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RESEARCH ARTICLE

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Food web properties vary with climate and land use in South African streams

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Abstract

1. Land use intensification and climate change are two prominent drivers of variation in biological communities. However, we know very little about how these two potential environmental stressors interact. Here we use a stable isotope approach to quantify how animal communities respond to urban and agriculture land use, and to latitudinal variation in climate (rainfall and temperature), in 29 streams across South Africa.
2. Community structure was shaped by both land use and climatic factors. The taxonomic diversity of invertebrates was best explained by an independent negative effect of urbanization, while abundance declined in summer. However, we could not use our variables to predict fish diversity (suggesting that other factors may be more important).
3. Both trophic functional diversity (quantifed using *isotopic richness*) and food chain length declined with increasing temperature. Functional redundancy (quantifed using *isotopic uniqueness*) in the invertebrate community was high in wet areas, and a synergistic interaction with urbanization caused the lowest values in dry urban regions. There was an additive effect of agriculture and rainfall on abundance-weighted vertebrate functional diversity (quantified using *isotopic dispersion*), with the former causing a decline in dispersion, with this partially compensated for by high rainfall.
4. In most cases, we found that a single dominant driver (either climate or land use) explained variation between streams. We only found two incidences of combined effects improving the model, one of which was amplified (i.e. the drivers combined

to cause an effect larger than the sum of their independent effects), indicating that management should first focus on mitigating the dominant stressor in stream ecosystems for successful restoration efforts.

5. Overall, our study indicates subtle food web responses to multiple drivers of change, only identified by using functional isotope metrics—these are a useful tool for a whole-systems biology understanding of global change.

KEYWORDS

agriculture, climate change, macroinvertebrates, multiple stressors, South Africa, stable isotope, urbanization

1 | INTRODUCTION

In our changing world, there is an increasing urgency to understand interactions among multiple environmental stressors such as global warming, species invasions, habitat destruction and pollution (Darling & Cote, 2008; Jackson, Loewen, Vinebrooke, & Chimimba, 2016; Jackson, Weyl, et al., 2016; Ormerod, Dobson, Hildrew, & Townsend, 2010; Reid et al., 2019). Land use intensification is a major driver of change which is already having global consequences for biodiversity and ecosystem services (Clapcott et al., 2012; Feld et al., 2016; Gutiérrez-Cánovas, Sánchez-Fernández, Velasco, Millán, & Bonada, 2015; Mantyka-Pringle, Martin, Moffatt, Linke, & Rhodes, 2014; Newbold, Hudson, Hill, Contu, & Lysenko, 2015). Although other drivers such as climate change and species invasions are also having negative effects (Dossena et al., 2012; Jackson et al., 2014; Mollot, Pantel, & Romanuk, 2017), habitat destruction associated with human activity is often considered the predominant driver of biodiversity loss in both freshwater and terrestrial ecosystems (WWF, 2018). With the global human population continuing to grow, this effect can be expected to increase over time, but we know very little about how whole communities of interacting species will respond (Bracewell et al., 2019; Kroeker, Kordas, & Harley, 2017). Climate change adds further complexity, and our knowledge of how food webs and functional diversity respond to combined land use and climate drivers is very limited (Bruder, Frainer, Rota, & Primicerio, 2019; de Vries et al., 2012; Gray et al., 2014).

Our planet is warming as a result of human activity and maximum temperature records across the world continue to be broken (Coumou & Rahmstorf, 2012). The Intergovernmental Panel on Climate Change predicts at least a 1.5°C average temperature increase by the end of the century, as well as global changes in patterns of precipitation (IPCC, 2014). Despite this, we know very little about how whole ecosystems will respond, particularly when a second driver of change is involved, which is becoming increasingly inevitable. There has been an increased focus recently on combined impacts of 'multiple stressors', with most evidence suggesting that they interact to cause effects which are non-additive (i.e. not the sum of their parts; Jackson, Loewen, et al., 2016; Jackson, Weyl, et al., 2016; Piggott, Townsend, & Matthaei, 2015b). A meta-analysis in 2016 found that just 88 papers had empirically quantified multiple stressor effects in freshwaters and of these, only one considered species interactions (Jackson, Loewen, et al., 2016; Jackson, Weyl, et al., 2016). This is arguably our biggest blind spot in ecology, as the effects of stressors will be transmitted through the food web. Moreover, freshwater ecosystems are particularly vulnerable with average population declines in vertebrates standing at >80% since 1970 (WWF, 2018).

The combined effect of human land use and climatic stressors is usually measured on the performance, abundance or distribution of a single species, without considering the consequences for food webs and whole ecosystems (Gray et al., 2014; Jackson, Evangelista, et al., 2017; Jackson, Wasserman, et al., 2017). Food web interactions are important in determining ecosystem stability and in distributing the cascading indirect effects (e.g. trophic cascades) of environmental stressors, and so it is fundamental that this knowledge gap is addressed. Food webs can shift dramatically in disturbed ecosystems (Gray et al., 2014; Shurin, Clasen, Greig, Kratina, & Thompson, 2012; Thompson et al., 2016; Yvon-Durocher, Montoya, Trimmer, & Woodward, 2011) due to the loss and/or addition of network nodes (the species in a food web), and changes in the strength or direction of network links (the trophic pathways in a food web). Different stressors will disproportionately affect different trophic levels, and evidence from terrestrial ecosystems suggests that predators are the feeding group most at risk following land use change (Barnes et al., 2014; Munguía, Trejo, González-Salazar, & Pérez-Maqueo, 2016; Ripple et al., 2014). Similarly, in freshwater ecosystems some studies have found that disturbance results in loss of rare predators (Ledger, Brown, Edwards, Milner, & Woodward, 2012) or causes declines in the trophic position of top consumers (McHugh, McIntosh, & Jellyman, 2010).

The independent effects of land use and climate change in freshwaters has been well-studied in some parts of the world including Europe and North America (Mantyka-Pringle et al., 2014; Martinuzzi et al., 2014; Woodward et al., 2012), but not usually using a food web approach. Those that do employ a food web approach have found that single stressors tend to simplify freshwater food webs, with empirical evidence for this in response to warming (O'Gorman et al., 2019), drought (Ledger et al., 2012), pollution (Thompson et al., 2016), and land use intensification (Yule, Gan, Jinggut, & Lee, 2015). More recently, studies have started to quantify the combined effects of land use and climatestressors, usually with experimental approaches. For instance, Piggott, Salis, Lear, Townsend, and Matthaei (2015) and Piggott, Townsend, and Matthaei (2015a) found that temperature had different effects on biofilm communities depending on the presence or absence of stressors associated with land use (sediment and nutrient pollution). Changes in precipitation can also impact stream food webs by altering flow, water quality and habitat availability (Kroll, Ringler, de la Cruz Cano Costa & De las Heras Ibanez, 2017). However, few studies employ a food web approach when considering realistic multiple stressor scenarios, while those that do only consider one part of the web (e.g. microbial webs; Cabrerizo, Medina-Sánchez, Villar-Argaiz, & Carrillo, 2019), use simple 'modules' of few species (Schrama et al., 2017), or use conceptual models rather than empirical data (Bracewell et al., 2019). There is a need to empirically quantify the combined effects of climate and land use change on freshwater food webs in natural environments to better understand how these stressors modulate ecosystem processes and services. Freshwaters provide many vital ecosystem services (such as drinking water, fish protein and flood mitigation) and support high levels of biodiversity, making them a priority for conservation efforts (Harrison et al., 2018). Feeding interactions (e.g. predator–prey) are often more important than horizontal interactions within populations (e.g. competition) in driving these processes, but most studies usually only consider one species or trophic level in multiple stressor research (see references in Jackson, Loewen, et al., 2016; Jackson, Weyl, et al., 2016).

Stable isotope analysis is an ideal tool to test how food webs respond to global change because it provides time- and space-integrated information about trophic relationships in communities of interacting species (Jackson et al., 2012; Layman, Arrington, Montaña, & Post, 2008). Emerging tools provide metrics of functional food web structure that can be compared across communities to address specific hypotheses relating to global change (Cucherousset & Villéger, 2015; Layman et al., 2012). For instance, this approach has recently been used in freshwater ecosystems to show that increased sedimentation from human land use caused a decline in trophic diversity (i.e. less diversity in diet between species; Burdon, McIntosh, & Harding, 2019); and that urbanization caused a decline in trophic redundancy (i.e. fewer species at each trophic level; Price, Sertić Perić, Romero, & Kratina, 2019). Here we use this approach to measure functional diversity as 'a component of biodiversity that generally concerns the range of things that organisms do in communities' following Petchey and Gaston (2006). Our isotopic metrics of functional diversity provide a holistic and functional view of how whole communities (and food webs) respond to stressors.

Understanding how multiple stressors interact within food webs is essential for understanding human impacts on ecosystems. However, to our knowledge, no studies have empirically quantified the response of freshwater food webs to human land use and climate change in Africa. Here we investigate food webs using 29 streams across a latitudinal climate gradient and an anthropogenic land use gradient. South Africa has experienced rapid population growth and increased migration to urban centres over the past 30 years (Kok & Collinson, 2006), resulting in an expanding urban footprint and increased demand for agricultural land with negative impacts on the environment (Todes, 2012). Although river systems had historically been negatively affected by agricultural run-off and water abstraction (Abalu & Hassan, 1998), they are increasingly coming under pressure from the effluent emanating from urban settlements (Jagals, 1997). Studies from Africa suggest that macroinvertebrate diversity in streams is negatively impacted by urban effluent, in particular from wastewater treatment works (e.g. Kasangaki, Chapman, & Balirwa, 2008). However, the impacts of urban and agricultural development on food webs and functional diversity have not been quantified. We address this knowledge gap using a stable isotope approach and hypothesize that: (a) land use and climate will interact non-additively to structure stream communities and food webs; (b) streams highly disturbed by human land use will have simpler isotopic food webs due to a loss of taxonomic and functional diversity; and (c) maximum trophic level will be low at impacted sites in comparison to pristine streams due to a loss of predatory species.

2 | MATERIALS AND METHODS

2.1 | Food web sampling

We sampled 29 first or second order streams from across a latitudinal gradient in South Africa covering seven ecoregions—these are defined as areas which contain characteristic, geographically distinct assemblages of species (Figure 1; Table S1). Five sites were sampled during both summer (December 2014) and winter (August 2014), two sites were additionally sampled during a second summer (December 2015), and the remaining 22 were sampled once during summer (December 2015). At each of the sites, a 25-m reach of stream was sampled. The stream invertebrate community was characterized based on four Surber samples (50 cm × 50 cm, 230 μm mesh) from riffles in each stream. All samples were preserved in 70% ethanol in separate containers for later enumeration and identification to family level. Additional invertebrates were sampled from 22 of the sites (those sampled in December 2015) using a kick net and allowed to gut clear (in clean river water) before being prepared for stable isotope analysis. At these 22 sites, an electrofisher was used to quantify fish and amphibian diversity and abundance in each stream-reach using a standardized two-pass sampling method (Kimberg, Woodford, Roux, & Weyl, 2014). All fish and amphibians were measured (fork or snout to vent length) and identified before up to five individuals of each species were fin or tail-clipped for stable isotope analysis and returned to the stream upon completion of sampling. Stream temperature, pH, conductivity and width (all measured at >3 points and averaged) were also taken on each sampling occasion and incorporated into our analyses.

2.2 | Stable isotope analyses

All stable isotope samples were frozen and then oven dried at 60°C, ground to a homogenous powder and analysed for their carbon and nitrogen ratios at the Mammal Research Institute (MRI), University of Pretoria, Pretoria, South Africa using a continuous flow isotope ratio

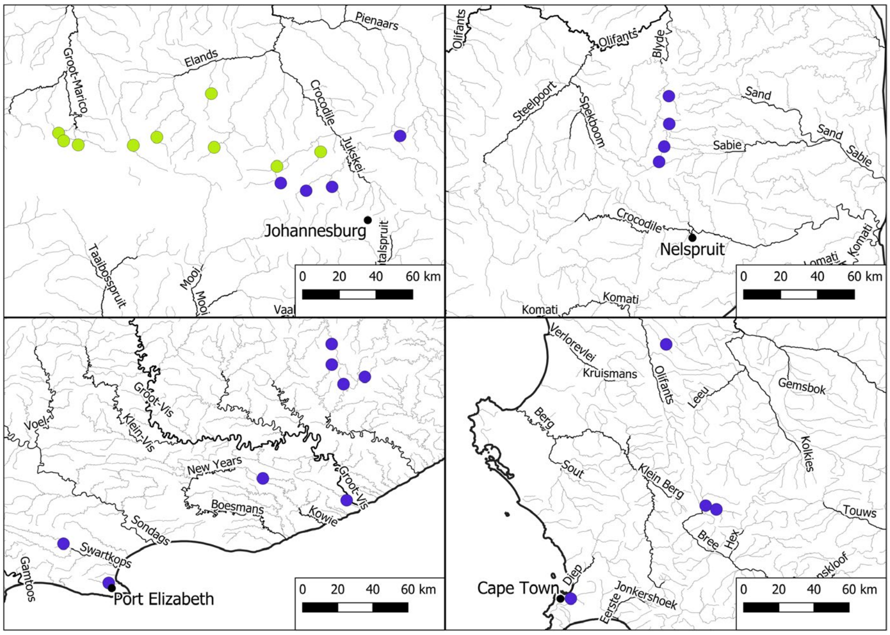

FIGURE 1 A map of the 29 streams in four areas of South Africa sampled, once in December 2015 (purple) or multiple times in 2014 and 2015 (green)

mass spectrometer (DeltaV IRMS coupled with a Flash 1112 elemental analyser with a ConFloIV interface). Laboratory standards (referenced to V-PDB for carbon and atmospheric nitrogen for nitrogen) and blank samples were run after every 12th sample to correct for drift if present. We analysed three samples of each taxon (1–10 individuals per sample) at each sampling site. The total number of species (i.e. nodes in the food web) at each site ranged from 6 to 24. Samples from one site were lost and, therefore, we only present isotope data from 21 streams.

2.3 | Stable isotopes: Functional diversity

Carbon and nitrogen stable isotope analyses of individuals can be used to estimate population diet and food web structure because the isotope signatures of an individual reflect what it has consumed. Stable isotope analyses give a time-integrated measure of diet by reflecting what an individual has consumed over a period of weeks (depending on body size and temperature; Vander Zanden, Clayton, Moody, Solomon, & Weidel, 2015). The distribution of populations in isotopic space can be used to quantify food web metrics (Jackson et al., 2012). Firstly, we calculated the food chain length of each community as the highest trophic level of any species in both the invertebrate and vertebrate community at each site. Tropic level was calculated using a Bayesian approach (using the tRophicPosition package in the R Computing Programme; Quezada-Romegialli, Jackson, & Harrod, 2019; R Core Team, 2017). We used common grazing mayflies of the families Leptophlebiidae, Baetidae and Caenidae as our baseline (except one site where we also used herbivorous chironomids (sub-family Orthocladiinae) due to low sample sizes of mayflies; $n = 3–9$ for each site), with trophic enrichment factors of 1.3 ± 0.3‰ and 2.9 ± 0.3‰ for carbon and nitrogen respectively (McCutchan, Lewis, Kendall, & McGrath, 2003). One site was omitted from the food chain length analyses because we did not have a reliable baseline (i.e. no mayflies and only one chironomid sample). The $\delta^{13}C$ and $\delta^{15}N$ data were then corrected by a community centroid approach before calculating any further stable isotope-derived metrics to allow comparisons between sampling sites with different isotopic baselines. This was computed by converting the isotope data, where values for each node (i.e. species) were expressed as the average distance from the community isotope mean for each individual site on both the carbon and nitrogen axis (Cucherousset & Villéger, 2015; Schmidt, Olden, Solomon, & Vander Zanden, 2007).

We combined the scaled invertebrate, fish and amphibian stable isotope and abundance data to produce comparable isotopic food webs (IsoWebs) and calculate metrics of trophic functional diversity. First, we calculated the area occupied by the convex hull surrounding the most extreme points in scaled isotopic space as a measure of the total isotopic functional diversity (hereafter, *Isotopic richness*; Rigolet, Thiébaut, Brind'Amour, & Dubois, 2015). A reduction in functional diversity can be due to loss of species and/or a loss of functional roles (i.e. the species is still present but switches diet)—our approach will reflect both of these mechanisms. However, to account for differences in abundance, next we calculated three abundance-weighted metrics (separately for vertebrates and invertebrates). Usually, stable-isotope metrics do not take species abundance or biomass into account—providing equal functional weight to both rare and common species (Rigolet et al., 2015). Here we accounted for abundance variation using the following metrics described by Cucherousset and Villéger (2015):

1. *Isotopic dispersion* ranges from 0 to 1, and the higher the value, the further most nodes (or their weight) are far from the centre of gravity. Low values indicate that most organisms are packed within a small area of isotopic space near the centre of gravity.
2. *Isotopic divergence* ranges from 0 to 1 and the higher the value, the more variance in trophic ecology in the food web (i.e. the taxa with the most extreme stable isotope values dominate the food

web). Low values indicate that most organisms (or nodes) are close to the centre of gravity of the convex hull.

3. *Isotopic uniqueness* ranges from 0 to 1 and the higher the value, the more unique each node is in the isotopic space. Low values indicate lots of overlap, indicating that species have similar functional roles in the food web (i.e. high functional redundancy).

2.4 | Stressor classification

We quantified land use by first defining the catchment area upstream of each individual site using a combination of quaternary drainage region boundaries (provided by the South African Department of Water and Sanitation (DWS); https://www.gov.za/about-sa/water-affairs) and hand-drawing catchment boundaries using elevation data in ArcGIS. Land cover for the upstream catchment at each site was then quantified using the South African National Land Cover Database (http://egis.environment.gov.za) from 2013/2014 which categorizes land at a 1:75,000–1:100,000 scale. We calculated the percentage of each catchment comprising agricultural (cultivated, plantation) and urban land (Appendix S1). Within each region, we selected at least one site which was predominantly natural, agricultural or urban.

We extracted the following climate variables for each sampling site from the WorldClim database using the R Computing Programme (Version 3.6.1; R Core Team, 2017): (a) mean annual air temperature; (b) monthly variation in annual air temperature; (c) total annual rainfall and (d) monthly variation in annual rainfall (all averages from 1970 to 2000). These measures provide a good proxy of each stream's hydrology, since stream temperature is correlated with air temperature (Mohseni & Stefan, 1999; Morril, Bales, & Conklin, 2005). Finally, fish invasion status was classified as a binary presence or absence of invasive fish species based on our electrofishing data and included in our ordinations (see below).

2.5 | Statistical analyses

All statistical analyses were performed using the R Computing Programme (R Core Team, 2017). Firstly, we performed principle component analysis (PCA) on our predictor variables: (a) sampling temperature; (b) mean annual air temperature; (c) monthly variation in annual air temperature; (d) total annual rainfall; (e) monthly variation in annual rainfall; (f) latitude; (g) stream width; (h) pH; (i) conductivity; (j) per cent urban land in catchment; (k) per cent agriculture land in catchment and (l) fish invasion status (presence or absence). This, and simple Pearson's correlations, indicated that not all variables were statistically independent and so we selected mean annual air temperature, total annual rainfall, urbanization and agriculture for further analysis (Figure S1). Next, canonical correspondence analysis (CCA) was used to examine relationships between our chosen environmental variables and binary presence and absence data of both invertebrates and vertebrates (at the 22 sites where both were sampled) using the VEGAN package (Oksanen et al., 2019). The significance of the environmental predictors was tested using type 3 analysis of variance (ANOVA).

Next, we calculated beta diversity using the BETAPART package (Baselga & Orme, 2012). This method quantifies the dissimilarity between the animal communities at each site (presence or absence of invertebrates and vertebrates), and shows how much variation is due to species turnover (i.e. replacement of species at one site by a different species in the second site) and nestedness (i.e. sites with low richness have a subset of species present at more diverse sites). We then used simple linear models to test for an effect of air temperature, total rainfall, urbanization and agriculture differences between sites. We then analysed whether any of these land use or climate variables exerted any significant independent or combined effects on stream communities (fish and invertebrate abundance and richness, and the functional isotopic food web metrics; all log(x + 1)-transformed) using general linear mixed effect models (using the NLME package; Pinheiro, Bates, DebRoy, & Sarkar, 2019). Here all 29 sampling sites were used for the taxonomic invertebrate responses, and 20–22 sampling sites were used for all other response variables. The random effect of ecoregion (seven levels) was included to account for the close proximity (and therefore, similarity) between streams in each catchment area. Per cent urban and agricultural land use and two climate variables (total annual rainfall and mean temperture) were our fixed effects. Additionally, season was included as a fixed effect for the taxonomic variables (except fish abundance which was only quantifed in summer). We ran models for individual, additive and interactive effects of all single drivers and driver pairs and selected the best model based on Akaike information criterion (corrected for small sample sizes; AICc). The significance of the models was tested by comparing with a null model (where we removed all fixed effects but the intercept), and conditional R^2 values were calculated for the best models using the SJPLOT package (Lüdecke, 2020). The effects of multiple drivers were considered non-additive if models including interaction terms had the lowest AICc values (Table S2). In these cases, the nature of the interaction was determined by comparing effect sizes between additive and non-additive models. Interaction effect sizes (*F*-values) were subtracted from the sum of the main effect sizes producing values representing the difference between additive and interactive effects (following Lakeman-Fraser & Ewers, 2014). If the value was positive (i.e. additive effect was greater than the interactive), then the relationship was considered to be antagonistic (the impact of the drivers was reduced when acting interactively); if however, the value was negative (i.e. additive effect was less than the interactive), then the relationship was considered to be synergistic (the impact of the drivers was increased when acting interactively).

3 | RESULTS

3.1 | Taxonomic community structure

The turnover component of beta diversity significantly increased with increasing site differences in climate (temperature and rainfall; Figure 2a,b) and land use (agriculture and urbanization; Figure 2c,d),

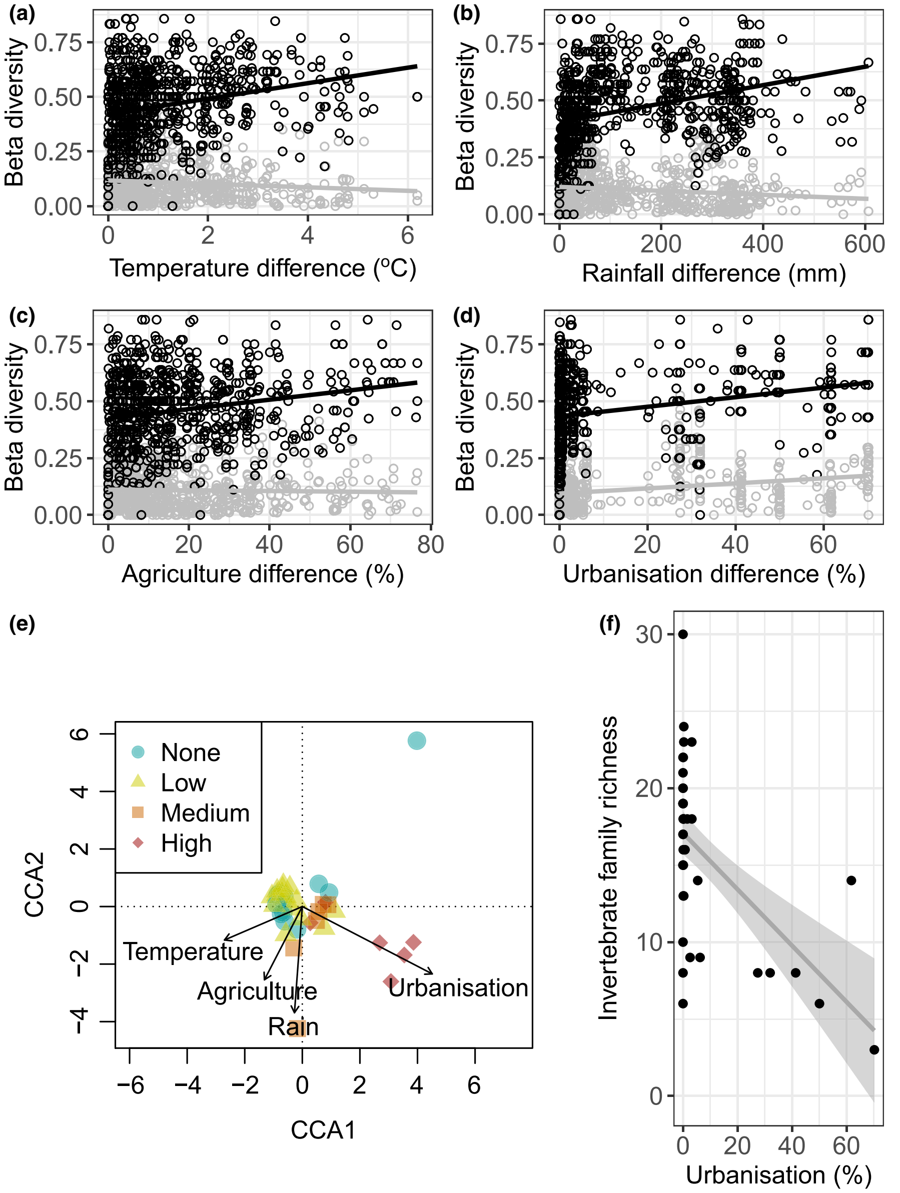

FIGURE 2 Taxonomic responses to climate and land use: (a–d) The dissimilarity in the animal communities with increasing pairwise site differences in temperature (a), rainfall (b), agriculture (c) and urbanization (d). Dissimilarity is measured as beta-diversity separated into turnover (black) and nestedness (grey) and the fitted lines represent a simple linear model. (e) A canonical correspondence analysis (CCA) scatterplot showing the relationship between the animal community and environmental variables, where each point represents streams with no (blue circles), minimal (<0.1%, yellow triangles), medium (1%–10%; orange squares) and high (>20%; red diamonds) coverage of urban land in the catchment. (f) The negative effect of urbanization on invertebrate richness, where the shaded area indicates the 90% confidence intervals around a linear model

TABLE 1 The effect of pairwise site differences in our four predictor variables (mean air temperature, total annual rainfall and urban and agriculture land cover (%)) on beta diversity

Predictor	Response	*df* (residuals)	Sum square (residuals)	Mean square (residuals)	*F*-value	*p*
Temperture	Turnover	1 (1598)	2.7 (45.0)	2.7 (0.03)	95.9	<0.001
	Nestedness	1 (1598)	0.2 (15.5)	0.1 (0.01)	14	<0.001
Rainfall	Turnover	1 (1598)	5.0 (42.7)	5.0 (0.03)	187.1	<0.001
	Nestedness	1 (1598)	0.2 (15.6)	0.2 (0.01)	24	<0.001
Agriculture	Turnover	1 (1598)	1.9 (45.8)	1.9 (0.03)	64.7	<0.001
	Nestedness	1 (1598)	0.01 (15.6)	0.01 (0.01)	1.1	0.29
Urbanization	Turnover	1 (1598)	3.2 (44.5)	3.2 (0.03)	114.5	<0.001
	Nestedness	1 (1598)	0.9 (14.7)	0.9 (0.01)	97.3	<0.001

while nestedness decreased with increasing differences in climate (Figure 2a,b; Table 1). Nestedness also increased with increasing pairwise site differences in urbanization (Figure 2d; Table 1). The first two CCA axes explained 40.5% of the total variation in the animal communities (Figure 2e). The first CCA axis accounted for 20.6% of the total variance and was positively correlated with urbanization, but negatively correlated with temperature. The second CCA axis accounted for 19.9% of the total variance and was negatively correlated with total annual rainfall and agriculture (Figure 2e). The distribution of sampling sites in the CCA revealed a strong separation between pristine and heavily urbanized sampling sites (Figure 2e), and this was one of three significant predictors (F_1 = 206; *p* = 0.005) of variation in the community, along with temperature (F_1 = 1.90; *p* = 0.015), and rainfall (F_1 = 1.70; *p* = 0.025).

Urbanization alone was the best predictor of invertebrate family richness, which declined with increasing urban land use (Figure 2f; Table 1; full model selection for all variables is presented in Table S2). Invertebrate abundance was best explained

TABLE 2 The best model for each response variable. Full model selection is shown in Table S2. All models included a random effect of ecoregion

Response	Best fit model	*df*	AICc	BIC	logLIK	*F*-value	R^2	Main effects – Interactive effects	Interaction type
Invertebrate family richness	Urbanization	4	31.3	36.9	−11.1	28.2	0.45		Independent
Invertebrate abundance	Season	4	104.1	109.7	−47.5	30.66	NA		Independent
Fish species richness	Intercept	3	53.1	56.5	−23.1	175.76			
Fish abundance	Intercept	3	29.6	31.6	−11.1	31.73			
Food chain length	Temperature	4	−29.5	−28.2	20.1	4.26	0.36		Independent
Isotopic richness	Temperature	3	32.8	34.5	−11.2	3.25	0.15		Independent
Invertebrate isotopic dispersion	Intercept	3	−35	−33.2	21.2	82.89			
Invertebrate isotopic divergence	Intercept	3	−25.8	−24.1	16.6	317.48			
Invertebrate isotopic uniqueness	Urbanization * rainfall	6	−21.5	−21.23	19.8	6.83	NA	4.09 – 8.63 = −4.54	Synergistic
Vertebrate isotopic dispersion	Agriculture + rainfall	4	−7.3	−8.6	11.4	4.64 + 6.60	0.501		Additive
Vertebrate isotopic divergence	Intercept	3	−16.7	−16	12.3	61.92			
Vertebrate isotopic uniqueness	Intercept	3	−4.6	−4	6.2	117.63			

Abbreviations: *, interaction term; +, additive term; AICc, Akaike information criterion corrected for small sample sizes; BIC, Bayesian information criterion; logLIK, Log-Likelihood; R^2, conditional *R*-squared.

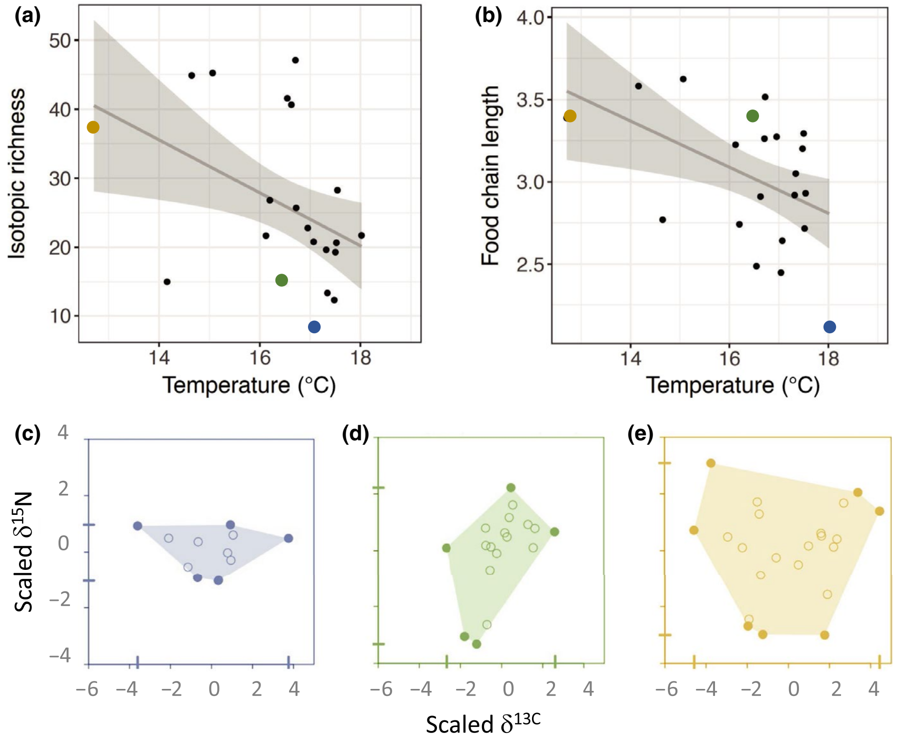

FIGURE 3 The negative effect of temperature on (a) isotopic richness and (b) food chain length, where the shaded area indicates the 90% confidence intervals around a linear model and the coloured points represent three reference sites, with the corresponding IsoWebs shown in (c) (blue, Keiskamma), (d) (green, Magalies) and (e) (gold, Klipplaat). Here the solid hulls surround each community's trophic functional space and the carbon and nitrogen isotope data are presented on scaled axis to ensure it is comparable between sampling sites

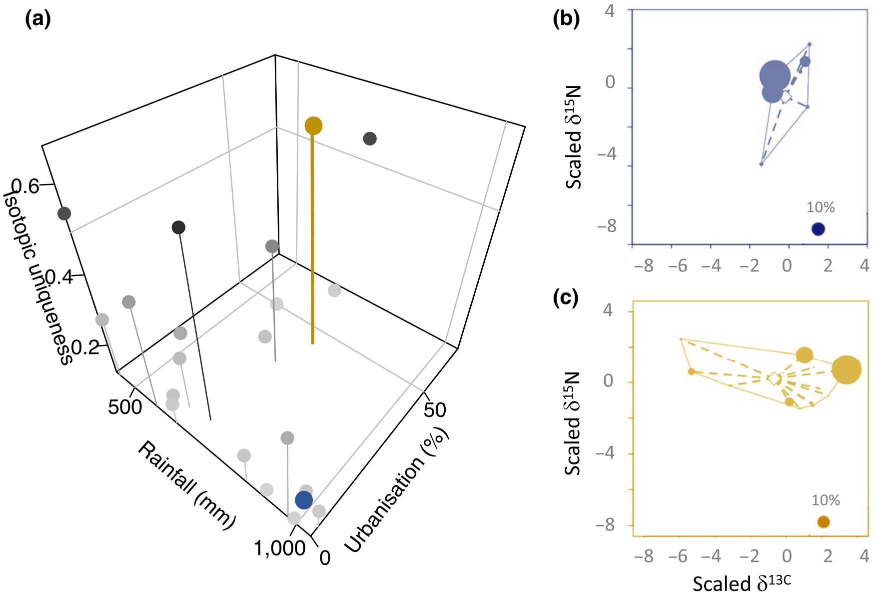

FIGURE 4 (a) The interactive effect of urbanization and rainfall on invertebrate isotopic uniqueness. Metric values are on a scale of low (grey) to high (black) and the coloured points represent two reference sites, with the corresponding IsoWebs shown in (b) and (c). Here point size represents abundance (per cent) and the solid hulls surround each community's trophic functional space. Dashed lines show the distance of each node from the centre (i.e. the community mean) of the IsoWeb. Isotopic uniqueness was negatively affected by rainfall (e.g. Klein-Sabie, b, blue), but this was compensated for by urbanization in some sites, such as Liesbeek (c, gold). Carbon and nitrogen isotope data are presented on scaled axis to ensure it is comparable between sampling sites

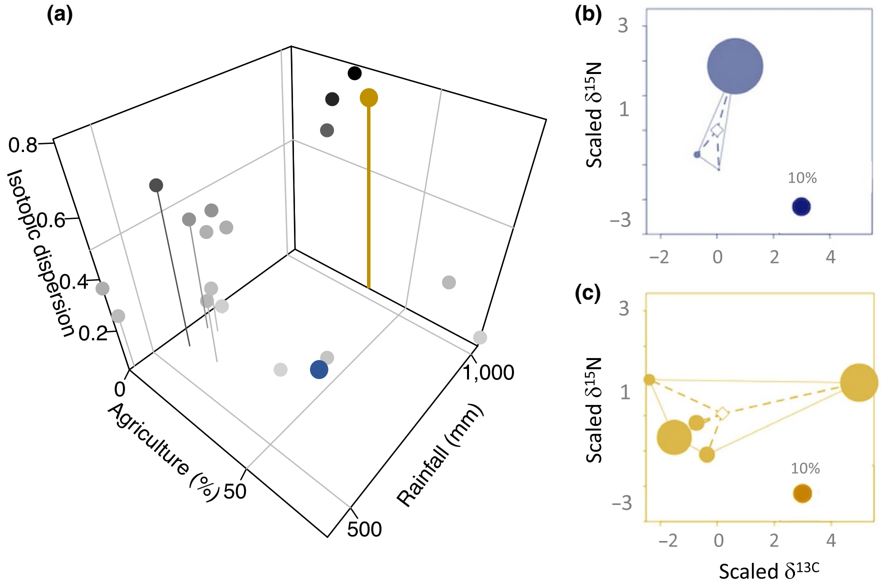

FIGURE 5 (a) The interactive effect of agriculture and rainfall on vertebrate isotopic dispersion, Metric values are on a scale of low (grey) to high (black), and the coloured points represent two reference sites, with the corresponding IsoWebs shown in (b) and (c). Here point size represents abundance (per cent) and the solid hulls surround each community's trophic functional space. Dashed lines show the distance of each node from the centre (i.e. the community mean) of the IsoWeb. Isotopic dispersion tended to decrease with increasing agriculture (e.g. Swartspruit, blue, b), but this was compensated for by high rainfall (e.g. Treur, gold, c), except for at heavily impacted sites. Carbon and nitrogen isotope data are presented on scaled axis to ensure it is comparable between sampling sites

by season, where it was lower during summer (Table 2; Figure S2). None of our land use and climate driver combinations could improve the null model and accurately predict fish species richness or abundance (Table 2).

3.2 | Functional diversity

The isotopic food webs (IsoWebs) varied in structure across the sites with the extracted metrics revealing that this was caused by a combination of land use and climate. Both total *isotopic richness* and food chain length decreased with temperature (Figure 3; Table 2). Rainfall was a strong driver of abundance-weighted invertebrate *isotopic uniqueness*, which declined in wetter areas, indicating high functional redundancy (Figure 4; Table 2). However, there was also a synergistic interaction with urbanization, with the highest invertebrate *isotopic uniqueness* (and therefore low functional redundancy) found in areas with low rainfall and high urbanization (Figure 4). There was an additive effect of agriculture and annual rainfall on abundance-weighted vertebrate *isotopic dispersion*, with the former causing a decline in dispersion, with this partially compensated for by high rainfall (Figure 5; Table 2). None of our driver combinations could improve the null model and accurately predict invertebrate *isotopic dispersion* and *isotopic divergence*, or vertebrate *isotopic divergence* and *isotopic uniqueness* (Table 2).

4 | DISCUSSION

Our results suggest that a combination of land use and climate variables drive variation in community and food web structure among South African streams, supporting our first hypothesis. However, we only found one non-additive interaction between land use and climate stressor variables (when quantifying effects on invertebrate *isotopic uniqueness*). In all other cases, independent or additive effects prevailed. In contrast to our second and third hypotheses (that streams highly disturbed by human land use will have simpler food webs and lower trophic levels), temperature was the most important variable explaining food chain length and *isotopic richness* (i.e. total functional diversity). This, combined with increasing species turnover and increasing pairwise site differences in temperature, suggests that food webs will become less diverse due to a loss of predators in a warmer world. Total annual rainfall and land use (agriculture and urbanization) were the most important variables in explaining our weighted-functional food web metrics, while urbanization alone explained invertebrate taxonomic diversity. Our second hypothesis was partially supported when considering vertebrate *isotopic dispersion* (i.e. weighted-functional diversity), which declined with increasing agriculture, although high rainfall appeared to compensate for this.

4.1 | Effects of land and climate change on food webs

We found that food webs were significantly compressed (i.e. low *isotopic richness*) by elevated temperatures. Food chain length also decreased with temperature, suggesting that this decline in trophic richness was caused by the loss of predators. This is further supported by patterns in beta diversity, which showed that species turnover increased with increasing temperature differences between sites. This suggests a loss of the predatory functional feeding group in a warmer world, rather than decline in species richness. In other words, populations or species which occupy lower trophic levels are replacing those in more predatory roles, without a loss of taxonomic diversity. Disturbance, resource availability, ecosystem size and habitat heterogeneity also play key roles in determining food chain length (Jackson, Evangelista, et al., 2017; Jackson, Wasserman, et al., 2017; Post, 2002). However, we expected food chain length to show strong declines in response to human-dominated landscapes (i.e. following predictions on the trophic-down-grading of Earth; i.e. predator loss, Estes et al., 2011), but it was best explained by temperature. This might suggest that climate change will be more important than land use in driving changes in freshwater predator distribution and abundance, or predatory behaviour, in the future. As temperatures increase, metabolic demand also increases. If resources are limited, larger bodied predatory species will not be able to keep up with the rising metabolic demands in warmer streams (Vucic-Pestic, Ehnes, Rall, & Brose, 2011). As such, reduced resource availability is directly linked to shorter food chain lengths (Post, 2002).

Vertebrate *isotopic dispersion*, a measure of functional diversity which takes abundance into account, declined with increasing agriculture, perhaps because agriculture effectively removes a resource (Burdon et al., 2019). Agricultural landscapes will have less diverse riparian communities reducing the diversity of allochthonous resources and, although we did not quantify this here, many studies suggest that run-off from agricultural practices (contaminants, sediments) can reduce the abundance and diversity of freshwater algae and plants (e.g. Piggott et al., 2015a, 2015b; Piggott, Salis, et al., 2015). Pesticides from agricultural run-off for example, can result in changes in primary producer and macroinvertebrate community composition which has been shown to result in bottom-up impacts on aquatic food webs elsewhere (e.g. Macneale, Kiffney, & Scholz, 2010). This is supported by the fact that high rainfall, which can flush out contaminants, had a positive effect on vertebrate functional diversity. South Africa is predicted to receive progressively less rainfall in the coming decades, particularly in the south-west, as the climate continues to warm (Archer et al., 2018), which suggests that vertebrates in running waters may become more vulnerable to agricultural intensification in the region in the coming decades, as the mitigating effects of rainfall weaken.

Rainfall was also an important driver of invertebrate *isotopic uniqueness*, a measure of functional redundancy (which also takes abundance into account). *Isotopic uniqueness* declined with total annual rainfall, indicating higher functional redundancy in wetter areas. This suggests that species' diet overlapped in wet regions, but were more unique in dry regions. Rainfall can drive the hydrology of streams and rivers by altering flow and seasonal discharge, which in turn will alter habitat (macrophyte growth, sediment retention) and resource (algal growth, detritus retention) availability for animals—with direct food web implications (Power, Holomuzki, & Lowe, 2013). Urbanization magnified the effect of low rainfall, suggesting that functional redundancy is lowest in dry urban regions. This can be partly explained by the loss of taxonomic invertebrate diversity with urbanization; in more pristine streams there are multiple species with similar diets (i.e. high functional redundancy), but they differ in their sensitivity to human disturbance (Olds et al., 2018). Therefore, taxonomic diversity and functional redundancy are lost in parallel (Galand, Pereira, Hochart, Auguet, & Debroas, 2018).

4.2 | Functional versus taxonomic metrics

Ecologists have been studying taxonomic diversity for centuries, and there is value in understanding how biodiversity at this level will shift in the face of ongoing global change, particularly for endemic, rare and/or iconic species (Hawkins et al., 2003; Kondratyeva, Grandcolas, & Pavoine, 2019). However, using a purely taxonomic approach may overlook the more subtle food web effects of stressors, such as changes in trophic structure, functional diversity and diet (Devictor et al., 2010; Petchey & Gaston, 2006). Here we found that a stable isotope approach, which considers both the abundance and trophic ecology of species, detected shifts in the food web in response to climate and land use, which our taxonomic measures missed. However, our taxonomic metrics allowed us to identify the mechanisms driving the observed changes in functional diversity. Going forward, there is a need for a more holistic approach in the bio-monitoring of freshwaters to detect the subtle food web effects of multiple stressors (Jackson, Loewen, et al., 2016; Jackson, Weyl, et al., 2016).

4.3 | Caveats

As with any field study, it is important to note that other factors might have a role in driving the observed relationships. For instance, elevated temperatures are often correlated with other variables which could be driving the patterns in trophic diversity and food chain length (e.g. low dissolved oxygen concentrations and flow; Du, Shrestha, Ficklin, & Wang, 2018). Additionally, across our study sites, air temperature was mildly correlated with latitude, pH, stream width, and rainfall (Figure S1). However, we are confident that temperature is a strong driver of food web structure, since similar results have been reported elsewhere (e.g. O'Gorman et al., 2019). Agricultural land use also tended to be higher in areas with high rainfall and rainfall variation, and was positively correlated with fish invasion. Although this is not surprising, it suggests that the additive effect of rainfall and agriculture on the functional diversity of vertebrates might be more complex and also involve both seasonal variation in precipitation, and the negative effects of invaders in these streams (Jackson, Evangelista, et al., 2017; Jackson, Wasserman, et al., 2017).

5 | CONCLUSIONS

Past studies have demonstrated the utility of stable isotopes in detecting changes in food webs as a result of invasions, habitat alteration and pollution, and here we have proven their ability to reveal the combined effects of land use and climate on isotopic functional diversity and functional redundancy. Our results suggest that global warming will cause food webs to become less diverse, with shorter food chain lengths. Vertebrate functional diversity will decline with increasing agriculture and reduced rainfall, while invertebrates will be subjected to a loss of functional redundancy with urban expansion and reduced rainfall. Multiple stressors have received a lot of research attention over the last 5 years because of concerns that stressors regularly combine to cause impacts which are worse than the sum of the independent effects (i.e. a synergistic interaction, or amplified effects). Here we show that, in South African streams, either the dominant stressor alone explains variation between streams (in terms of invertebrate taxonomic richness and abundance, *isotopic richness* and food chain length) or, alternatively, the stressors combined in a simple additive manner (when effects were measured on vertebrate *isotopic dispersion*). Non-additive effects were found in only one of the six cases where our models improved predictive power beyond the null model (1 of 12 cases in total). This suggests that management should identify the dominant stressor for the response of interest for successful conservation or restoration efforts. For instance, if there is need to preserve invertebrate diversity, our results suggest that urban spread should be reduced. However, if the priority is to maintain top predators and vertebrate functional diversity, mitigating the effects of climate change should be considered. Conservation of freshwater ecosystems in human-dominated landscapes in our warming world is critical both from a biodiversity and an ecosystem service perspective, and our results further support the importance of sustainable land use and good management practices. Given the longitudinal aspect of rivers, threats associated with agricultural and urban expansion can affect areas downstream from the disturbance proportional to the scale and nature of the disturbance (Davies, O'Keeffe, & Snaddon, 1993). This highlights the need for considering current and future land use patterns in conservation planning initiatives aimed at protected area expansion. Therefore, efforts should be made to preserve natural freshwater ecosystems in human-dominated landscapes, and to create more protected areas. This may be achieved by identifying catchments of strategic importance for both biodiversity and water resource provision (e.g. freshwater ecosystem priority areas; Nel et al., 2011), and enforcing their protection from urban and agricultural expansion through long-term spatial planning.

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AUTHORS' CONTRIBUTIONS

M.C.J. conceived the ideas, designed the methods, analysed the data and wrote the first draft. All authors collected the data, contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available on figshare: https://doi.org/10.6084/m9.figshare.11807097.v1 (Jackson et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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