=9.14, p-value <0.0001). Controlling for non-native species resulted in roughly 30% reduction in mean abundance of birds in intensive croplands but did not change the abundance in other land uses significantly (Table 8).

Table 8: Estimated mean abundance (per 1km transect) of all bird species and native bird species in different land-use types during winter and summer. Subscripts along the means indicate grouping according to Tukey's post-hoc test at 95% significance level.

Season	Parameter	Protected Grasslands	Rangelands	Non-irrigated Croplands	Irrigated Croplands	p-value
Winter	Mean (SE) Overall	287 (46.14)	189.3 (36.7)	189.5 (50.95)	475.2 (68.37)	0.005
	Mean (SE) Native	287 (46.14)	188.8 (36.75)	176.8 (47.11)	374.7 (73.5)	0.053
Summer	Mean (SE) Overall	135.9 (26.88)	109.5 (14.59)	130 (16.59)	484.2 (94.4)	<0.0001
	Mean (SE) Native	135.9 (26.88)	107 (14.4)	121.4 (16.4)	317.9 (68.2)	<0.0001
Overall	Mean (SE) Overall	211.4 (32.22)	149.4 (21.61)	159.7 (30.48)	479.7 (71.8)	<0.0001
	Mean (SE) Native	211.4 (32.22)	147.9 (21.57)	149.1 (28.87)	346.3 (61.7)	0.002

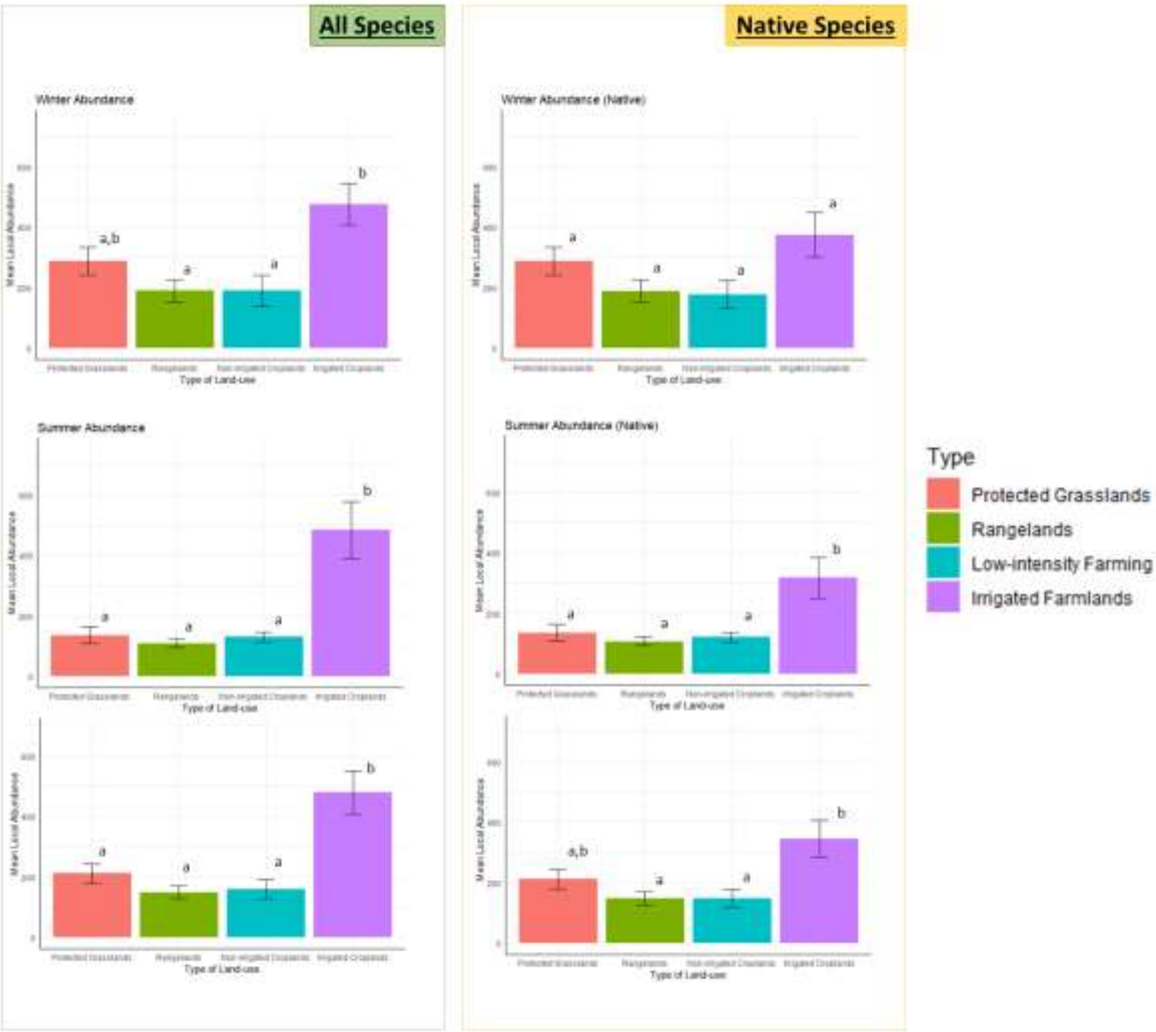


Figure 5: Bar plot representing the mean abundance (per sq.km) of all species (left) and native species (right) across land-use types during winter (top), summer (middle) and both seasons together (bottom). The error bars represent the standard error on the mean. The superscript on the error bars represents the grouping of different land-uses according to multiple comparisons with Tukey's post-hoc test.

6.4 Bird community composition across land uses

Community composition, at the landscape scale, changed progressively with intensification of land use. Protected grasslands had two unique species across the year that were not found in any other land-use, while low-intensity agriculture and rangelands respectively had two and one unique species. However, this could be an artefact of detection and more sampling could've revealed these unique species in other land uses. On the other hand, fourteen species were unique to Intensive agriculture, which is substantial even after considering the species that could have been missed due to imperfect detection in other land-uses. Two threatened species – Great Indian Bustard (Critically Endangered) and McQueen's Bustard (Vulnerable) – were recorded during the study and both were found only in protected grasslands.

Ordination using NMDS displayed perceivable differences in bird communities of different land use types during both seasons Permutational test of multivariate dispersion showed that multivariate dispersion amongst the groups was homogenous and the data was suitable for performing perMANOVA analysis (Permutational test for multivariate dispersion: p_{winter}= 0.83, p_{summer} = 0.64, $p_{overall}$ = 0.41). The perMANOVA results indicated strong evidence against the null hypothesis that 'there is no significant difference in bird communities between land use types' (perMANOVA: p_{winter}= <0.001, p_{summer} = <0.001, $p_{overall}$ = <0.001). Pairwise post-hoc comparison of perMANOVA results with Bonferroni correction of p-values suggested that during both the seasons and year-round, the communities of Intensive croplands were significantly different from the communities of all other land use types (perMANOVA – All combinations: p_{winter}= <0.01, p_{summer} = <0.01, $p_{overall}$ = <0.01). Communities in protected grasslands did not differ significantly from communities in rangelands (perMANOVA: p_{winter}= 1.00, p_{summer} = 1.00, $p_{overall}$ = 1.00) and low-intensity croplands (perMANOVA: p_{winter}= 0.43, p_{winter} = 0.26) during individual seasons, but year-round species composition in protected grasslands differed from that of low-intensity croplands (perMANOVA: $p_{overall}$ = <0.01). Bird communities in rangelands were not significantly different from the communities in low-intensity croplands (perMANOVA: p_{winter}= 1.0, p_{summer} = 1.0, $p_{overall}$ = 1.0) during any season or year-round.

The inferences remained largely similar to the earlier results even after controlling for non-native species, showing difference in native community for at least one land use type (perMANOVA – All combinations: p_{winter}= <0.01, p_{summer} = <0.01, $p_{overall}$ = <0.01). The average community structure of native species was different in intensive cropland than any other land-use type during all seasons (perMANOVA – All combinations: p_{winter}= <0.01, p_{summer} = <0.01, $p_{overall}$ = <0.01). Low-intensity croplands had different native communities than protected grasslands in winter (perMANOVA: p_{winter}= 0.024) but similar communities in summer (perMANOVA: p_{summer} = 1.0). Native communities in rangelands were very similar to communities in both protected grasslands and non-intensive croplands during both the seasons.

The significant difference in community composition even after controlling for non-native species indicated that the change in overall community composition between land-uses is partly driven by change in composition of native species. To further substantiate the claim, Analysis of Similarity was carried out between combinations of land uses in both seasons and all species as well as only native bird species. The magnitude of difference between Intensive croplands and other land uses reduced when non-native species were excluded. This shows that newly ingressed species are also influencing the overall community structure to a significant extent in intensive croplands but not in other land-use types (Figure 7).

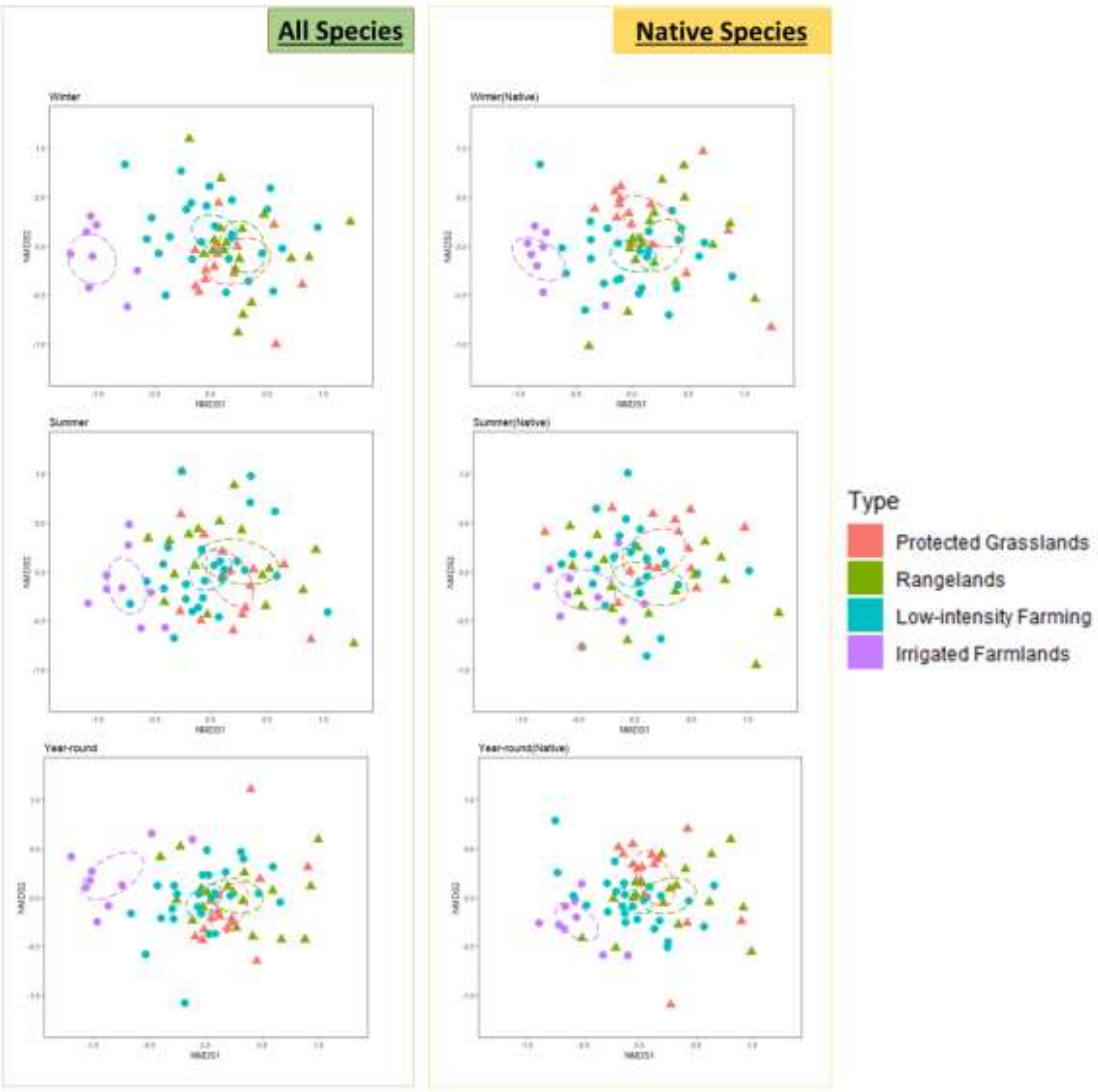


Figure 6: NMDS ordination showing bird community composition (above) of all bird species (left) and native bird species (right) in different land-use types during winter (top), summer (middle) and both seasons together (bottom). The ellipsoids are centred at mean MDS value of both axis and the radius is determined by the standard error of mean at 95% C.I. Stress values of all plots were less than 0.25 and the non-metric fit was more than 90%.

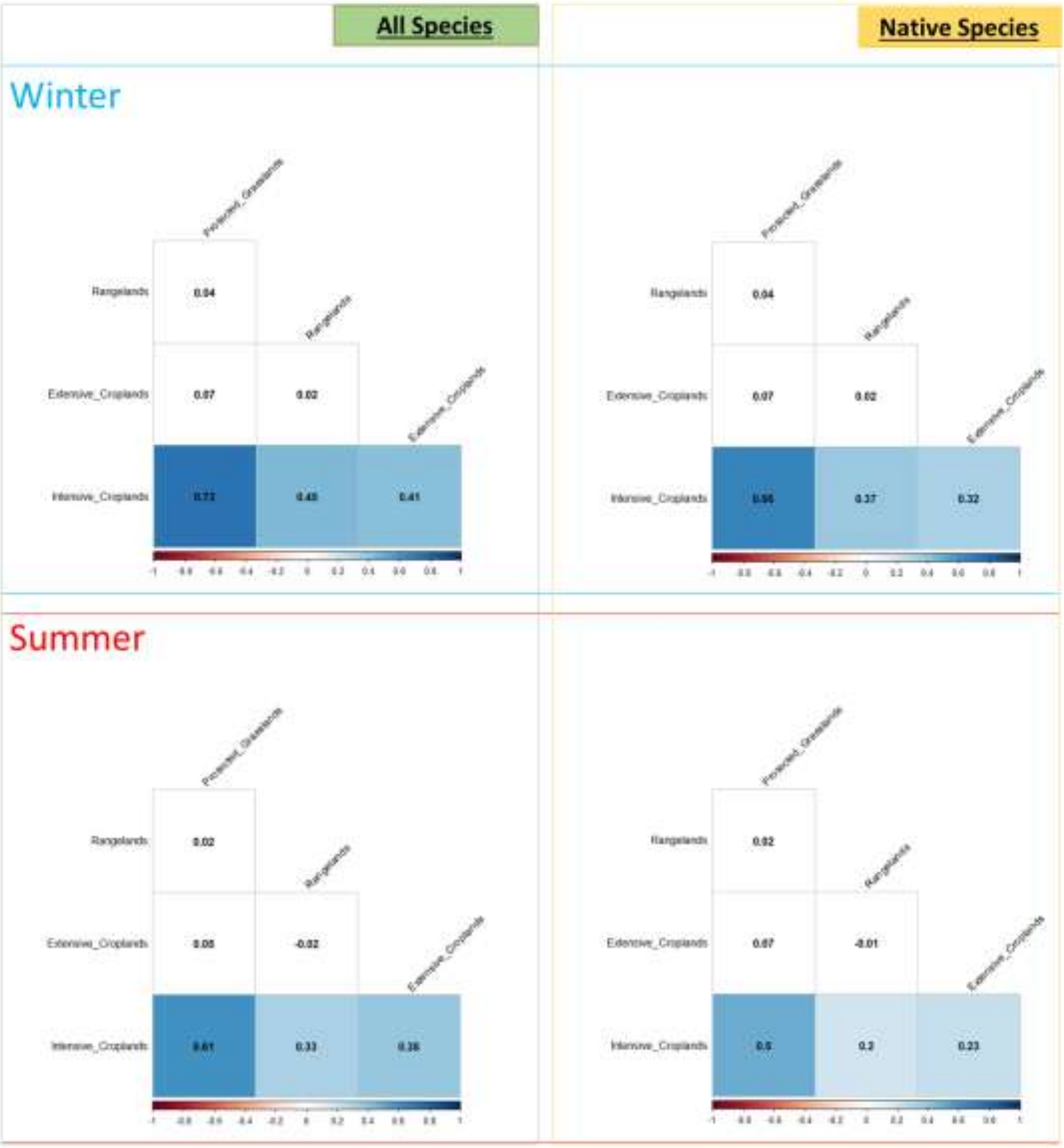


Figure 7: ANOSIM R-values indicating similarity of bird communities between respective combinations of land-use types during winter (above) and summer (below), with all species (left) and only native species (right). The values range from -1 to 1 with values close to 0 indicating random grouping or low dissimilarity in communities and values closer to the extremes indicate grouping or higher dissimilarity in communities. Every square has two land-use types associated with it and indicates the R-value between the particular combinations. The values in colour represent significantly different values at 95% significance and the values without any colour (white) represent an insignificant difference.

6.5 Drivers of species richness and abundance

The factors influencing species richness varied between the two seasons. In winter, comparison of alternate hypotheses showed that species richness was positively influenced by crop volume ($\beta_{\text{top model}} = 0.12$ (0.03), $p < 0.05$) and foliar biomass of woody plants ($\beta_{\text{top model}} = 0.10$ (0.03), $p < 0.05$) and negatively influenced by forb volume ($\beta_{\text{top model}} = -0.15$ (0.005), $p < 0.05$). The best fitting model explained the data fairly well with a McFadden's R^2 value of 0.40 (Figure 8, Table 9)

Table 9: Comparisons of best fitting models with the global model. The model was selected based on the AICc criterion.

Season	Model	df	logLik	AICc	delta	R^2
Winter	~Crop+Forb+wpd (Best)	4	-165.47	339.60	0	0.52
	~Crop+Forb+GBH+wpd	5	-164.69	340.40	0.80	0.53
	~Crop+veg_diversity+Forb+I(Forb^2) + GBH+ Grass+wpd (Global)	8	-164.22	347.02	7.41	0.16
Summer	~wpd+Forb+veg_diversity (Best)	4	-162.97	334.60	0	0.65
	~Crop+veg_diversity+Forb+wpd	5	-162.96	336.95	2.34	0.65
	~Crop+veg_diversity+Forb+I(Forb^2) + GBH+ Grass+wpd (Global)	8	-162.66	343.90	9.29	0.65

During summer, the species richness was positively affected by foliar volume of woody plants (beta $_{\text{top model}}$ = 0.18 (0.03), p-value <0.0001), compositional heterogeneity of vegetation (beta $_{\text{top model}}$ = 0.10 (0.04), p-value=0.01) and negatively affected by the forb biomass (beta $_{\text{top model}}$ = -0.28 (0.07), p-value < 0.001) (Figure 8).

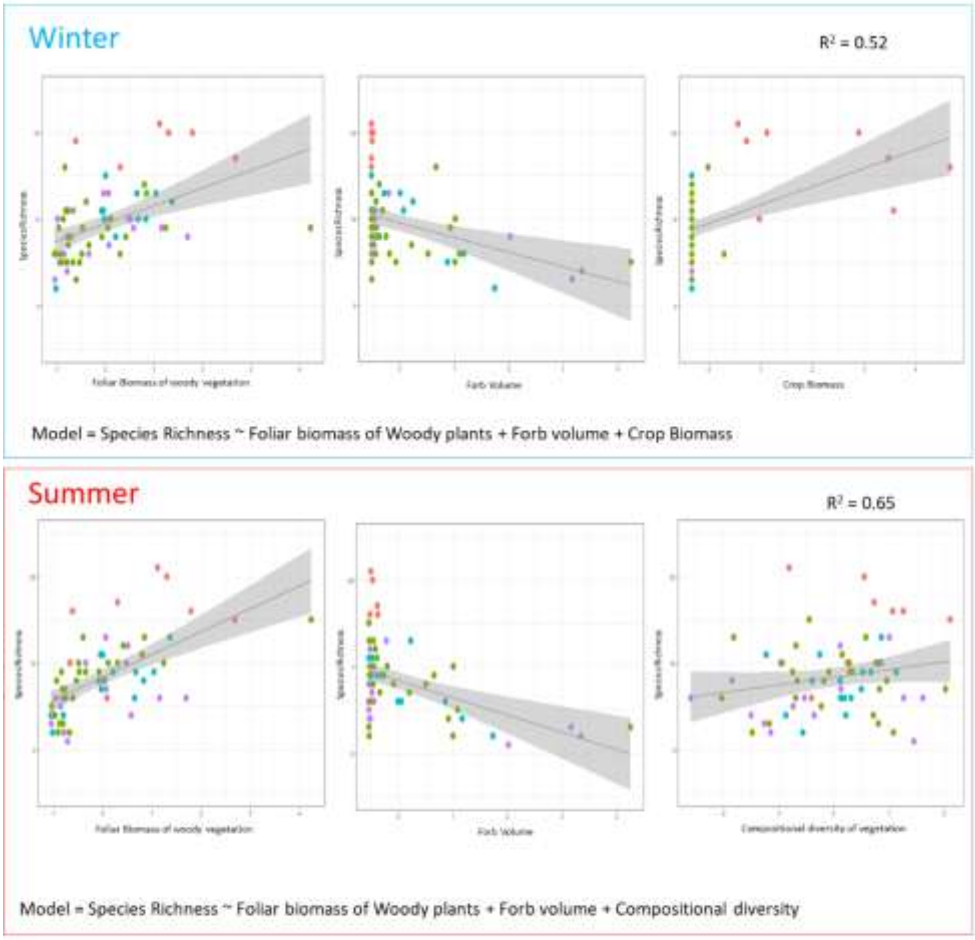


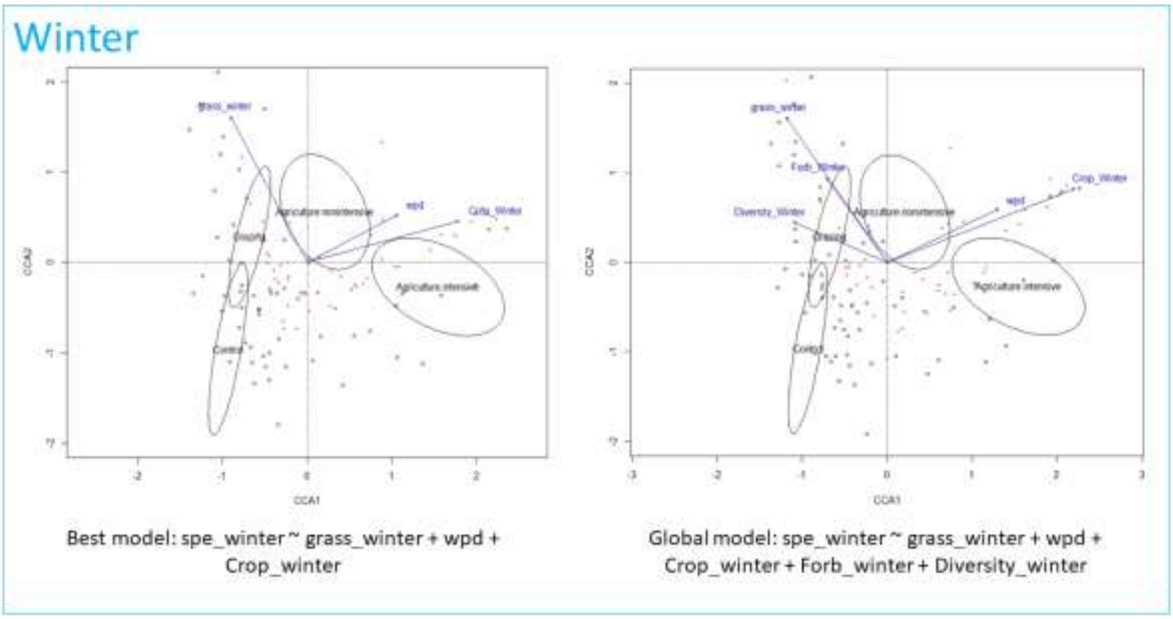
Figure 8: Habitat correlates of species richness during winter (top) and summer (bottom). The parameters were based on the best fitting model for each season. The significantly influential variables in winter were foliar biomass of woody vegetation (left), forb biomass (middle) and crop biomass (right). Similarly, the explanatory variables in summer were foliar biomass of woody vegetation (left), forb biomass (middle) and compositional heterogeneity of vegetation (right).

Results of canonical correspondence analysis, conducted to understand the habitat correlates of bird composition are depicted in Table 7. In winter, the global model with all the variables explained 19% of the variance after constrained ordination but had two variables that were correlated (Variance inflation factor (GBH_winter and wpd = 3.4). Term-wise permutational MANOVA on the models suggested that Crop volume, Grass volume and woody plant foliar volume were significantly influencing bird community composition in winters (Table 10). The final constrained ordination with three significantly influential variables explained 14% variance in the data (Figure 1).

Table 10: Results of Canonical Correspondance Analysis for both the seasons. a) represents the entire global model; b) represents the global model without collinear variables and c) is the simple model with only significantly influential variables

<table>
<tr><th>Model</th><th colspan="4">Formula</th><th>Proportion (constrained)</th></tr>
<tr><td rowspan="7">Winter</td><td colspan="4">a) Winter_spe ~ Crop_winter+ grass_winter + wpd + Forb_volume_Diversity_winter+GBH_winter</td><td>0.19</td></tr>
<tr><td colspan="4">b) Winter_spe ~ Crop_winter + grass_winter + wpd + Forb_volume_Diversity_winter</td><td>0.17</td></tr>
<tr><td colspan="4">c) Winter_spe ~ Crop_winter + grass_winter + wpd</td><td rowspan="5">0.14</td></tr>
<tr><td>Variable</td><td>dF</td><td>F</td><td>Pr</td></tr>
<tr><td>Crop_winter</td><td>1</td><td>6.2739</td><td>0.001</td></tr>
<tr><td>grass_winter</td><td>1</td><td>2.4758</td><td>0.005</td></tr>
<tr><td>Wpd</td><td>1</td><td>1.758</td><td>0.107</td></tr>
<tr><td rowspan="6">Summer</td><td colspan="4">a) Summer_spe ~ Crop_summer+grass_summer+ wpd + Forb_volume_Diversity_winter+GBH_winter</td><td>0.18</td></tr>
<tr><td colspan="4">b) Summer_spe ~ Crop_summer+grass_summer+ wpd + Forb_volume_Diversity_winter</td><td>0.15</td></tr>
<tr><td colspan="4">b) Summer_spe ~ Crop_summer+ wpd</td><td rowspan="4">0.11</td></tr>
<tr><td>Variable</td><td>dF</td><td>F</td><td>Pr</td></tr>
<tr><td>Crop_summer</td><td>1</td><td>4.409</td><td>0.001</td></tr>
<tr><td>Wpd</td><td>1</td><td>4.1341</td><td>0.016</td></tr>
</table>

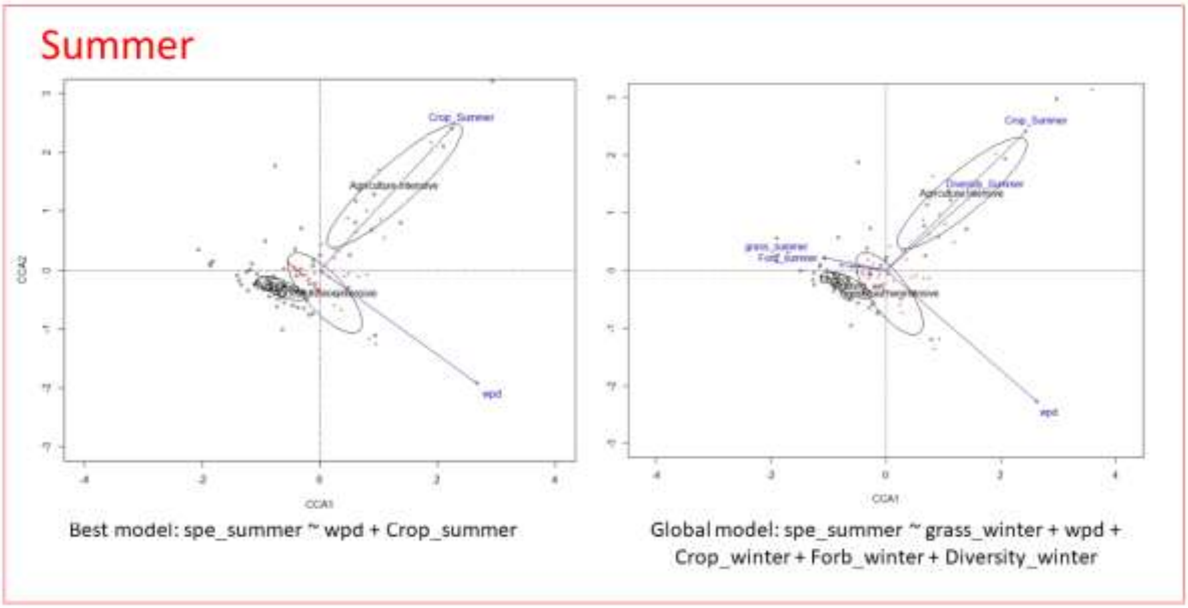
The same procedure was repeated in summers, and the results indicated that crop volume and woody plant foliar biomass were significantly affecting bird community composition in summer (Table 10). The final model with two variables explained 11% of the constrained variance in community composition data (Figure 10).


Winter

Best model: spe_winter ~ grass_winter + wpd + Crop_winter

Global model: spe_winter ~ grass_winter + wpd + Crop_winter + Forb_winter + Diversity_winter

Figure 9: CCA biplot for Winter with full global model (left) and simple model with significantly influential variables (right).


Summer

Best model: spe_summer ~ wpd + Crop_summer

Global model: spe_summer ~ grass_winter + wpd + Crop_winter + Forb_winter + Diversity_winter

Figure 10: CCA biplot for Summer with full global model (left) and simple model with significantly influential variables (right).

7. Discussion

The results of the study broadly suggested that bird communities do not change significantly in response to low-impact land-uses like pastoralism and extensive agriculture but change drastically as agriculture intensifies with the advent of irrigation. This pattern is conserved across different seasons, although the magnitude of difference within communities changes with season. The change in bird communities correlates with the sequential change in structure and composition of vegetation in both the seasons. Analysing patterns of species richness against environmental variables suggests that the process of community assembly across land-uses is affected by habitat factors such as forb biomass, crop biomass, vegetation heterogeneity and woody plant foliar biomass. The results of this study provide novel information regarding the effects of land-use change on avifauna of the landscape and progresses our understanding of how anthropogenic processes lead to change in community assembly.

7.1 Patterns of vegetation across space and time

The composition and structure of vegetation changed progressively with intensifying change in land use. The similarity in vegetation structure of rangelands and extensive croplands is superficially caused by two factors: 1) High pressures of grazing in rangelands have reduced the grass biomass so drastically that the understory is now very similar to the largely tilled understory of extensive croplands. 2) Low-intensity farming does not change woody plant species like Capparis decidua, Zizypus nummularia, significantly. The slight difference of bird composition in extensive croplands and rangelands was potentially due to loss of perennial grass species after tilling and due to presence of early successional species like *Aerva pseudotomentosa, Dipterygium glaucum* in the fallow regenerating croplands. On the other hand, the vegetation composition of intensive agriculture was expectedly different from all the other land uses. This was due to four reasons: 1) Progressive clearance of original vegetation over the course of agriculture intensification; 2) Plantation of new, originally non-native species such as *Acacia nilotica, Dalbergia sisoo, Acacia senegal, Prosopis juliflora* etc. on hedges; 3) Change in understory due to farming and presence of crops. 4) The selective proliferation of certain native species (eg. Calotropis procera, *Zizypus nummularia*) owing to changed conditions. This change in composition was also associated with a change in structure as farm-crops and newly planted were very different from originally present plants in their structural profile.

Temporally, two major changes were likely to occur in the vegetation of the study area during the sampling period. The most noticeable change that predictably occurred was the change in structure of vegetation understory in intensive agriculture after harvest of crops in late winter. Most croplands were left fallow after harvest and thus became structurally very similar to extensive agriculture. Additionally, succession of vegetation in these newly fallow fields resulted in structural and compositional convergence between intensive agriculture and the other land-uses, especially non-intensive agriculture (Figure 2). The second change that could have potentially changed vegetation was removal of biomass due to livestock grazing in rangelands and extensive croplands. However, this change was minimal in the current scenario as most of the palatable biomass in the rangelands and extensive croplands was already grazed out by the start of winters. Thus, the grass biomass was largely unchanged across seasons in these two land-uses. Protected grasslands remained unaffected by both these changes and were similar in composition and structure during both the seasons. Vegetation in rangelands and extensive croplands also did not differ significantly between the two seasons. Intensive agriculture, however, changed notably in structure during the two seasons and became structurally similar to other land uses in the summer.

To summarise, the results suggest that rangelands and extensive croplands are very similar to protected grasslands in terms of vegetation structure and composition during both seasons. Intensive agriculture at the current levels has notably distinct habitat during the winter but become relatively more similar to extensive agriculture and other two land-uses after turning fallow during the summer.

7.2 Bird community responses to intensifying land use

The patterns of species richness, abundance and composition of local bird communities can be summarised on two distinct fronts –

a) Protected grasslands with regulated low-intensity grazing and rangelands with unregulated high-intensity grazing had very similar bird communities in terms of species richness, abundance and composition. This suggests that livestock grazing does not notably alter the niches available for bird species. However, notably, the current year being a drought resulted in many protected grasslands being grazed by livestock reducing the herbaceous height and cover; and making it more similar to rangelands with unregulated grazing compared to good rainfall years. Thus, it would be important to replicate the study in good rainfall years when protected grasslands are actually less grazed, to see if these inferences hold true. Similarly, bird communities in extensive croplands having low-intensity unirrigated agriculture were also not very different from communities in protected grasslands and indicated only a slight change in the niche space. These results did not differ even after controlling for non-native species, thus confirming that the converging parameters were not due to replacement of native species by new ones. The almost identical community parameters also show that livestock grazing and extensive agriculture at the current level of intensity is not very detrimental for bird communities and alternately provides secondary habitat for many bird species. This compatibility of low-intensity land-uses with birds may have resulted from a very long association as these landscapes have experienced human footprint and moderate human modification of landscape from historical times, allowing wildlife to adapt and co-occur (Rangarajan x, Dutta 2018).

b) On the other hand, irrigated croplands with high-intensity agriculture had much higher species richness and abundance at the local scale but also had significantly different community composition. The higher species richness and overall abundance were due to ingression of originally non-native mesic species, whose colonization was potentially facilitated by the presence of surface water and the associated creation of a new microhabitat. Local bird richness and abundance remained significantly higher even after controlling for non-native species and indicated that the new habitat can fundamentally be used by the native species. However, the significant change in bird community composition even after controlling for newly colonised species suggested that individual species respond differentially to this new habitat and some native species are negatively affected or lost entirely due to this intensification of land-use.

These patterns at the local scale species richness, abundance and composition apparently indicate that expansion of low-impact land-use does not have negative impacts on native bird communities until irrigation driven intensification sets in. However, this notion cannot be fortified without looking at these patterns from a landscape perspective, while also checking seasonal differences in patterns and studying effects on populations of individual species. Apart from this caveat, my results at the local scale indicate that – a) intensively grazed grasslands and extensive croplands can be important habitats for grassland birds as the communities of these land-uses are very similar to protected grasslands in terms of richness, abundance and community composition. b) Irrigated high-intensity croplands can also sustain native bird communities but cause significant change in community structure potentially due to differential changes in abundance of individual species. c) High-intensity/Irrigated agriculture supports the colonisation of erstwhile non-native bird species, thus increasing local-scale species richness and abundance. The potential causes, mechanisms and correlates of these patterns are discussed in the upcoming sections.

The findings of this study corroborate results of many others across the globe in suggesting that low-impact land use types like rangelands and low-intensity croplands can provide important habitat for open-habitat species (Dutta & Jhala, 2014; Kamp et al., 2011; Leonard A. Brennan, 2005; Wright et al., 2012). Similarly, the results are also congruent with studies that have found intensification of agriculture beyond a certain threshold to have negative impacts on native bird communities in both grasslands (Chamberlain et al., 2000; Donald et al., 2001; Kamp et al., 2011; Phalan et al., 2011) and forests (Elsen, Ramesh, & Wilcove, 2018).

7.3 Effect of changing land-use on regional bird species pool

As the local composition of birds was not very different between protected grasslands, rangelands and extensive agriculture, it is fair to assume that the latter can act as secondary refugia for most of the species. However, community composition at the local scale does not tell us the effects of land use on all species especially the intrinsically rare species. Hence, it is important to check the effects of land use on regional species pool to check whether some species get lost due to change in habitats. This would essentially involve checking the landscape scale species richness and how it changes with change in habitats.

Similar to local species richness, landscape-scale species richness was also highest in intensive agriculture, followed by extensive agriculture. However, this regional species richness reduced drastically in both seasons when non-native species were excluded from the analysis, and was significantly lower than protected grasslands. The higher naïve and estimated species richness in protected grasslands suggests that none of the production land uses can independently sustain all species in the native regional pool. But at the same time, the presence of only two unique species in protected grasslands indicates that a combination of multiple low-impact production landscapes, extensive agriculture and rangelands in this case, can together sustain most of the regional species pool. This further highlights the importance of these two low-impact land-uses as secondary habitats for bird species.

7.4 Seasonality of patterns

The patterns of local community structure in terms of species richness, abundance were fairly similar between two seasons for protected grasslands, rangelands and extensive croplands. The major change in patterns was with intensive agriculture. Community composition in intensive agriculture was very different during the winter but became similar to other land-uses during the summer. The use of intensive agriculture by native birds during summer suggests that at the current level of intensity, it can still form a secondary habitat for birds during the breeding season. Unlike many other studies which show the ubiquity of primary habitat during the breeding season (Elsen et al., 2016), the results of this study suggest that native birds use production land-uses even during the breeding season. My observations indicate that some species such as Black-crowned Sparrow-Lark, Common Babbler, White-eared bulbul etc. were using them as their breeding sites. Many other species such as Purple sunbird, Eurasian collared-dove, Indian silverbills locally migrated to these irrigated croplands in cropping season because of the availability of food. Their presence however could’ve been due to the availability of natural habitats in the vicinity that could act as a potential refugia. In the absence of such natural habitats in surroundings, as would be the case for complete agricultural landscape, these birds are unlikely to persist.

7.5 Habitat correlates of species richness and composition at local scales

Species richness across all land uses was influenced by crop biomass, woody plant biomass and forb biomass. During winter, species richness increased with crop biomass, a parameter intimately associated with intensification of agriculture; probably because of the associated increase in productivity and creation of new microhabitats due to irrigation. Increase in foliar biomass of woody trees expectedly increased species richness as they provide important resources in terms of food (especially insects) and cover (nesting substrate, thermal refugia). Whereas, forb biomass was inversely related to the bird richness, during both the seasons. The decrease in species richness with increase in forb biomass was due to proliferation of unpalatable species like *Aerva javanica, Haloxylon salichornium* and *Dipterigyium glaucum,* which did not allow regeneration of other trees or grass in the vicinity. These species commonly colonise regenerating agricultural fields and overgrazed grasslands and are hence a direct consequence of land use. During summer, compositional diversity of vegetation also increased bird species richness potentially suggesting that birds use more heterogeneous habitats during the breeding season. . This may perhaps result from the need of different microhabitats to complement contrasting ecological needs of breeding birds that would corroborate the concept of landscape complementation.

Similar to species richness, community composition was also affected significantly by crop volume and woody plant foliar volume. Additionally, grass volume also had an effect on composition in the winter season. During summer, crop volume and woody plant foliar biomass were influential in driving bird community composition. Most native species had lower than average optimum for crop volume during both the seasons suggesting that farming and associated factors negatively influence native bird communities.

7.6 Conservation implication: Reconciling human needs with wildlife conservation

Primary habitats are often associated with greater richness and abundance as compared to production land-uses and considered irreplaceable for biodiversity conservation (Lee et al., 2011). Results from my study suggest that although primary grassland habitat is essential to save the full spectrum of the regional species pool, low-impact land-uses can act as important secondary habitats for conservation of bird species. The local level patterns suggest that livestock grazing and extensive agriculture do not have drastic negative impacts on bird community structure and are together able to sustain most of the species even at a regional scale. My findings further support the notion that strategically managed production landscapes can be important sites for conservation, and a secondary alternative to protected areas where the creation of one is not feasible (Dutta & Jhala, 2014; Elsen et al., 2016; Wright et al., 2012). However, these findings need to be augmented with species-level population data that examines how species' densities and not just occurrence (as reflected by species richness) depends on land-use types and habitat structure, as proposed by Green et al, Phalan et al.

A landscape approach for conservation has often been advocated for the conservation of grasslands in India but very few studies have investigated whether such an approach is ecologically feasible (Dutta et al., 2011). Evidence from this study supports the approach of conserving grasslands as large-landscapes strategically managed as agro-pastoral mosaics with small protected areas embedded in them. This strategy can potentially conserve all the regional species while not compromising on the human needs, as shown by empirical evidence gathered in this study and many others (Dutta & Jhala, 2014).

In the Thar desert, the Desert National Park Wildlife Sanctuary is the largest protected area with more than 3000 sq.km. under protection (Dutta et al., 2017). However, it is also home to more than 50,000 people who depend completely on agro-pastoralism within the sanctuary. Unsurprisingly, the use of land within the sanctuary has been the epicentre of unrest between the local people and the local forest department for many years. Evidence from this study suggests that low-impact use of land coupled with habitat management like removal of forb species, controlling lopping by provision of alternate firewood supply and reseeding of grass in forb affected area can help conserve general bird diversity without hampering livelihood needs. Another alternative could be setting up sustainable community farms where agro pastoralism can be strategically managed to achieve biodiversity conservation while also sustaining human livelihoods.

7.7 Caveats and methodological issues

The biggest caveat of the study comes from the fact that birds can travel large distances and are not bound to a particular habitat. Thus, the landscape scale species richness estimate can only be interpreted as the number of species able to use a particular habitat and does not indicate whether the habitat or land-use is able to sustain a particular species. Similarly, mean local richness also indicates the number of species using the habitat on an average, without giving any information about the identity or abundance of the species. Further the results are averaged across a large number of sites and can potentially be inflated by rare species, abnormal plots or by species which are vagrant to the habitat. This problem can be overcome by additionally inferring results from the ordination of community composition data, in which every independent point is at the site level and then grouped at the habitat level. Community composition data can reveal the broad patterns with consideration of species identity and is robust to some of the problems associated with univariate measures such as species richness. However, most common ordination techniques are not sensitive to individual species and similar compositional patterns of dominant species can often mask a differential pattern shown by a relatively rare species. Considering these caveats, it is essential to look at all the community parameters like species richness, abundance and composition together before making generalised inferences. Data on occurrence and abundance of individual species and other community-level properties like functional diversity can make the inferences even more robust.

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