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Research Article

Modelling habitat quality of high conservation priority vertebrates in an arid ecosystem with limited baseline data

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ABSTRACT

Few arid nations have the baseline data needed to map high value habitat at local scales. We used remote sensing to model local habitat value across Saudi Arabia, an arid nation with degraded ecosystems and limited baseline data. First, we digitally mapped the ranges of Saudi Arabia's 199 high conservation priority terrestrial vertebrate species to produce a Conservation Priority Species Score for every point in the Kingdom. We then used ArcGIS to score five landscape attributes (to 30-m resolution) that correlate with vertebrate occupancy rates in arid ecosystems (urban development, land-use naturalness, hydrology, protected area status, and terrain complexity) to produce a Site Quality Score for every location. By multiplying the broadscale Conservation Priority Species Score by the local Site Quality Scores, we generated a Site Conservation Value Score for every location in Saudi Arabia. Modelled Site Conservation Value Scores correlated significantly with species counts from field surveys conducted at 12 sites, suggesting our model has value. We review the literature from arid ecosystems to test the assumptions inherent in our model and acknowledge the limitations of our approach. These results suggest our interim model can help identify local site value in arid ecosystems until more refined models are generated.

Key words: ArcGIS, Biodiversity conservation, Conservation triage, Protected Areas, Saudi Arabia

INTRODUCTION

To mitigate the global biodiversity crisis, conservation agencies, land managers, industries and governments require accurate and efficient mapping of habitat quality at local scales. However, such data can be prohibitively expensive to collect in the field and can take too long to obtain. As a result, remotely sensed data are increasingly used to model species distributions in time and space (Nagendra, 2001; Turner *et al*., 2003; Abdullah *et al*., 2018).

Like most arid ecosystems, Saudi Arabia's biodiversity is under threat from increasing urbanization, desertification, agricultural intensification, excessive hunting, climate change, and numerous other processes (Abuzinada *et al*., 2005; Al-Rowaily *et al*., 2015; Barichievy *et al*., 2018). Consequently, 113 species in Saudi Arabia are listed as vulnerable, 40 are endangered, 16 are critically endangered, three are regionally extinct, and one is globally extinct. Only one of the 21 extant nationally endemic species is listed as least concern and none are stable or increasing (IUCN, 2021). Furthermore, desert ecosystems are highly sensitive to disturbance and recover slowly, if at all (Bainbridge, 2012). Hence, it is essential to conserve any remaining high value habitat in the Kingdom. However, to date there are no published models of Kingdomwide habitat quality and very little baseline data about species distributions, making it challenging for organizations to avoid damaging high value habitat or to prioritize which habitat to protect. Therefore, the purpose of this study is to use remote sensing to develop a preliminary model of habitat quality that can be used by conservation agencies, industries and land managers to help identify and protect Saudi Arabia's highest conservation priority habitat.

In previous work, we developed an empirical scoring methodology to identify and rank Saudi Arabia's highest conservation priority species based on their global and regional conservation and population statuses, national responsibility, national abundance, level of endemicity, and phylogenetic distinctness (see Boland & Burwell, 2020, 2021 for details). Using this methodology, 199 species (five amphibians, eight freshwater fish, 29 mammals, 55 reptiles, and 102 bird species) are identified as high conservation priority to Saudi Arabia, each with a relative conservation priority score ranging from 0 to 100 (highest conservation priority).

In this study, we first aim to model the location of Saudi Arabia's 199 high conservation priority vertebrate species. Given that these high conservation priority species are more likely to occur in high value habitat within their range, we then model five landscape variables that are known to correlate with presence/absence of high conservation priority vertebrate species: (i) urban development, (ii) land-use naturalness, (iii) hydrology, (iv) protected area status, and (v) terrain complexity. Our premise is simple: in arid environments high conservation priority terrestrial vertebrates are more likely to occur amongst natural vegetation, near a wadi, in complex terrain, away from human structures, and within a protected area, than in a flat, barren site, far from a

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wadi, close to urban structures, with no formal protection. We review the literature from arid environments that supports and tests these assumptions and discuss the limitations inherent in our approach.

MATERIALS AND METHODS

Modelling landscape level conservation priority scores

To model landscape level conservation priority scores, we used ArcGIS 10.6.1 (ESRI, 2018) to superimpose digitized range maps for each of Saudi Arabia's 199 high conservation priority terrestrial vertebrate species, and then applied the Weighted Sum tool to calculate the summed Conservation Priority Species Scores for every point in the Kingdom (cf. Mateo, 2012; Domisch *et al.*, 2015). We used the Reclassify by Function tool with a linear transformation to rescale the map to values between 0 and 100.

Modelling site habitat value

To model site habitat value, we first scored five habitat attributes for every point in the Kingdom: infrastructure, naturalness, hydrology, protected area status, and terrain complexity. For each attribute, we used ArcGIS to score every location according to its habitat value, ranging from 0 (indicating the point has the lowest habitat value) to 100 (indicating the site has maximum habitat value) as described below.

First, we created an input layer to score habitat value according to its proximity to populated centers and associated infrastructure (cf. Rüdisser *et al.*, 2012; Wanghe *et al.*, 2020). Urban spatial data were obtained from Navteq. Populated centers were categorized according to latest available population estimates: major cities (>1,000,000 people), cities (100,000–1,000,000), large towns (50,000–100,000), medium towns (10,000–50,000), small towns (5,000–10,000) and villages (<5,000). Each populated area was buffered a distance according to its population size (with larger population centers having a larger buffer: Table 1). Points inside populated area buffer zones were scored 0, with habitat value scores increasing linearly to 100 at a variable distance from the buffer perimeter (with larger population centers having a wider zone of impact: Table 1).

Infrastructure was categorized as highways, secondary roads, railway lines, pipelines and powerlines and buffered to 20 m. Areas inside infrastructure buffer zones were scored 0, with habitat value scores increasing linearly to 100 at 3 km from the edge of the highway buffer or 1 km from the edge of other infrastructure buffers (Table 1). Once the urban and infrastructure grids were created, we used the Cell Statistics tool to create a composite urban and infrastructure input layer by selecting the minimum habitat value score for each location.

Second, we created an input layer to score local habitat value according to the relative naturalness of three principal land use types: (i) high intensity agriculture, (ii) mixed woodlands / low intensity agriculture, and (iii) rangelands (cf. Krosby *et al.*, 2015; Cao *et al.*, 2020). We used the Normalized Difference Vegetation Index (NDVI) to extract vegetation data from the multispectral imagery obtained from the Sentinel-2 satellite sensor. We used NDVI thresholding to classify the vegetation layer into three the land use types. Using the Euclidian Distance tool, distance grids were created for each vegetation type. High intensity agriculture was scored as 0, while surrounding areas were rescaled using a linear function to a score of 50 at 5 km from the perimeter of each farm. Areas of mixed woodlands / low intensity agriculture were scored as 100 with surrounding areas rescaled using a linear function to a score of 50 at 1 km from the perimeter of the habitat type. Rangelands were scored as 50. Cities and towns were excluded from this analysis.

Third, we created an input layer to score habitat value according to its proximity to wadis (drainage channels) and wetlands (both natural and artificial). We used a 30-m digital elevation model to calculate wadi drainage patterns (publicly available from Ministry of Economy, Trade and Industry of Japan and the United States National Aeronautics and Space Administration). We used the Fill tool to fill in low-lying sinks and imperfections in the dataset, and the Flow Direction tool to determine the direction of flow from each cell to its steepest downslope neighbour. We then used the Flow Accumulation tool to calculate the accumulated flow for each cell. The Conditional Operator tool extracted the drainage patterns, and the Stream Order tool assigned a wadi order number to each branch of the drainage network from 1 (the smallest wadi tributary) to 7 (the largest wadi). We used the Stream To Feature tool to convert the data to a vector network (cf. Magesh *et al.*, 2012; Omran *et al.*, 2016). Dendritic patterns in sand seas were excluded from the analysis. The centre line of each wadi was then buffered to a distance equal to wadi order number multiplied by 1,000 m (thus the largest wadis were buffered to 7,000 m and the smallest wadi tributaries to 1000 m). Areas inside wadi buffer zones were scored 100, with habitat value scores decreasing linearly to 0 at 1 km from the edge of the buffer. We used satellite imagery to identify significant wetlands. Each wetland was buffered to 1 km from the perimeter. Wetlands and their buffer zones were scored 100 with habitat value scores decreasing linearly to 0 at 10 km from the perimeter of the buffer.

Fourth, we created an input layer to score habitat value according to its protected area status with the following categories: (i) national protected areas, (ii) Important Bird and Biodiversity Areas (Birdlife International, 2021), (iii) Important Plant Areas (Plantlife International, 2021), (iv) coastal 400-m setback areas, (v) proposed protected areas, and (vi) other identified protected areas (World Database on Protected Areas; Saudi Aramco Biodiversity Protection Areas). Areas inside protected areas and their buffer zones were scored as per Table 1, with habitat value scores decreasing linearly to 0 with increasing distance from the protected area buffer (see Table 1). Once the protected area grids were created, the Cell Statistics tool was used to create a composite protected area input layer by selecting the maximum habitat value score for each location.

We created an input layer to score habitat value according to its terrain complexity (cf. Huang *et al.*, 2020). Terrain complexity is grouped into six variables: slope, terrain undulation, surface cutting depth, profile curvature, surface roughness and elevation variation coefficient. These variables were derived from GDEM 30-m elevation data. We used the Reclassify By Function tool to score terrain complexity at each location from 0 (least complex, lowest habitat value) to 100 (most complex, highest habitat value). Once the terrain complexity grids were created, we used the Cell Statistics tool to calculate the mean habitat value score for the six terrain complexity variables for each point in the Kingdom.

Table 1. The scoring system used for each of the site attributes.

Attribute	Habitat value score (max: 100)	Buffer (km)	Zone of influence (km)
Land use			
High intensity agriculture	0	0	5
Traditional agriculture / woodlands	100	0	1
Rangelands	50	0	1
Hydrology			
Wadi order 7 (largest wadis)	100	7,000	1
Wadi order 6	100	6,000	1
Wadi order 5	100	5,000	1
Wadi order 4	100	4,000	1
Wadi order 3	100	3,000	1
Wadi order 2	100	2,000	1
Wadi order 1 (smallest wadis)	100	1,000	1
Wetlands	100	1,000	10
Infrastructure			
Major cities	0	10	200
Cities	0	10	100
Large towns	0	10	50
Medium towns	0	5	20
Small towns	0	2	10
Villages	0	2	5
Highways	0	.02	3
Secondary roads, railways	0	.02	1
Pipelines	0	.02	.3
Powerlines	0	.02	1
Protected areas			
National Protected Areas	100	1,000	10
Important Bird and Biodiversity Areas	75	1,000	5
Important Plant Areas	75	1,000	1
Other identified protected areas	50	1,000	1
Proposed protected areas	25	1,000	1
Coastal setback areas	100	400	5
Terrain complexity			
Slope	0 – 100	n/a	n/a
Terrain undulation	0 – 100	n/a	n/a
Surface cutting depth	0 – 100	n/a	n/a
Profile curvature	0 – 100	n/a	n/a
Surface roughness	0 – 100	n/a	n/a
Elevation variation coefficient	0 – 100	n/a	n/a

Modelling site conservation value

After scoring each location out of 100 for each of the five habitat value attributes, we used the Cell Statistics tool to calculate the Mean Habitat Value Score for each location. We then used the Map Algebra tool to divide the Mean Habitat Value Score by 100 to obtain a Site Quality Score (ranging from 0 to 1) for every point in the Kingdom. We used the Map Algebra tool to multiply the summed Conservation Priority Species Score by the Site Quality Score to create a Modelled Site Conservation Value Score for every point in the Kingdom.

Testing the model

Field surveys were conducted between 2014 and 2017 at 12 designated or proposed Saudi Aramco Biodiversity Protection Areas by five independent third-party consultancies. The 12 sites are distributed across Saudi Arabia and cover most major habitat types (Table 2). At each site, two experienced field biologists conducted five-day / four-night surveys during spring (late February to early May). Vertebrate species were recorded using direct and indirect observations (including active searches, linear transects, sit and wait recordings, nocturnal spotlighting searches), and by setting 30 Sherman traps, eight pitfall trap lines, six remote camera traps, and four ultrasonic bat detectors at appropriate locations throughout each site, and (if wadis or wetlands were present) by conducting amphibian sound recordings and freshwater fish searches. We tested the final model by running a linear regression between our Modelled Site Conservation Value Score and the number of vertebrate species recorded in field surveys at 12 locations across Saudi Arabia. Statistical analyses were conducted using JMP 16.1 statistical software (SAS, 2021).

Table 2. Location and date of field surveys.

Site ID	Location	Habitat type	Year of survey
1	Abha	Alpine	May 2015[a]
2	Abqaiq	Wetlands	April 2016[b]
3	Abu Ali	Coast	April 2015[c]
4	Bahrah	Woodlands	May 2016[b]
5	Dhahran 1	Jebels	April 2014[a]
6	Dhahran 2	Wetlands	April 2014[a]
7	Khurais	Scrub desert	May 2017[a]
8	Manifah	Coastal	April 2015[c]
9	Medinah	Woodlands	May 2016[b]
10	Shaybah	Sand seas	February 2017[d]
11	Tanajib	Coastal	April 2015[c]
12	Udhailiyah	Scrub desert	March 2017[e]

Field surveys were conducted by [a] Clean Environment Technology, [b] Arensco, [c] Conseco, [d] Royal Society for the Conservation of Nature Jordan, [e] SNC Lavalin

RESULTS

We generated a landscape level conservation priority heat map, which depicts summed relative High Conservation Priority Scores for all terrestrial vertebrates in Saudi Arabia (Figure 1). We then generated site habitat value heat maps for each of the five modelled habitat variables: infrastructure, land use naturalness, hydrology, protected area status, and terrain complexity (Figure 2), and a relative Site Quality Score map (Figure 3), which depicts modelled habitat quality at a 30-m level.

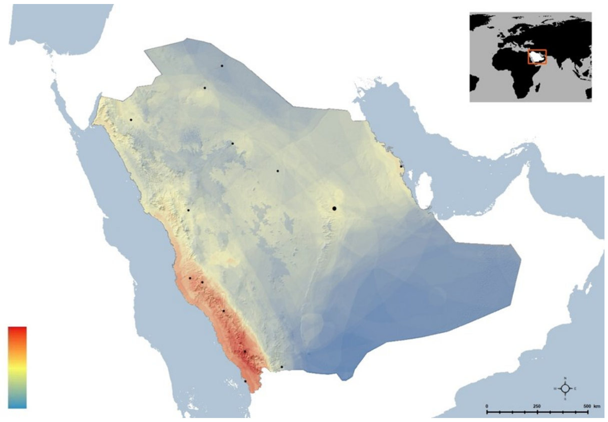

Figure 1. Heat map of summed conservation priority scores for all terrestrial vertebrates in Saudi Arabia. Warmer colors depict areas of higher conservation priority; cooler colors depict areas of lowest conservation priority. Black dots denote regional capital cities.

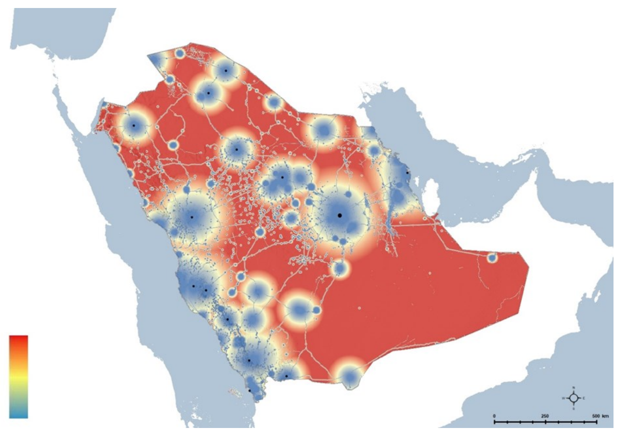

Figure 2a. Heat map of infrastructural impact on habitat value. Warmer colors depict areas of lower infrastructural impact on habitat value; cooler colors depict areas of greater infrastructural impact on habitat value. Black dots denote regional capital cities.

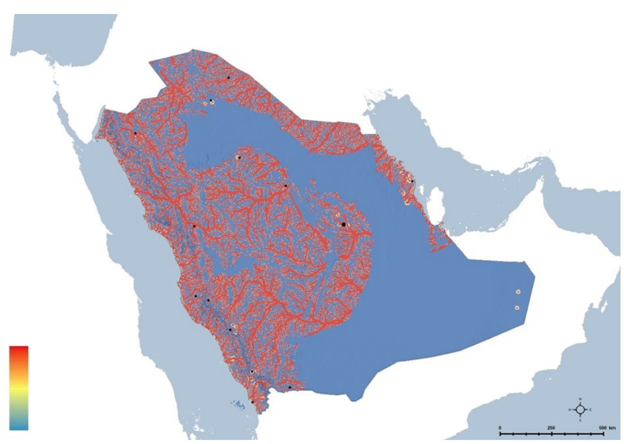

Figure 2b. Heat map of hydrological impact on habitat value. Warmer colors depict areas of higher habitat value due to the presence of wadis or wetlands; cooler colors depict areas further from wadis or wetlands. Black dots denote regional capital cities.

Table 3. Modelled areas of influence for major land use types in Saudi Arabia.

Land use	Direct footprint km^2 (% of KSA)	Indirect impact km^2 (% of KSA)
High intensity agriculture	7,222 (0.3%)	171,911 (7.4%)
Traditional agriculture / woodlands	12,355 (0.5%)	51,794 (2.2%)
Rangelands	1,882,261 (80.7 %)	1,882,261 (80.7 %)
Populated areas and infrastructure	85,526 (4%)	1,528,735 (65.6%)
National Protected Areas	342,885 (14.7%)	419,991 (18.0%)

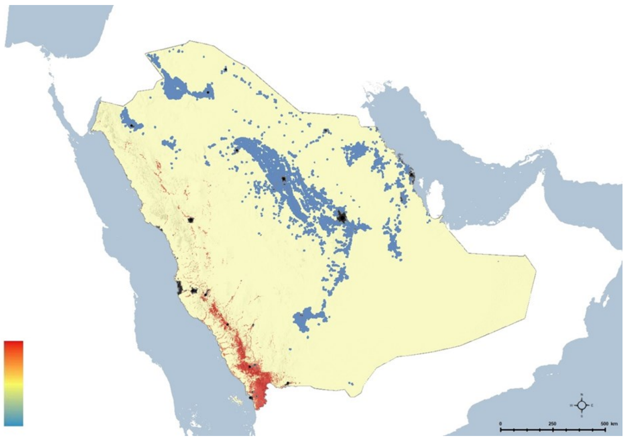

Figure 2c. Heat map of vegetation impact on habitat value. Warmer colors depict areas of higher habitat value due to the presence of woodlands and traditional low intensity agriculture; cooler colors depict areas of lower habitat value due to high intensity agriculture; tan areas depict rangelands; black polygons denote regional capital cities.

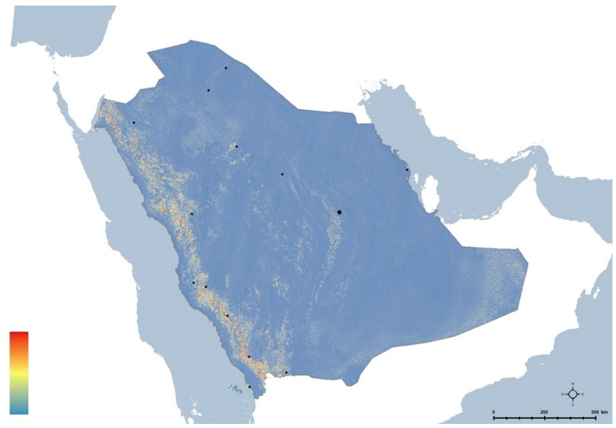

Figure 2e. Heat map of terrain complexity impact on habitat value. Warmer colors depict areas of higher habitat value due to the presence of more complex terrain; cooler colors depict flatter areas of lower habitat value; black dots denote regional capital cities.

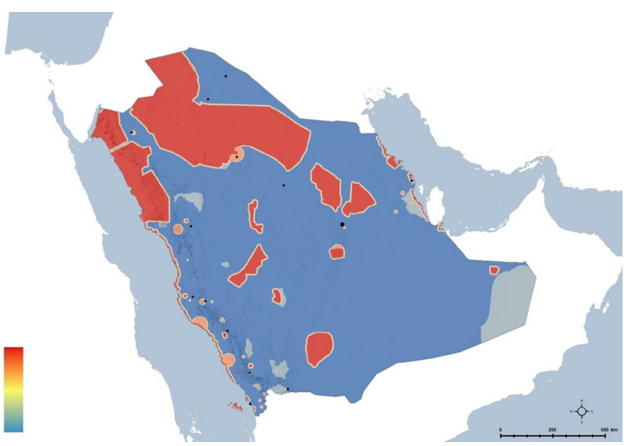

Figure 2d. Heat map of protected area status impact on habitat value. Warmer colors depict areas of higher habitat value due to the presence of protected areas of variable status; cooler colors depict areas further from protected areas or of low protection status; black dots denote regional capital cities.

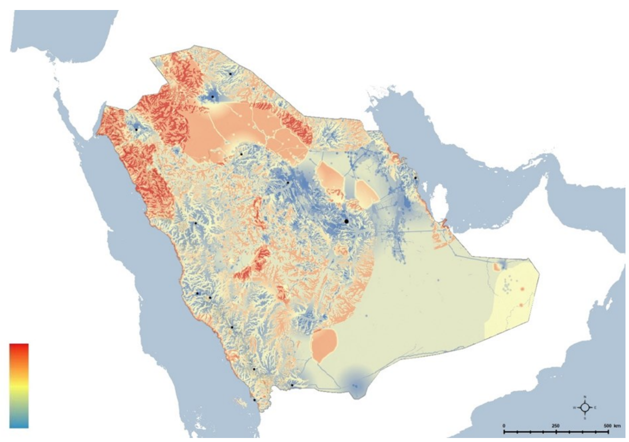

Figure 3. Heat map of overall site habitat quality. Warmer colors depict areas of higher habitat value; cooler colors depict areas of lower value; black dots denote regional capital cities.

Finally, we generated a map of the Modelled Site Conservation Value Score for every point in the Kingdom (summed Conservation Priority Species Score multiplied by Site Quality Score), to model the relative likelihood that high conservation priority vertebrates will occur at any given site (Figure 4). The total areas of Saudi Arabia covered by major land use types (both their direct footprint, and their surrounding areas of attenuating impacts) are presented in Table 3.

A linear regression revealed a significant positive relationship between Modelled Site Conservation Value Score and the number of vertebrate species recorded at the 12 surveyed sites (Linear regression $F_{1,10}$=12.2, P=0.01; Figure 5).

DISCUSSION

We used a novel method to produce a heat map that depicts the summed conservation priority scores for every vertebrate species in Saudi Arabia (Figure 1).

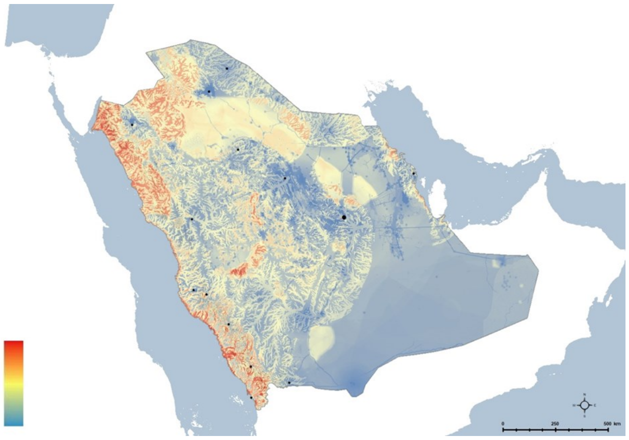

Figure 4a. Heat map of site conservation value. Warmer colors depict areas of higher conservation value due to the presence of high conservation priority species *and* high value habitat; cooler colors depict areas of lower conservation value; black dots denote regional capital cities.

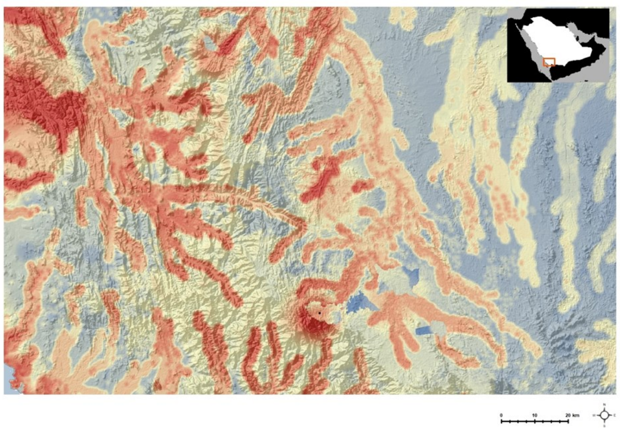

Figure 4b. Detail of the final habitat model from southwest Saudi Arabia showing local variation in site conservation value; black dot denotes Abha city.

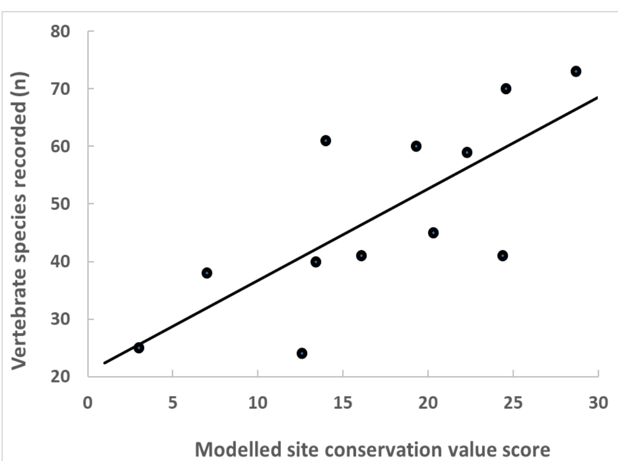

Figure 5. Linear regression of the number of vertebrate species recorded from field surveys conducted at 12 sites across Saudi Arabia versus modelled site conservation value score. Numbers next to points denote site number (see Table 2).

This map demonstrates that the highest vertebrate conservation priority areas occur in the southwest coastal plains and the ‘Asir Mountains. While this map is useful, it is ultimately based on broadscale, expert range maps of low resolution that do not take into account local variations in habitat quality. High conservation priority species are more likely to occur in patches of high value habitat within their range. Therefore, we used ArcGIS to map and score five landscape attributes that are known to correlate with vertebrate presence/absence in arid ecosystems: infrastructure, land use naturalness, hydrology, protected area status, and terrain complexity (Figure 2). By taking the mean scores of these five attributes at each point, we developed a map of local site quality, which depicts the attractiveness of any given site to high conservation priority vertebrates (Figure 3). We then multiplied the site quality score by the summed conservation priority score for each point in the Kingdom to generate a model of site conservation value to 30-m resolution (Figure 4). This modelled site conservation value was significantly related to the number of vertebrate species recorded in field surveys previously conducted at 12 sites across the Kingdom (Figure 5). This suggests the model is reasonably reliable, although more field surveys should be conducted to further test and enhance the model’s robustness.

While ours is a novel approach, comparable methodologies have been applied to model and map habitat values in numerous conservation programs (e.g., Nagendra 2010; Hefley *et al*., 2015; Fabris *et al*., 2018; Corradini *et al*., 2021; Zheng *et al*., 2021).

The impacts of populated areas and infrastructure on arid biodiversity

The first attribute we modelled was populated areas and associated infrastructure. For the myriad reasons outlined below, very few high conservation priority species persist in viable numbers in arid urban centers, and thus all points within our populated or industrial areas layer were scored as zero for this attribute.

Urbanization is one of the most ecologically damaging of any land-use types and has profound effects on biodiversity (Hansen *et al*., 2005; Newport *et al*., 2014). Accordingly, metanalyses demonstrate that species richness and diversity (especially vertebrates and plants) usually decline in urban and peri-urban environments (Grimm *et al*., 2008; Faeth *et al*., 2012). Within cities and their surrounding areas, the vast majority of native biodiversity is displaced by infrastructure and artificial, impermeable ground surfaces. The few native species that are able to thrive within cities are generally commensal and/or invasive (McKinney, 2006), and thus not of high conservation priority, by definition. Some predators proliferate in cities, especially introduced species, such as cats, dogs and rats, as well as commensal native predators (especially Arabian Red Fox *Vulpes vulpes arabica* in Saudi Arabia). These abundant predators further reduce the reproductive success and survivorship of native prey species attempting to colonize an urban environment. Native animals in cities may also suffer from drastically altered microclimates, radical changes in community composition, reduced primary productivity, highly modified food supply, and novel diseases (Chace & Wallace, 2006; McKinney, 2006; Faeth *et al*., 2012).

The impact of cities on biodiversity is likely to be especially high in Saudi Arabia (and in most cities in arid environments) where urban councils rarely plant native desert species; instead, they tend to utilize fast-growing,

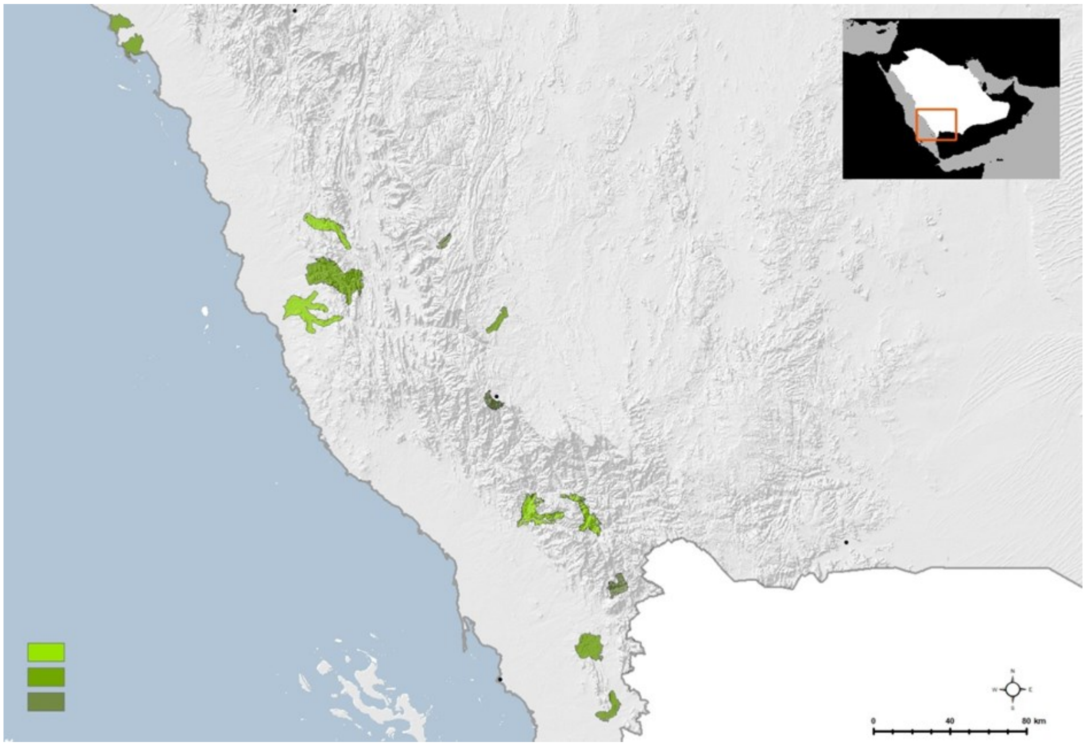

Figure 6. The 13 patches of highest modelled conservation value not currently in designated protected areas. Darker green patches represent especially high conservation value patches; black dots denote regional capital cities.

non-native species in ornamental parks and streetscapes (Abudjain, 2003). Furthermore, Saudi Arabian cities typically exhibit a sprawling style of urban development with limited interstitial natural spaces and small residential yards containing very few native plants. Such development results in a relatively high rate of local extinctions in built areas (Sushinsky *et al*., 2013).

There are, of course, exceptions, and a few of Saudi Arabia's high conservation priority species can be found in urban areas: specifically, Fan-tailed Raven *Corvus rhipidurus*, Tristram's Starling *Onychognathus tristramii* and African Straw-colored Fruit Bat *Eidolon helvum* (Boland & Alsuhaibany, 2020; Cooper-Bohannon *et al*., 2020). However, none of these species prefer these habitats, whereas the vast majority of high conservation priority species actively avoid or are unable to persist in urban areas. Thus, we suggest the score of zero for habitat value within urban areas is justified.

A city's impact on biodiversity is not limited to the immediate urban area; indeed, it can be felt for many kilometers as infrastructure, people, pest species, and pollution radiate from the city center (Grimm *et al*., 2008; Mcdonald *et al*., 2009). These impacts have not been quantified in Saudi Arabia (or in other arid countries). For the purposes of our analysis, we assumed that the sum of these negative impacts decreases linearly with increasing distance from urban perimeters (Table 1). Below we review some of the negative effects on desert biodiversity surrounding urban areas, starting with the most proximal and acute.

Areas immediately around cities suffer most heavily from hunting, which is a national pastime in Saudi Arabia. For example, a recent analysis estimated that over 1.7 million wild birds are killed illegally in Saudi Arabia every year (Brochet *et al*., 2009). This high rate of hunting is a major source of population decline in the Kingdom for birds, mammals, and reptiles alike (e.g., Al-Johany, 2007; Al-Shayaa *et al*., 2007; Brochet *et al*., 2009; Barichievy *et al*., 2018; Aloufi *et al*., 2019; AlRashidi *et al*., 2021; Wilms *et al*., 2021). Saudi Arabian hunters regularly travel 200 km or more in order to mount a multi-day hunting trip (Abdullah Alsuhaibany pers. comm).

In addition, biodiversity in areas surrounding urban centers is most prone to invasive, pest or commensal species that proliferate in cities and subsequently colonize the surrounding areas. In Saudi Arabia, large populations of omnivorous mammals (Hamadryas Baboons *Papio hamadryas* in the west and Arabian Red Fox throughout) have adapted to living on the edges of urban areas (Mori *et al*., 2007; Mohammad & Basuony, 2016) due to a combination of suboptimal waste management and meso-predator release. These large source populations facilitate colonization of surrounding natural areas, which is likely to negatively impact prey species with decreasing intensity as one moves further from the populated area.

Another major threat to biodiversity around arid cities is desertification caused by a combination of overgrazing by domestic livestock belonging to urban dwellers, off-road driving, and excessive firewood collection, which are common activities in Saudi Arabia (Al-Rowaily, 1999; Al-Nafie, 2007; Barichievy *et al*., 2018). These practices lead to significant loss of native vegetation cover and altered vegetation structure (with cascading effects on native fauna), as well as soil compaction, loss of soil stabilizers, increased exotic species, and nest and burrow destruction (Lovich & Bainbridge, 1999; Keshkamat *et al*., 2012; Assaeed *et al*., 2019). Extreme temperatures, intense solar radiation, high winds, limited moisture and low soil fertility ensure desert ecosystem recovery takes decades following such disturbance (Bainbridge, 2012). Biodiversity around Saudi Arabian cities also suffers from high levels of illegal solid waste dumping (Radwan & Mangi, 2019), smuggling and poaching (Islam *et al*., 2020), as well as a greater frequency of arterial roads and utility corridors with associated effects on biodiversity.

Less direct impacts of urban areas on biodiversity include light, noise, water and air pollution, which can affect the physiology, behaviour and reproduction of a range of animal taxa for 200 km or more from the edge of urban areas (Mcdonald *et al*., 2009; Newport *et al*., 2014). For example, dryfall of particulate compounds from urban air pollution can be a major source of supplemental nitrogen for plants, favouring exotic plant species over native ones (Mcdonald *et al*., 2009), with demonstrated effects on biodiversity for at least 180 km from some major urban areas in USA (Lovich & Bainbridge, 1999). Such air pollution is likely to have similar impacts on Arabian native flora and associated fauna where particulate dryfall is often very high (e.g., Ali-Mohamed & Jaffar, 2000; Ali-Mohamed & Ali, 2001).

While the negative effects of urban areas certainly decrease with increasing distance from the urban periphery (Mcdonald *et al*., 2009; Benítez-López *et al*., 2010), not enough research has been conducted to determine if this relationship is linear or otherwise. For simplicity, we assumed urban impacts decrease linearly with increasing distance from the urban area (depending on the size of the population: Table 1).

The infrastructure supporting human population centers also significantly impacts vertebrate distribution and abundance. Highways and other roads not only cause habitat loss, they also result in direct mortality and injury of wildlife through wildlife-vehicle collisions, which affects large numbers of animals per annum (Forman & Alexander, 1998; Dean *et al*., 2019). In Saudi Arabia, the animal road mortality rate has not been quantified, but is likely to be relatively high because both dispersal and home range size of arid-adapted animals tend to be larger in comparison to that of similar species in higher rainfall environments (Harestad & Bunnel, 1979; Dickman *et al*., 1999; Badgery *et al*., 2021), meaning that desert species are more likely to interact with roads (Fahrig & Rytwinski, 2009). For example, recent surveys in pre-Saharan Tunisia revealed that roughly one vertebrate is killed per kilometer of road, every day (Dhiab & Selmi, 2021).

The negative impacts of roads extend beyond the limits of the road itself. Roads facilitate human access to surrounding areas for hunting, firewood collection, off-road driving, camping, littering, and illegal dumping, which are all very common in Saudi Arabia (Barth, 1999; Al-Nafie, 2007; Brochet *et al*., 2009; Al-Mutairi *et al*., 2015; Al-Mosa *et al*., 2017; Radwan & Mangi, 2019). Vehicle disturbance around road verges in arid areas causes soil compaction, facilitates invasion by non-native plants, and crushes vegetation, ground-nesting birds, and burrowing animals (Milton & Dean, 2010; Assaeed *et al*., 2019). Roads are often associated with transmission lines, which have large impacts on soaring bird mortality in areas of high bird abundance in Saudi Arabia (Shobrak, 2012; Shobrak *et al*., 2021). The habitat surrounding roads can also be influenced by air, land and water pollution from salt, sediment, chemical run-off, exhaust, and dust. Such road-related pollution makes surrounding areas unsuitable for certain flora and fauna (Bennett, 2017).

Roads also serve as corridors for many alien and invasive species (Gelbard & Belnap, 2003; Coffin, 2007; Von der Lippe & Kowarik, 2007), wildlife diseases (McCormack & Allen, 2007) and predators (Wysong *et al*., 2020; Quintana *et al*., 2021), which can further supress surrounding biodiversity (Frey & Conover, 2006; DeGregorio *et al*., 2014). In Saudi Arabia, the high density of ravens, Black Kites *Milvus migrans*, Arabian Red Foxes and Hamadryas Baboons near roadsides is obvious and is likely to reduce the abundance of small prey species in adjacent habitat (Mori *et al*., 2007; Mohammad & Basuony, 2016; Boland & Alsuhaibany, 2020). Likewise, most invasive plant species in Saudi Arabia occur adjacent to roadsides (Thomas *et al*., 2016), outcompeting native plants and reducing habitat value.

Roads also result in noise and light pollution, which impacts biodiversity for a kilometer or more from the road itself in temperate and woodland habitats (Forman & Alexander, 1998), and likely further in arid environments where there is little vegetation to help mitigate these effects (Dean *et al*., 2019). Noise pollution from vehicles using roads can significantly impact species that use vocalizations in mate attraction, territory defence, group cohesion, and alarm calling (Hanna *et al*., 2011; Tennessen *et al*., 2014). Traffic noise impedes species that rely on sound to navigate, forage and avoid predators, such as bats, owls and amphibians (Berthinussen & Altringham, 2012; Lukanov *et al*., 2014; Luo *et al*., 2015; Senzaki *et al*., 2016). Among birds, traffic noise can reduce reproductive success (Halfwerk *et al*., 2011), which is a particular concern in arid ecosystems where lifetime reproductive success tends to be lower than in comparable temperate species (Tieleman *et al*., 2004). Traffic noise can induce a chronic stress response in amphibians, birds, freshwater fish, mammals and reptiles (Blickley *et al*., 2012; Shier *et al*., 2012; Tennessen *et al*., 2014; Lunde *et al*., 2016; Mickle & Higgs, 2018). For example, a recent study of Egyptian Spiny-tailed Lizards *Uromastyx aegyptia* in pre-Saharan Tunisia revealed that corticosterone levels increased with proximity to roads (Kechnebbou *et al*., 2019). Persistent traffic noise can also reduce telomere length in birds, diminishing longevity (Meillère *et al*., 2011). Many species simply abandon areas of high traffic noise (Slabbekoorn & Ripmeester, 2008; McClure *et al*., 2013; Bennett, 2017), as demonstrated in Goitered Gazelles *Gazella subgutturosa* in Iran (Ghadirian *et al*., 2019).

In addition, roads can impede animal movement and dispersal, both physically and behaviorally, thereby increasing habitat fragmentation. For example, Cream-coloured Courser *Cursorius cursor* avoid coming within 135 m of paved roads in semi-arid Canary Islands (Palomino *et al*., 2008). Reptiles in arid and semi-arid environments suffer population fragmentation and home range reduction due to roads (Jones *et al*., 2011; Peaden *et al*., 2011). Molecular studies across multiple taxa confirm a significant and rapid loss of genetic diversity in small populations isolated by roads (Holderegger & Di Giulio, 2010; Dean *et al*., 2019), including in arid ecosystems (Epps *et al*., 2005).

These combined effects can affect vertebrate distribution and abundance for up to 3,000 m either side of a road, with most impacts occurring closer to the road. Busier roads have wider-reaching impacts on biodiversity than narrower roads with lower traffic volume (see reviews in Reijnen *et al*., 1995; Forman *et al*., 2003; Riitters & Wickham, 2003; Benítez-López *et al*., 2010; Silva *et al*., 2012; Bennett, 2017). Therefore, our model assumes highways and secondary roads have impacts on arid vertebrates that attenuate linearly for 3,000 m and 1,000 m, respectively.

Our model also considered the impacts of railway lines on biodiversity. Like roads, railways can cause habitat loss and fragmentation, noise and air pollution, wildlife collision, soil compaction (from maintenance vehicles), and creation of dispersal corridors for invasive species, pathogens and predators (Borda-de-Água *et al*., 2017; Popp & Boyle, 2017). In Saudi Arabia freight and passenger trains occur at a low frequency. Therefore, we scored their impact on habitat value as per secondary roads (Table 1).

The construction of pipelines can also have negative impacts on biodiversity due to habitat loss, plant mortality and altered plant and animal community structure and composition (Richardson *et al*., 2017), particularly in arid environments where ecological recovery is slow. During construction, native vegetation and topsoil are removed, facilitating the introduction and spread of non-native and invasive plant species (Naeth *et al*., 2020). Pipelines can also present a linear, physical barrier that impedes or alters animal movements and fragments arid habitat (Fiori & Zalba, 2003). Most pipelines are associated with an adjacent vehicular track for regular maintenance, which widens the area of impact, and increases accessibility to remote areas thereby facilitating hunting, habitat loss and degradation (Finer *et al*., 2008; Butt *et al*., 2013).

The zone of impact of pipelines on biodiversity seems to vary between different locations. Impacts on surrounding vegetation were limited to a few meters of the pipeline corridor in arid North America (Jones *et al*., 2014), and within 25 m of the corridor in semi-arid Uzbekistan (Naeth *et al*., 2020). But in China, the effects of pipelines on vegetation were detectable up to 300 m away (Shi *et al*., 2014). Given the large number of vehicle tracks that accompany pipelines in Saudi Arabia, our model assumes that pipelines impact biodiversity with decreasing effect for up to 100 m from the pipeline itself.

Power lines cause much the same impacts on biodiversity as pipelines, though the power lines themselves can result in additional direct mortality of birds and bats through collision and electrocution (Richardson *et al*., 2017). Such mortality is a significant conservation concern for many threatened species (Jenkins *et al*., 2010), including in arid environments (e.g., Uddin *et al*., 2021). A 28-year study revealed that electrocutions and collisions with overhead power lines have contributed to population declines of Egyptian Vultures *Neophron percnopterus* in East Africa (Angelov *et al*., 2013), while a more recent study demonstrated that the rate of mortality was equally high in Saudi Arabia (Oppel *et al*., 2020). The few other studies conducted in Saudi Arabia to quantify the rates of mortality and injury from power lines also suggest that power lines pose a conservation concern (Shobrak, 2012). In one study, 236 White Storks *Ciconia ciconia* were found dead below a single power line (Shobrak *et al*., 2009); in another, 532 birds from at least 22 species were recorded below a 6-km power line (Shobrak, 2021). The actual rate of mortality is likely to be much higher because of inherent sampling limitations (Schutgens *et al*., 2014). Consequently, some mammals and birds avoid coming within close proximity of power lines. For example, Great Bustard *Otis tarda* in semi-arid Spain have altered their migration patterns to avoid power lines (Palacín *et al*., 2017).

While power lines may provide some bird species with additional nesting sites (D'Amico *et al*., 2018), these birds often have reduced breeding success due to increased exposure to weather, electromagnetic pollution, and electromagnetic fields (Janiszewski *et al*., 2015; D'Amico *et al*., 2018). Furthermore, such adaptable species tend not to be of high conservation priority. In Saudi Arabia, power lines may have facilitated range expansions of ravens and introduced House Crows by providing nesting substrate in treeless landscapes (as documented in Pied Crows *Corvus albus* in arid South Africa: Cunningham *et al*., 2016). Since these birds are efficient generalist predators, an increase in distribution and abundance of these species is likely to have negative impacts on surrounding biodiversity.

A meta-analysis covering 234 bird and mammal species found that the impacts of powerlines and other infrastructure can be detected for up to a kilometer on bird populations and for up to five kilometers in mammals, with variation according to taxa and habitat type. Such avoidance behavior tends to be particularly strong in open habitats, such as arid environments, due to enhanced visibility (Benítez-López *et al*., 2010). In our model, we assumed that powerlines reduce biodiversity for up to 1 km with diminishing effect with distance. If our assumptions regarding the impacts of populated areas and infrastructure on biodiversity are roughly correct, then such infrastructure impacts biodiversity across at least 66% of Saudi Arabia's mainland (Table 3).

The impacts of land use naturalness on arid biodiversity

The second attribute we modelled was vegetation density and naturalness. One of the biggest predictors of biodiversity presence/absence is proximity to natural vegetation (Rüdisser *et al*., 2012), particularly in arid environments where vegetation provides scarce food, shelter and nest sites in an otherwise barren landscape. Our model classified vegetation within the Kingdom into three broad categories: (i) high intensity agriculture, (ii) low intensity agriculture / mixed woodlands, and (iii) rangelands, each with very different impacts on biodiversity.

Our model assumes that modernized, high intensity agriculture has a strong net negative impact on biodiversity. Most farming in Saudi Arabia now employs a high intensity approach, consisting of pivot-irrigated monocultures (typically wheat, barley, sorghum, millet or alfalfa), with regular applications of agrichemicals, including insecticides, molluscicides, rodenticides, fumigants, plant growth regulators and other chemicals (World Bank, 2012; Alzaidi *et al*., 2013). This type of high intensity agriculture is often regarded as the biggest driver of biodiversity loss globally (e.g., Tscharntke *et al*., 2005). The loss of ecological heterogeneity at multiple spatial and temporal scales, repeated tillage, and the application of agrichemicals significantly reduces invertebrate and vertebrate diversity (Hails, 2002; Benton *et al*., 2003; Green *et al*., 2005; Vandermeer *et al*., 2005), including in arid and semi-arid areas. For example, very large losses of biodiversity were recorded in high input cotton monocultures in semi-arid African savannah (Baudron *et al*., 2009).

In arid environments, agricultural irrigation creates more mesic habitats with significantly elevated plant and insect abundance. Consequently, high intensity farms usually support relatively large numbers of individuals from a narrow range of generalist species that are more resilient to environmental perturbation and able to utilize these abundant novel resources. Conversely, specialists have narrower niche requirements and are thus disproportionately affected by the reduced niche availability on high intensity farms (Siriwardena *et al*., 1998). The few studies from Arabia tend to support this effect. For example, a survey of rodents in the Jordan Rift valley found the generalist Dwarf Gerbil *Gerbillus nanus* was abundant on and around farms whereas the specialist Lesser Egyptian Gerbil *G. gerbillus* was absent (Talbi, 2009). The Desert Hedgehog *Paraechinus aethiopicus*, a generalist omnivore (Mohamed, 2021), was more abundant (and heavier) on farms in Qatar due to the abundance of resources compared to natural desert areas (Abu Baker *et al*., 2017). Likewise, a radio-tracking study from central Saudi Arabia found very high densities of the highly omnivorous Arabian Red Fox around farms (Macdonald *et al*., 1999).

High intensity farms appear to have a strong net negative impact on the conservation status of birds in Saudi Arabia. While at least 101 of Saudi Arabia's 401 regularly occurring bird species can be found foraging in high intensity farms, often in high numbers (Boland & Alsuhaibany, 2020), the great majority of these species (n=91) are of low conservation priority (Boland & Burwell, 2020). Many adaptable species have colonized Saudi Arabia as a result of the intensification of agriculture since the 1970s (Jennings, 2010; Boland & Alsuhaibany, 2020). Conversely, most high conservation priority species are unable to utilize high intensity farmland. Of Saudi Arabia's 102 high conservation priority bird species, 55 have ranges that overlap with high intensity farmland (the rest are restricted to the coasts, wetlands or alpine areas). Only ten of these 55 species forage regularly on high intensity farms, while the other 45 species have suffered significant habitat loss due to the conversion of their natural habitat into high input agriculture (Boland & Alsuhaibany, 2020). Thus, while some high conservation priority species utilize high intensity farms (for example, the best place to see the critically endangered Sociable Lapwing *Vanellus gregarius* in Saudi Arabia is in farmlands around Tabuk and Haradh), on balance, high intensity farming has a significant net negative impact on vertebrate conservation status in Saudi Arabia.

The biodiversity impacts of high intensity agriculture are felt several kilometers beyond the perimeter of the farm itself. One study in southwest Jordan demonstrated that irrigated farms have an impact on bird assemblages up to 2.6 km from the farm edge, even though the surrounding habitat was structurally intact. Characteristic ground-dwelling species of open sand dune habitats were absent within 1 km of farms, and then began to increase with increasing distance from farms for an additional 1.6 km. Again, species that were more abundant on farms were primarily widespread, opportunistic species and therefore of low conservation priority (Khoury & Al-Shamlih, 2006).

Poisoning and persecution of vertebrate predators and scavengers in and around agricultural areas further alters community structure and diminishes biodiversity values for many kilometers from the farm itself. This is a significant problem in Saudi Arabia: in a recent survey, half of the farmers interviewed admitted to setting poison traps while all of them admitted to shooting predators (Oppel *et al*., 2020). Most poisoned animals in Saudi Arabia remain unburied, resulting in secondary poisoning of vultures and other scavengers (Oppel *et al*., 2020; Shobrak *et al*., 2020).

An even broader impact of pivot-irrigated agriculture in arid regions is the gradual lowering of the surrounding water table due to groundwater pumping, which leads to progressive xerification of vegetation at a landscape scale (Dilts *et al*., 2012). In Saudi Arabia, excessive groundwater pumping for irrigation (which is responsible for 88% of freshwater removal in the Kingdom: World Bank, 2012) has caused a dramatic reduction in surface and sub-surface water, which has sunk over 95 m in agricultural regions, significantly increasing soil salinity (Al-Saleh, 1992; Grindle *et al*., 2015; Al-Ghumaiz, 2016; Alharbi & Helmy, 2017). This in turn results in the loss of *rawdah* (temporary meadows) that would appear after rainfall and support a relative abundance of native biodiversity, including nomadic desert species such as Arabian Lark *Eremalauda eremodites* (which appears to have declined precipitously in recent years: Boland & Alsuhaibany, 2020), and landscape level mortality of acacia trees, which are keystone species throughout much of Saudi Arabia. For these reasons, our model assumes the biodiversity impact of high intensity farming areas diminishes linearly with increasing distance for 5 km from the edge of each farm.

The second vegetation class we identified was woodlands mixed with traditional, low intensity farming. Our model assumes this mosaic habitat has a net positive impact on biodiversity. This land use type occurs in the 'Asir mountains (southwestern Saudi Arabia) where precipitation is the highest in the Kingdom and large-scale pivot irrigation is unsuitable due to the complex terrain. Farmers grow a mixture of crops, typically alongside fallow fields, mixed hedgerows, and patches of native juniper and acacia woodlands.

This habitat type contains the richest, most diverse, and most heterogenous vegetation in the Kingdom. According to the 'habitat heterogeneity hypothesis', such habitat contains relatively more niches and should support a greater density and diversity of fauna than open scrub habitat or barren desert (Rosenzweig, 1995; Tews *et al*., 2004). The positive relationship between vegetation density and vertebrate abundance has been well demonstrated in Saudi Arabia and neighbouring arid countries for birds (Newton & Newton, 1997; Van Heezik & Seddon, 1999; Khoury *et al*., 2007), mammals (Al-Hazmi & Ghandour, 1992; Hackett *et al*., 2013), reptiles (Disi, 2011), and amphibians (Akram *et al*., 2015; Al-Qahtani & Al-Johany, 2018). The presence of vegetation is also an important predictor of presence for freshwater fish in arid environments (Filipe *et al*., 2002).

There are no data on the biodiversity impacts of traditional mixed farming in Arabia. However, studies from other traditional agricultural areas indicate that such farming practices typically have net positive impacts on biodiversity if patches of native vegetation are retained (Fischer *et al*., 2012; Queiroz *et al*., 2014). Indeed, the conservation value of traditional farming landscapes is often exceptional, with many species able to persist because their habitat remains well connected, land use intensity is low, and their remaining habitat has been lost (Fischer *et al*., 2012).

Studies from other arid areas support our assumption that low intensity farming in the remaining natural habitat in the ʻAsir is likely to benefit biodiversity. In the South Sinai Peninsula, traditional agriculture maintains wild plant diversity (Norfolk *et al*., 2013) and enhances bird density and species richness, compared to surrounding unmanaged habitat (Norfolk *et al*., 2015). In Tunisia, traditional low intensity agriculture of mixed production contains more birds and greater diversity compared to dense date palm plantations (Selmi & Boulinier, 2003). The same effect is reported from farms in semi-desert regions of Kazakhstan (Kamp *et al*., 2016). However, there are certainly some negative impacts of ʻAsir farming practices. For example, persecution and poisoning of predators and scavengers are significant issues in the ʻAsir (Cunningham *et al*., 2009; Oppel *et al*., 2020), perhaps even more than anywhere else in the Kingdom because of the relatively large number of predators and scavengers that occur in the southwest. Pesticide use is commonplace in these areas (Asiri *et al*., 2020; Ramadan *et al*., 2020) and usually associates with reduced biodiversity (Hole *et al*., 2005; Rahman, 2011; Jeliazkov *et al*., 2016), though it is likely to be less prevalent than on high intensity farms. Finally, lowering of water tables due to groundwater extraction is also likely to be an issue, though again not nearly as severe as in high intensity agricultural areas.

Furthermore, the ongoing clearing of woodlands in the ʻAsir to create more farmland poses a serious threat to many high conservation priority vertebrates (Boland & Burwell, 2020, 2021). Juniper and acacia woodlands once covered the upper slopes of the ʻAsir Mountains, but now no large uninterrupted tracts of woodlands occur in the highlands (Pellikka & Alshaikh, 2016) due to extensive clearing and dieback (Miyazaki *et al*., 2007). Thus, *any* existing woodland patches in the southwest is now critical, irreplaceable habitat. Given the importance of remaining alpine woodland habitat, and in light of data from other low intensity farming practices in arid regions, we assigned this habitat type the maximum score for this variable.

The third vegetation class we identified was rangelands where both nomadic and sedentary farmers graze domestic camels, sheep, and goats on native vegetation. This land use type occurs across 75-80% of Saudi Arabia (Al-Rowaily *et al*., 2015; Table 3). For the reasons outlined below, our model assumes that the biodiversity value of rangelands has been negatively impacted by livestock grazing, though not as severely as in high intensity farmlands.

Virtually all of Saudi Arabia's rangelands is declining in condition, productivity and naturalness due to pervasive overgrazing, abolition of the traditional *hema* system (communal stewardship of common land), excessive firewood collection, off-road driving, illegal dumping, destructive camping, meso-predator release, and clearing of wadis for gravel extraction (Al-Rowaily, 1999; Al-Nafie, 2007; Bakhashwain, 2010; Daur, 2012). Stocking rates have increased by orders of magnitude in recent decades (Al-Rowaily *et al*., 2015). Thus, what were once vast areas of natural steppe-like vegetation are now heavily desertified with altered soil structure and nutrient cycling, compacted soil, erosion, and much depleted plant density and diversity (Mirreh & alDiran, 1995; Barth, 1999; Al-Rowaily *et al*., 2009, 2012, 2015). Some degraded areas are thought to be beyond recovery (Ghazanfar & Osborne, 2010).

Studies from arid and semi-arid regions around the globe demonstrate that livestock grazing leads to significant habitat degradation by modifying fine-scale habitat features and food resources, increasing bare ground (Eldridge *et al*., 2017), reducing the seed bank for granivorous species (Pol *et al*., 2014), promoting woody plant cover, and altering microclimate, vegetation composition and structure (Yates, *et al*., 2000). Livestock grazing in arid regions markedly diminishes ecosystem services associated with habitat provision, biodiversity, and soil and water functions (Eldridge & Delgado-Baquerizo, 2017), reduces ecosystem resilience (Jones, 2000), and impedes the response of wildlife to drought and other disturbances (Howland *et al*., 2014).

Rangeland degradation thus has significant impacts on vertebrate conservation. Numerous studies have shown that livestock grazing in arid ecosystems results in a considerable reduction in species abundance, richness and diversity in mammals (Eccard *et al*., 2000; Hoffmann & Zeller, 2005; Read & Cunningham, 2010), reptiles (Castellano & Valone, 2006; Howland et a, 2014; Val *et al*., 2019), and birds (Gonnet, 2001; James, 2003; Cardoni *et al*., 2015; Zarco *et al*., 2019; Faria & Morales, 2020; Tadey, 2021). In some places, the impacts of grazing on vertebrate fauna can be severe. For example, bird abundance in the Sahel has decreased by 80% since the 1960s due to increased grazing intensity (Zwarts *et al*., 2018). In Australian rangelands, grazing and agriculture are the presumed cause of extinction for at least 78 plant species and a major threat to 105 others (James *et al*., 1999).

While livestock grazing in arid ecosystems may actually benefit some abundant generalist species adapted to open habitats, it negatively impacts specialists with narrow ranges (James, 2003; Tabeni & Ojeda, 2003; Macchi & Grau, 2012; Schieltz & Rubenstein, 2016; Marone *et al*., 2017). For example, studies from semi-arid North America show that livestock grazing causes the loss of entire sets of grassland birds and the disappearance of the most sensitive species, which are replaced by widespread generalists (Zalba & Cozzani, 2004).

Although livestock grazing in Arabia has obvious impacts on vegetation cover (Abuzinada, 2003) – which are visible when comparing fenced and unfenced areas, both in the field and on satellite imagery – these impacts have rarely been quantified. Exclusion experiments in western Saudi Arabia demonstrate that livestock grazing significantly decreases vegetation cover, density and species richness, and increases the abundance of weeds and unpalatable species (Al-Rowaily *et al*., 2015). In Emam Saud Bin Abdulaziz Protected Area (formerly Mahazat as-Sayd), livestock were excluded by fencing in 1989, which saw plant diversity increase 2.5-fold within the first four years of livestock exclusion (Newton & Newton, 1997) and "has allowed a spectacular recovery of native vegetation" (Al-Sodany *et al*., 2011). A brief study from a wadi in the UAE showed that fenced areas contained 74 plant species, whereas unfenced areas grazed by goats contained only two (Shahid, 2017).

The impacts of rangeland degradation on vertebrate conservation have not been quantified in Arabia. Anecdotal reports indicate that faunal abundance and diversity is much higher in fenced areas free from domestic livestock (Abuzinada, 2003). The fenced Emam Saud Bin Abdulaziz Protected Area contains a far greater diversity and density of birds, reptiles, and mammals than the surrounding desertified landscape (Al-Sodany *et al*., 2011). When sheep and goats (but not camels) were removed from Harrat al-Harrah and Al-Khunfah protected areas, the resident populations of Arabian Sand Gazelles *Gazella marica* noticeably increased within a few years. Likewise, the removal of camels from core areas of the Ibex Reserve resulted in a considerable increase in Nubian Ibex *Capra nubiana* (Abuzinada, 2003). Unfortunately, most or all of those animals were subsequently killed by hunters (Barichievy & Sandouka, 2015; Barichievy *et al*., 2018). Bird diversity and abundance increased in Harrat al-Harrah after most livestock were removed (van Heezik & Seddon, 1999). In Saudi Arabia, bird species primarily associated with rangelands tend to be decreasing regionally (Boland & Alsuhaibany, 2020). In Kuwait, preliminary surveys revealed that livestock exclusion areas contained twice as many native vertebrate species as surrounding grazed habitat (Al-Khalifa *et al*., 2012). For these reasons, our model assumes that rangelands contain significantly reduced biodiversity value and were scored accordingly.

The impacts of hydrology on arid biodiversity

The third landscape attribute we modelled was surface drainage. In Saudi Arabia, the main hydrological features are drainage channels (wadis), which are usually dry but can support ephemeral streams and pools after sporadic rainfall, and may occasionally flood (Bajabaa *et al*., 2014). As a result, wadis invariably contain a much greater density and diversity of plants compared to surrounding habitats (Schulz & Whitney, 1986; Mandaville, 1990; Miller *et al*., 1996; Ali *et al*., 2000; Brinkmann *et al*., 2009; Moosavi *et al*., 2019). For example, while only 37 plant species occur throughout the wadi-free 640,000-km^2 Rub' al-Khali desert (Mandaville, 1986), at least 126 plant species occur in Wadi al-Noman in Makkah province (Khalik *et al*., 2013), 196 species in Wadi 'Ar'ar in the Northern Borders (Osman *et al*., 2014), and 266 species in Wadi Turbah Zahran in the 'Asir Mountains (Al-Robai *et al*., 2017). Even in the most biodiverse areas of southwestern Saudi Arabia, plant diversity is significantly greater in wadis than in surrounding habitat (Heneidy & Bidak, 2001).

Plant diversity is a primary determinant of animal diversity (Rosenzweig, 1995; Siemann *et al*., 1998; Schuldt *et al*., 2019). Accordingly, the considerably more diverse and far more dense plant communities in Arabian wadis have been demonstrated to support comparatively rich populations of invertebrates, reptiles, birds, amphibians and mammals (van Heezik & Seddon, 1999; Jennings, 2010; Tourenq *et al*., 2011; Al-Qahtani *et al*., 2018; Milto *et al*., 2019), while freshwater fish in Saudi Arabia occur almost exclusively in wadis (Hamidan & Shobrak, 2019).

Certainly, some species may avoid wadis. For example, studies from Saudi Arabia show that Egyptian Spiny-tailed Lizards avoid burrowing in wadis (because the substrate cannot support burrows), but nonetheless build their burrows *near* wadis, presumably to benefit from the extra shade and forage available (Wilms *et al*., 2009; AlRashidi *et al*., 2021). Even the Arabian Oryx *Oryx leucoryx*, almost legendary for its ability to endure hyper-arid conditions, is more likely to be found in Acacia-rich wadis than in barren dune habitat (Tear *et al*., 1997; Landau *et al*., 2021).

Our model assumes that larger wadis have a wider zone of influence than smaller wadis. Larger wadis receive a larger catchment, and therefore tend to be more wooded and support a greater density of vegetation compared to smaller wadis and tributaries. Thus, larger wadis are likely to support a larger number and diversity of vertebrates, which are likely to travel from further distances to utilize the wadi's resources. Furthermore, because vegetation density and habitat heterogeneity gradually decrease with increasing distance from wadis (Mandaville, 1990; Miller *et al*., 1996; Heneidy & Bidak, 2001), we assigned decreasing biodiversity value with increasing distance from wadis.

Another significant predictor of vertebrate presence/absence is surface water. The vast majority of Saudi Arabia's landmass contains very little or no surface water. There are no natural rivers or lakes, and only a few small springs, primarily in the southwest (Cox *et al*., 2012; Garcia *et al*., 2015). Thus, artificial wetlands represent the most reliable source of surface water in the Kingdom. In Saudi Arabia, the number of artificial wetlands has steadily increased since the first treated wastewater systems were established in the 1960s. Large artificial wetlands now exist near every city and large town (Al-Obaid *et al*., 2017).

Wetlands are hotspots of biodiversity in Saudi Arabia because primary productivity is orders of magnitude higher than in surrounding habitat. At least 220 (55%) of Saudi Arabia's 401 regularly occurring bird species have been recorded from a 1-km^2 artificial wetland in Dhahran (Boland *et al*., 2017). At least 287 bird species have been recorded at the 10-km^2 Malaki dam on the edge of the 'Asir foothills, which includes one of the most diverse assemblage of breeding birds in Arabia (Jennings, 2010). Likewise, 89 (41%) of Saudi Arabia's 219 breeding bird species have been recorded nesting within the 60-km-long wastewater stream that runs through Riyadh (Jennings, 2010; Boland & Alsuhaibany, 2020). High levels of biodiversity have been recorded in other wetlands in the region. For example, a constructed wetland at Nimr in Oman recorded over 117 species of bird within the first three years of operation (Al-Rawahi *et al*., 2014), and a wetland at Al Wathba in UAE contains over 21% of Abu Dhabi emirate's terrestrial animal and plant species, including 10 mammals, 16 reptiles, and 262 bird species (Soorae *et al*., 2020).

In arid environments, wetlands enhance the biodiversity value of surrounding habitats for several kilometers from the wetland itself. For example, avian species richness and abundance have been demonstrated to increase with increasing proximity to surface water in arid and semi-arid regions of Africa, North America and Australia (Fisher *et al*., 1972; Bock, 2015; Abdu *et al*., 2018). In Australian deserts, bird abundance is elevated for at least 5 km, even from small waterholes (James *et al*., 1999). Likewise, in the Kalahari, wetlands influence bird community composition for several kilometers (Abdu *et al*., 2018). In North Africa, sandgrouse nesting density is higher within 8 km of a wetland, and some will fly 70 km each way to drink from a waterhole (Yosef & Zduniak, 2011; Winkler *et al*., 2020). Similar results have been recorded in mammals: in semi-arid Australia, large mammals may travel up to 20 km to attend a waterhole (James *et al*., 1999); and in dry season Kenyan savannahs, water-dependent mammals are ten times more abundant within 10 km of a waterhole (Western, 1975).

The area surrounding a wetland is also important as it can provide a buffer for biodiversity using the wetland itself. Wetland birds, for example, are notoriously vulnerable to disturbance, and wetland occupancy rates can be affected by disturbance events at least 500 m away (Glisson *et al*., 2017), and in some instances can be directly impacted by noise and/or construction occurring 1,800 m away or more (Van der Zande *et al*., 1980). Indeed, bird occupancy at wetlands can be affected by events at the catchment level (Stevens & Conway, 2020). Given the density and diversity of terrestrial vertebrates utilizing wetlands in arid environments, their ability to attract and support wildlife from many kilometers away, and the importance of habitat surrounding wetlands, we ascribed maximum site value to wetlands, with the zone of influence extending for 10 km around the wetland perimeter.

The impacts of protected area status on arid biodiversity

Another key factor in determining the likelihood of vertebrate presence/absence is the degree of formal protection afforded a site. Protected areas can act as citadels against numerous threatening processes. Consequently, threatened species, rare species, and indeed common species, are typically more abundant and more likely to occur within a protected area than outside one (Fabricius *et al*., 2003; Devictor *et al*., 2007).

The differential between vertebrate species abundance inside versus outside a protected area is likely to be especially great in arid ecosystems where poor land management practices outside of protected areas can cause desertification. In Saudi Arabia, there are usually stark differences in species diversity and abundance in protected versus unprotected areas, particularly when the protected area is fenced and/or patrolled. For example, Emam Saud Bin Abdulaziz Protected Area contains a far greater diversity and density of native plants, birds, reptiles, and mammals than the surrounding desertified landscape (Islam and Knutson, 2008; Al-Sodany *et al*., 2011). While unfenced protected areas are not immune to threats, such as chronic hunting, poaching, livestock grazing, firewood collection, and off-road driving (Islam *et al*., 2011; Barichievy *et al*., 2018), our model assumes they are nonetheless likely to support far more plants and animals than unprotected areas.

What's more, the locations of most protected areas were chosen specifically to cover areas of high biodiversity value. Saudi Arabia's Protected Area System Plan was formulated to strategically protect key habitats containing endangered biotopes and high conservation priority species (Child & Grainger, 1990; Abuzinada, 2003). Some protected areas were designated precisely because they contain high value, endangered species, such as Ibex Reserve and At-Tubayq Reserve, which were established to protect Nubian Ibex *Capra nubiana*, while also protecting gazelles, Arabian Grey Wolf *Canis lupus arabs* and numerous other high conservation priority species (Abuzinada, 2003; Wronski & Macasero, 2008; Wronski *et al*., 2012). Other protected areas were established to serve as reintroduction sites for otherwise regionally extinct species. For example, Emam Saud Bin Abdulaziz Protected Area is a reintroduction site for Arabian Oryx and Common Ostrich *Struthio camelus*, both of which went extinct in the wild in Arabia during the 20th century (Islam *et al*., 2008, 2011); likewise Arabian Gazelle *Gazella arabica* and Arabian Sand Gazelle *Gazella marica* have been reintroduced into two and three protected areas, respectively. All native ungulates and large carnivores are now completely dependent on conservation management within the protected area network (Barichievy *et al*., 2018).

The biodiversity benefits of protected areas extend beyond the site boundary. For example, protected areas are important source populations for recolonization of surrounding degraded landscapes by animal and plant species, stepping stones between otherwise separated habitats, temporal retreats or nesting areas for dispersing species, and staging posts for migratory species. The benefit of each protected area is likely to diminish with increasing distance from the site boundary. Therefore, our model assumes protected areas enhance the biodiversity value of surrounding habitat with decreasing influence up to 10 km from the protected area boundary (Table 1).

Our model also incorporated proposed protected areas. The Saudi government proposed these sites as potential protected areas on the basis of their intrinsically high biodiversity values. However, since the sites are not formally or actively protected, our model assumes they suffer from additional threats not experienced at designated protected areas, such as excessive hunting, off-road driving, grazing, illegal dumping, firewood collection, that diminish their biodiversity value. Consequently, the model assumes the biodiversity value of proposed protected areas is significantly lower than designated protected areas (Table 1).

The model also included other areas of known high biodiversity value, including designated Important Plant Areas and Important Bird and Biodiversity Areas. Saudi Arabia currently has four Important Plant Areas designated under the auspices of Plantlife International. Important Plant Areas are regarded as the most important places in the world for wild plant and fungal diversity (Plantlife International, 2021). One of the sites, the Farasan Archipelago, is not included in this study as it is offshore (Hall *et al*., 2010). Another, Uruq Bani Ma'arid, is a designated Protected Area (Hall *et al*., 2011) and thus is assigned as full biodiversity value in our analysis. Jabal Qaraqir (roughly 80 km south of Tabuk) is an important site for both plant and animal diversity, including over 160 plant species, and several vertebrate species of high conservation priority, such as Nubian Ibex, Arabian Grey Wolf, Striped Hyaena *Hyaena hyaena*, Honey Badger *Mellivora capensis*, Arabian Partridge *Alectoris melanocephala*, Griffon Vulture *Gyps fulvus*, Desert Tawny Owl *Strix hadorami*, and Sinai Rosefinch *Carpodacus synoicus* (Llewellyn *et al*., 2010). Likewise, Jabal Aja' (about 10 km west of Hayil city) contains over 355 plant species, as well as Arabian Grey Wolf, Nubian Ibex, Egyptian Vulture, Griffon Vulture, and Desert Tawny Owl (Llewellyn *et al*., 2011).

Important Bird and Biodiversity Areas are designated as the places of greatest significance for the conservation of the world's birds. Saudi Arabia has 39 Important Bird and Biodiversity Areas designated by Birdlife International (Birdlife international, 2021). Each Important Bird and Biodiversity Area contains high conservation priority bird species, and often supports high priority mammals, reptiles, amphibians and freshwater fish. Unfortunately, none have been formally assessed in Saudi Arabia since 2013 and their condition is listed as unknown. Moreover, four sites are listed as under medium threat, four are highly threatened, and five are very highly threatened; six are receiving low levels of conservation action, 21 receive negligible conservation action, and none receive more than medium conservation action (Birdlife international, 2021). Given the lack of conservation action and their threatened status, we ascribed Important Bird and Biodiversity Areas as having partially diminished biodiversity value, with the zone of influence extending for 5 km around the perimeter of each site (Table 1).

The final protected area included in this attribute layer were coastal set-back areas. Globally, coastal areas support some of the most productive habitats. This is particularly the case in hot, arid ecosystems where coastlines often support highly productive mangrove forests, and the adjacent marine environment often contains prolific coral reef and seagrass ecosystems (Giri *et al*., 2011; McKenzie *et al*., 2020). Thus, there are typically stark differences in both productivity and species abundance between the arid interior and adjacent coastal areas (Burt, 2014). In Saudi Arabia, a government decree prohibits development from most areas within 400 m of the coastline, which has effectively created a very high value protected area along both coasts. Animals that utilize these coastal resources are likely to be concentrated closer to the coastline. The model assumes that vertebrates utilizing coastal areas would be concentrated closer to the coastal setback areas, and would decrease linearly with increasing distance from the coast for 5 km.

The impacts of terrain complexity on arid biodiversity

The final attribute we modelled was terrain complexity. Our model assumes that topographically more complex areas have greater conservation value than adjacent flatter areas. This is because greater topographic complexity typically correlates with greater taxonomic diversity, intraspecific genetic diversity, and ecological diversity (Garrick, 2011; Badgley *et al*., 2017; Morelli *et al*., 2020). Globally, a disproportionate share of taxonomic diversity occurs within topographically complex regions, such as large mountain ranges and deeply dissected plateaus (Antonelli *et al*., 2018; Morelli *et al*., 2020). This effect is pronounced in arid ecosystems where complex topography provides mesic refugia during episodes of climate change (Tapper *et al*., 2014; Byrne *et al*., 2017; Šmíd *et al*., 2017) and serves as reservoirs of endemic species (Di Virgilio *et al*., 2018). In Saudi Arabia, there is a significant positive correlation between terrain complexity and species diversity (Boland and Burwell, unpublished data). Accordingly, the mountainous areas in the southwest contain most of the Kingdom's endemic and high conservation priority plant and terrestrial vertebrate taxa (Mallon, 2011; Boland & Burwell, 2020, 2021).

Vertebrate occupancy rates are expected to be higher in more topographically complex areas, which contain more ecological niches, stronger environmental gradients, greater surface areas, refugia from extreme or fluctuating weather, places to hide, places to mount an ambush, shade, milder microclimate, reduced wind, reduced desiccation, greater soil moisture, enhanced germination rates, and greater productivity. Complex topography also enhances metapopulation dynamics: similar habitats in a weakly or sporadically connected patchwork can support donor populations for recolonization, thus reducing the risk of local extirpation (Brown & Kodric-Brown, 1977; Badgley *et al*., 2017; Fey *et al*., 2019). These effects are likely to be especially important in arid ecosystems where topographic complexity may provide the principal source of habitat heterogeneity in the near absence of vegetation.

Certainly, there are exceptions to this generalization. Sandgrouse, for example, avoid undulating surfaces where they are at risk of being ambushed by predators, and prefer instead to forage on flat, open surfaces (Ferns & Hinsley, 1995). But overall, complex habitats support greater species diversity and density and were scored accordingly in our model.

Limitations of the model

There are numerous limitations when developing a model based on so few baseline data. First and foremost, there are insufficient data to determine the relative values of each attribute used in the model. Thus, we had to make several simplistic assumptions. For instance, we scored rangelands as having half the value of mosaic woodland / traditional farming habitat, and we scored proposed protected areas as having one quarter the value of designated protected areas, and so on (Table 1). Although we support our scoring approach with a thorough review of data from other arid systems, the score we assigned for each landscape attribute is little more than a pragmatic estimate. Second, we assumed that landscape attributes will have impacts on biodiversity that attenuate linearly with increasing distance from a given attribute. Again, this is a simplistic assumption. Doubtless, the biodiversity impacts of roads, for example, will have a complex, non-linear relationship with increasing distance, confounded by taxa, the frequency and type of traffic, the specific ecological processes occurring in different habitat types, and other variables not considered in our model. However, there are no data at present to determine the precise nature of the interaction, and so we assumed a linear relationship as a simple approximation. Third, some of the remote data that we obtained are out of date and incomplete. As one example, our roads data layer does not include all roads. Many new roads have been added since the data layer was created, and some private roads may not be included in the map. Fourth, although the five landscape attributes that we modelled represent the most significant predictors of local vertebrate abundance, there are no doubt many other factors that influence the conservation value of any given site. Finally, although we found a significant positive linear relationship between our Modelled Site Conservation Value Score and species diversity, the sample size was very small (12 sites) for an area as large as Saudi Arabia.

Nonetheless, we contend that our model represents a very important contribution to biodiversity conservation planning in the Kingdom, because to the best of our knowledge this is the first attempt to develop a detailed conservation priority map at such a scale in the Arabian Peninsula. The model provides useful direction to conservation agencies, industries and land owners about the relative conservation value of sites across the Kingdom until a more robust map can be developed. We hope that our preliminary model stimulates others to build a more refined and more accurate model.

Implications of the model

According to the model, there are no extensive patches of very high-quality habitat remaining in Saudi Arabia. Instead, patches of high-priority land are scattered across the Kingdom, in fragments of alpine habitat in the southwest, in wadis along the coastal plains and northwest, in the sandstone jebels of Harrat al-Harrah in the north, and in a few wadis within the central Arabian shield. This makes biodiversity conservation in Saudi Arabia especially challenging.

The patches of highest conservation value habitat outside of designated protected areas all occur in the southwest, primarily in the highlands with some on the coast (Figure 6). These 13 patches range in size from 26 –359 km^2. Although these patches are small, we recommend that they be surveyed and considered for formal protection. We also recommend that some larger protected areas be established that connect multiple small patches of high value habitat to help conserve the Kingdom's precious and dwindling biodiversity.

CONCLUSION

We have used a novel approach to create a habitat model that can inform land owners, industries, and conservation agencies about the relative conservation value of every point in the Kingdom. Preliminary field surveys suggest the model is reasonably reliable, although more field surveys should be conducted to further test and enhance the model's robustness. Despite the limitations, we contend that our preliminary model is a very useful interim tool, and call on others to develop more refined and robust models to help conserve arid biodiversity.

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