

COMBINING NICHE MODELS AND REMOTE SENSING TO EXPLORE SHORT-TERM HABITAT SUITABILITY TEMPORAL DYNAMICS AND IMPROVING BIODIVERSITY MONITORING

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ABSTRACT

The on-going declines in biodiversity caused by global and local environmental changes call for improved monitoring and conservation schemes. Remote-sensing (RS) of earth surface stands at the forefront to tackle this challenge, by providing data at different spatial and temporal resolutions that can be related with a wide range of environmental variables. Spatiotemporal dynamics of ecosystems and vegetation functioning (depicting several facets of matter and energy fluxes) can affect habitat suitability and therefore the persistence of species and the patterns of biodiversity. In this study we analysed habitat suitability and species diversity patterns by combining Species Distribution Models (SDMs) with multi-temporal RS-based variables of vegetation primary productivity, seasonality and phenology calculated from MODIS products and also from MODIS/Landsat data fusion using the StarFM algorithm. Predictors' related to structural variables of landscape composition and configuration were compared to functional variables of vegetation dynamics calculated from RS NDVI time-series in a Multi-model Inference (MMI) framework, allowing to assess the relative predictive importance of each set of variables. Multi-annual RS data was used to explore post-fire alterations in biodiversity and short-term changes in habitat suitability dynamics. Overall, MMI results showed a good support for vegetation functioning variables (derived from RS data) in some cases exceeding the model performance of structural landscape variables. In addition, multi-annual RS data were capable of improving habitat suitability models, evaluating short-term changes and assessing post-fire variations in biodiversity. We argue that coupling SDMs with RS functional indicators can provide early-warnings of changes affecting habitat suitability well before assessments based on structural indicators. Possible applications of this methodology range from the improvement of biodiversity monitoring schemes to the design of more effective conservation strategies by explicitly considering the spatiotemporal dynamics of ecosystems.

INTRODUCTION

Despite the increasing number of conservation initiatives, the rate of biodiversity loss does not appear to be diminishing, nor do the pressures upon species and their habitats (1). Recent quantitative scenarios of biodiversity change consistently indicate that this decline will continue throughout the 21st century, with global change and local land uses leading to alterations in terrestrial ecosystems (2). These pressing challenges lay the need of ecological science to provide tools and long-term datasets to accurately assess, monitor and report on biodiversity status and trends (3) in order to scientifically inform and specify strategies for biodiversity monitoring, management and conservation.

Identifying the factors that drive the distribution of species is thus at the core of ecological research aimed to prevent further loss of biodiversity (1). Species distribution models (hereafter SDMs (4)) combine observations of species occurrence or abundance with the spatial distribution of environmental factors to predict species distributions (5). They are widely used to describe patterns, to deliver spatiotemporal predictions at several scales (6) and to address fundamental questions such as the ecological impacts of climate and land-use changes (7). Recent advances in RS have strongly contributed to improve SDMs as well as biodiversity monitoring (8-11). The remotely sensed Normalized Difference Vegetation Index (NDVI) is one of the most extensively used vegetation indices in ecological applications, and has shown to improve distribution models for tree species (12). Many of the RS-based variables currently employed in ecological applications, such as productivity, biomass and leaf area index, can be used to characterize functional gradients that can be associated to species responses (8). Continuous RS data may further contribute to SDMs by improving spatial and temporal resolutions and by expanding the range of input variables (13). Moreover, as change and uncertainty are intrinsic components of ecosystems, which are shaped by an ensemble of deterministic and stochastic forces (14), the potential of RS data to inform on short-term ecosystem and landscape dynamics is a valuable asset to anticipate changes in the status of threatened species and habitats (15).

In this context, the current study aimed to test: (i) the predictive ability of RS-based vegetation dynamics indices (calculated from annual NDVI time-series) to explain the distribution of species and general indicators of plant and bird species richness, and (ii) the usefulness of multi- multi-annual time-series of RS indices of vegetation dynamics to enhance the predictive power of models of habitat suitability and to explore changes in selected biodiversity indicators.

METHODS

Study-areas and response variables

Two study-areas were considered, both located in the North of Portugal. Study-area 1 (SA1) is bounded by -7.785°W to -7.471°W longitude and 41.391°N to 41.640°N latitude. It comprises the full extent of *Vila Pouca de Aguiar* municipality with an area of roughly 437 km². In SA1, we aimed to analyse the spatiotemporal patterns of habitat suitability for *Veronica micrantha* Hoffmanns. & Link, a rare and vulnerable species as considered by IUCN. This species is endemic to Iberian Peninsula and protected by European law (Annexes II and IV – EU Habitats Directive). In Portugal, SA1 hosts an important proportion of its national population, and 30.9% of this area is included in the Natura 2000 network. Preliminary compilation of presence records from herbarium data and field surveys (with locations selected by a model-assisted sampling design (16)) were used to collect a total of 27 presence/absence records of the target species at a spatial resolution of 1km².

Study-area 2 (SA2) comprises the full extent of the Vez river watershed, a small basin (263km²) bounded by -8.526°W to -8.257°W longitude and 41.837°N to 42.017°N latitude. Elevation ranges from 15m a.s.l. up to 1420m. This area holds important biodiversity values, being 13.6% included in the *Peneda-Gerês* National Park and 43.3% in Natura 2000. However, between year 2000 and 2012 roughly 37.0% of the area was burnt at least once and thus wildfires, along with LUC changes (mainly related to agricultural abandonment and scrub encroachment) present challenges for conservation. In SA2 we aimed to assess general indicators of species diversity for plants (overall species richness of vascular plants and richness of endemic species), as well as passerine bird species (including total diversity per sample unit (α), average β -diversity/dissimilarity of species assemblages, and species richness by feeding group including insectivorous, omnivorous and granivorous species). A two-stage sampling design (17), with stratified random sampling in the first stage and systematic sampling in the second, was implemented to select a total of 120 sample units with 200x200m for field-surveys on plant and passerine species diversity.

Remote-sensing data processing and calculation of vegetation dynamics indices

For SA1, the MODIS MOD13Q1 250m product, a NDVI time-series of 16-days composites, was used to calculate vegetation dynamics indices (VDI) for each year between 2001 and 2010 (calibration year). The double logistic function-fitting method was applied to reduce noise effects on data, generating a smoothed NDVI curve for each year which was used to calculate VDI (18, 19). These two procedures were performed using the TIMESAT software (20). The largest value for the fitted function during the growing season and seasonal amplitude were calculated to represent primary productivity. The time for the start of the growing season (in days) and the time for the mid of the growing season (zonal maximum; in days) were selected to represent phenology. All VDI variables were up-scaled to the same spatial resolution of species records (1km²) using the mean (for seasonal amplitude and start of growing season) or the maximum (for mid of growing season and the maximum value) as aggregation functions. To characterize water availability we used MODIS MOD16A3 actual evapotranspiration (mm.year⁻¹) product (21) with a spatial resolution of 1km². From soil data (obtained from national authorities) we calculated the % cover of different soil types. The national fire database was used to compute the average burnt area between year 2001 and 2009 and the trend slope (using Sen-Theil's method).

Vegetation indices for SA2 were calculated for years 2014 (calibration year) and 2007 from MODIS/Landsat data fusion using the StarFM algorithm (22). Surface reflectance data were obtained from MODIS MOD09Q1 data product at 250m/8-days composites for the red and NIR bands. Landsat post-processed data was obtained from the USGS/ESPA service. After determining the best MODIS/Landsat comparison pairs for performing data fusion, StarFM was employed to calculate surface reflectance values for both bands for each available MODIS date. A time-series of NDVI was then calculated and a Savitzky-Golay smoothing filter was applied to remove spurious observations and increase signal-to-noise ratio. To represent primary productivity we calculated the minimum, maximum, average and median values of the growing season based on the smoothed NDVI annual time-series. For representing seasonality during growing season we calculated the: standard-deviation, coefficient of variation, mean-absolute deviation, inter-quantile differences, as well as the green-up and senescence rates. Phenological aspects were portrayed by the day of maximum value during the growing season; using this variable, we also calculated the cosine and sine transformations to represent the degree of "summerness" and "winterness". In order to upscale Landsat/MODIS fusion data (30×30m) to the same spatial resolution of biodiversity data (200×200m) we used the zonal minimum, maximum, average and standard-deviation statistics. For both areas, spatial data on land use/cover (LUC; available from local authorities with a MMU of 1ha) was used to calculate landscape composition variables (e.g., % cover of agroforestry), and landscape configuration metrics (e.g., edge density, median patch size).

Modelling framework

Predictor variables were pre-selected based on their intrinsic ecological properties, current literature, field observations and exploratory statistical analysis (not shown) using correlation analyses and preliminary model fitting to investigate the relation between response variables and predictors. The response variables (SA1 – *V. micrantha* habitat suitability; SA2 – plant/bird species richness) were related to predictor variables using Generalized Additive Models (GAM). GAM are an extension of generalized linear models recognized as a powerful and versatile method (4) due to the ability of including non-linear and asymmetric responses in species-environment relations. A multi-model inference framework (MMI) based on Akaike Information Criterion, with a correction for finite sample size (AICc), was used for comparing and ranking multiple competing model hypotheses (23). Competing hypotheses were mainly related to vegetation functioning/dynamics (productivity, phenology and seasonality) and landscape composition/configuration. For each response variable, a null-model considering only an intercept term was also used for comparing model fitness. Models exhibiting substantial ($0 \leq \Delta AICc \leq 2$) and moderate support ($2 > \Delta AICc \leq 4$) were selected to the confidence set. Akaike weights (w_i), were used to represent the different degree of support of each model hypothesis ($w_i=0$, no support; $w_i=1$, full support). Additionally, as auxiliary measures of model fitness we also calculated the adjusted R-squared (R^2), explained deviance

(D), Area Under the ROC curve (AUC; only for SA1 with binomial response variable), and the Spearman correlation between the observed and predicted values (Sp. ρ ; only for SA2 response variables). To avoid spurious effects due to high correlation or collinearity between predictors we calculated Variance Inflation Factors (VIF) for the global model (a model incorporating all predictor terms from the various hypotheses tested) for each response variable; this verified that \sqrt{VIF} was lower than 2, thus signalling low to moderate multicollinearity (not shown).

Exploring multi-annual time-series of vegetation indices

With the purpose of evaluating the added value of including multi-temporal RS variables for explaining *V. micrantha* habitat suitability in SA1, we tested two types of model predictions (MPs) based on: (i) single-year predictions using data solely for the calibration year of 2010, and (ii) a multi-temporal mean, by hindcasting and then averaging predictions across the entire 2001-2010 period, generating a 10-year long habitat suitability time-series. These two types of MPs were then evaluated through holdout cross-validation (HCV; 500 evaluation rounds with 70%/30% train/test partition) by calculating the AUC and True-skill statistic (TSS) metrics.

In the Vez river watershed (SA2), wildfires are a prevailing ecological driver of disturbance, with a large wildfire in year 2006 consuming roughly 20% of the area. We tested the usefulness of VDI calculated from multi-temporal MODIS/Landsat data fusion to assess the potential rate of recovery and/or loss following the early post-fire (year 2007) and the current calibration date (year 2014). To illustrate this, we calculated the change rate of species richness of passerine birds by hindcasting the model (calibrated in 2014) for the year 2007 and comparing the two dates for locations that have not suffered another wildfire (besides the one recorded in 2006) between 2000 and 2013.

RESULTS

Overall, for SA1, MMI results for habitat suitability of *V. micrantha* (Table 1) revealed that, in decreasing order of support, competing models related to vegetation productivity, water availability, soil types, fire disturbance and landscape composition obtained substantial support ($\Delta AICc \leq 2$ and w_i between [0.25, 0.11]; Table 1). Competing models related to vegetation phenology and landscape configuration obtained moderate support ($2 > \Delta AICc \leq 4$). The intercept-only model obtained the lowest support.

Results for SA2, which analysed general indicators of species richness for plants and passerine birds, showed that total vascular plant species richness was largely explained by landscape composition variables ($w_i=1.00$; Table 2), mainly related with the % cover of agricultural areas and different types of forested areas, including evergreen needleleaf and deciduous broadleaf. However, when considering only the subset of Iberian endemic species, RS-based vegetation indices of seasonality obtained the highest support, followed by landscape composition, with model weights, w_i equal to 0.57 and 0.43 respectively (Table 2).

Table 1 – Multi-model rankings obtained for SA1, testing habitat suitability for *V. micrantha*. Only models included in the confidence set (represented by $\Delta AICc \leq 4$) are shown in table. K – number of model parameters, AICc – Akaike Information Criterion, w_i – Akaike model weights, LogLik – model log-likelihood, R^2 – adjusted R-squared, D – explained deviance, and, AUC – Area Under the ROC curve.

Response	Model hypothesis	K	AICc	$\Delta AICc$	w_i	LogLik	R^2	D	AUC
<i>V. micrantha</i> habitat suitability	Veg. productivity /seasonality	4	19.61	0.00	0.25	-4.94	0.66	0.55	0.81
	Water availability	4	20.02	0.42	0.20	-5.42	0.65	0.51	0.85
	Soils	2	20.22	0.61	0.18	-7.73	0.55	0.29	0.76
	Fire disturbance	4	20.86	1.25	0.13	-5.11	0.66	0.53	0.79

Landscape composition	3	21.19	1.59	0.11	-6.17	0.62	0.44	0.75
Veg. phenology	3	22.36	2.76	0.06	-7.07	0.58	0.35	0.76
Landscape configuration	3	23.11	3.50	0.04	-7.64	0.55	0.30	0.74

Table 2 – Multi-model rankings obtained for SA2 including plant and bird species general biodiversity indicators. Only models included in the confidence set ($\Delta AICc \leq 4$) are shown in table. K – number of model parameters, AICc – Akaike Information Criterion, w_i – Akaike model weights, LogLik – model log-likelihood, R^2 – adjusted R-squared, D – explained deviance, and, Sp. ρ – Spearman correlation between observed and predicted values.

Response	Model hypothesis	K	AICc	$\Delta AICc$	w_i	LogLik	R^2	D	Sp. ρ
Vascular plants species richness	Landscape composition	12	1537.23	0.00	1.00	-755.33	0.53	0.57	0.77
Endemic plants species richness	Veg. seasonality	6	551.60	0.00	0.57	-269.59	0.23	0.26	0.50
	Landscape composition	9	552.18	0.57	0.43	-266.51	0.23	0.29	0.54
Passerine birds species richness	Landscape composition	8	516.41	0.00	0.57	-249.31	0.15	0.19	0.42
	Veg. productivity	5	518.36	1.96	0.21	-254.23	0.12	0.13	0.46
	Veg. phenology	4	518.82	2.41	0.17	-254.79	0.10	0.12	0.35
Average β -diversity/ dissimilarity of passerine bird species	Landscape composition	7	433.63	0.00	0.33	-209.45	0.08	0.12	0.30
	Veg. phenology	5	433.75	0.12	0.31	-211.21	0.07	0.10	0.30
	Landscape configuration	6	434.92	1.29	0.17	-210.64	0.07	0.11	0.32
	Veg. seasonality	5	436.32	2.69	0.09	-212.46	0.04	0.07	0.35
	Veg. productivity	4	437.05	3.42	0.06	-214.69	0.02	0.04	0.20
Insectivorous passerine birds species richness	Landscape composition	8	423.64	0.00	0.61	-203.44	0.14	0.18	0.35
	Landscape configuration	4	425.57	1.93	0.23	-208.59	0.10	0.10	0.32
	Veg. phenology	4	427.63	3.99	0.08	-209.14	0.08	0.09	0.34
Omnivorous passerine birds species richness	Landscape configuration	5	308.29	0.00	0.22	-148.49	0.10	0.13	0.33
	Landscape composition	7	308.38	0.09	0.21	-146.78	0.14	0.16	0.40
	Veg. phenology	4	308.59	0.30	0.19	-150.21	0.12	0.10	0.33
	Veg. productivity	3	308.69	0.40	0.18	-151.44	0.08	0.08	0.31
	Veg. seasonality	4	308.82	0.53	0.17	-150.35	0.09	0.10	0.34
Granivorous passerine birds species richness	Veg. seasonality	5	320.70	0.00	0.90	-155.58	0.21	0.20	0.51

Also for SA2, when considering indicators related to total richness and average β -diversity of passerine species, features associated to landscape composition attained the highest support (w_i of 0.57 and 0.33, respectively). However, models including RS variables of vegetation phenology, seasonality and primary productivity also recorded good to moderate support for average β -diversity (respectively, $w_i=0.31$, 0.09 and 0.06); and also, productivity followed, with less support by phenology for total passerine species richness (respectively, $w_i=0.21$ and 0.17). When considering species richness of insectivorous birds, landscape composition and configuration obtained greater support (w_i equal to 0.61 and 0.23 respectively) and only moderate support for vegetation phenology ($w_i=0.08$; Table 2). In case of species diversity of omnivorous bird species, higher model complexity was found with very similar support obtained for landscape variables but also for vegetation dynamics. Regarding the species richness of granivorous birds, a very strong support of vegetation seasonality dynamics was found ($w_i=0.90$; Table 2).

Overall, MMI summary results for bird diversity indicators (Figure 1) showed that structural metrics related to landscape composition were highlighted as important an equal number of times as vegetation functional attributes related to phenology (80%). Also for bird diversity indicators, RS indices of vegetation seasonal variation and primary productivity along with landscape configuration were selected 60% of the times as having substantial or moderate model support in MMI. Regarding plant species indicators, overall structural landscape metrics, particularly landscape composition attained highest scores (100%) but closely followed by vegetation functional attributes related to seasonality (67%) and to a lesser extent productivity (33%) and phenology (33%) along with landscape configuration (33%).

Inter-annual dynamics

For SA1, two types of model predictions (MP) were performed and compared: (i) single-year predictions using solely data for the calibration year of 2010 (MP-1), and (ii) composite multi-temporal mean predictions, averaging predicted habitat suitability between 2001 and 2010 (MP-2). Although the performance statistics showed good results for MP-1, with AUC=0.88 and TSS=0.82, the inclusion of dynamic data in multi-temporal predictions further increased model accuracy in MP-2 (AUC=0.95, TSS=0.92). A considerable portion of the study-area was considered suitable for the test species, at least for one year of the focal period (Figure 2). However, when focusing on areas most often predicted by the averaged-model, this area decreased considerably as well as the spatial contiguity of suitable habitat (darker areas in Figure 2). Suitable areas of higher stability in the 10-year period are generally distributed along low-elevation areas and valleys, often close to rivers or areas with high water availability, and locations with high productivity and seasonality dynamics.

Results on the % change rate of passerine bird species richness between 2007 and 2014 evidence large areas that may have undergone a lagged loss in avifauna diversity following the 2006 wildfires (only

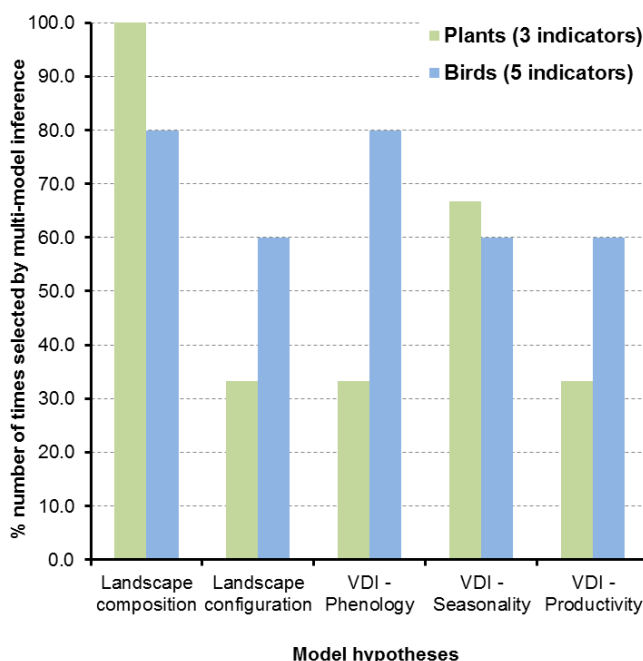


Figure 1 – Summary of multi-model results highlighting the % number of times that a given hypothesis was selected for plant species indicators (three total) and bird species indicators (five in total).

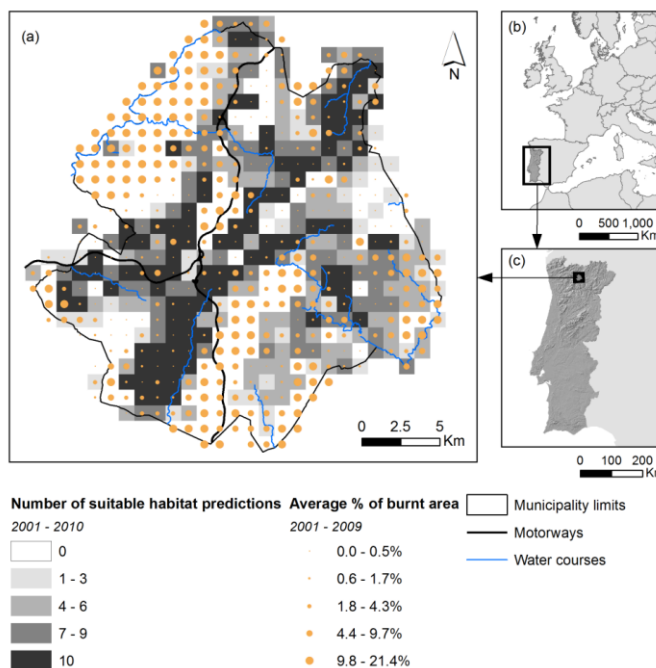


Figure 2 – Number of suitable habitat predictions between 2001 and 2010 for each grid unit in SA1 using model-averaged predictions (a); and, SA2 geographic location (b,c). Areas more often predicted in the temporal interval of the study have darker tones.

considering areas in recovery), as shown in Figure 3. However, other areas show an increase in species diversity towards 2014, probably evidencing some recovery to pre-fire conditions (Figure 3).

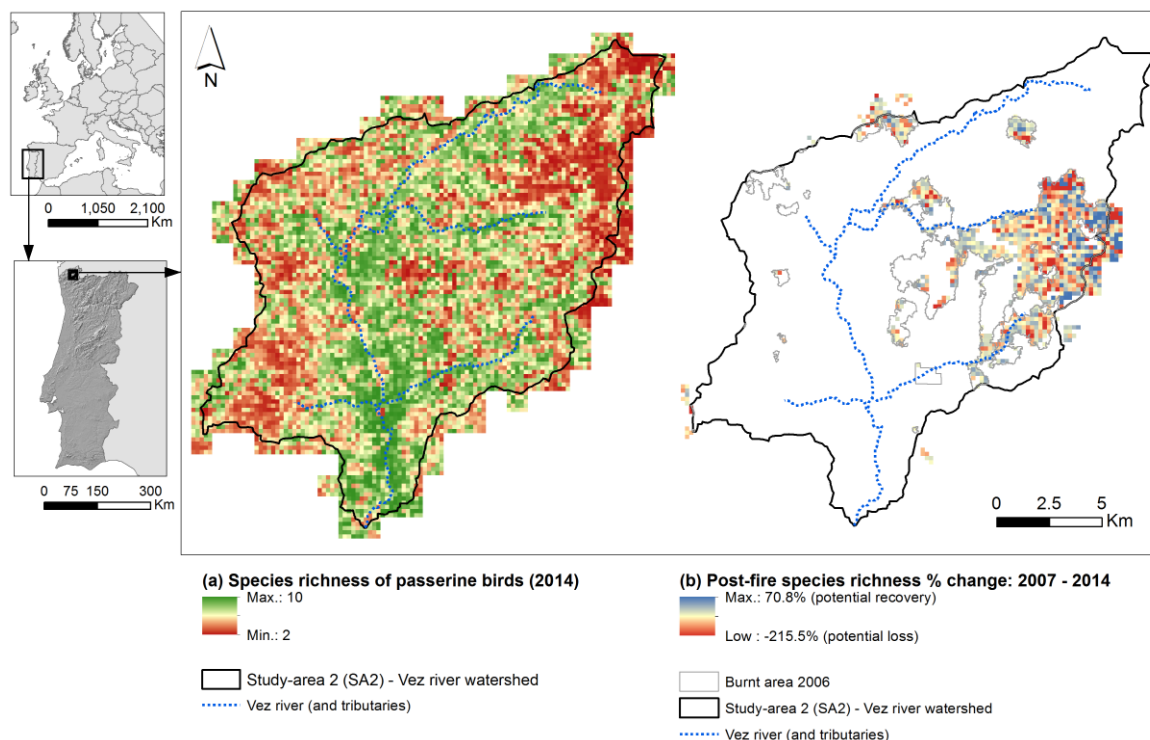


Figure 3 – (a) Species richness of passerine birds in SA2 as predicted by GAM including all predictors related with vegetation indices for calibration year of 2014 (greener areas indicate higher diversity), and (b) % change in species richness of passerine birds following 2006 wildfires in recovering areas (solely affected by fire in 2006 between 2000 and 2013).

DISCUSSION AND CONCLUSIONS

Multi-model inference showed the importance of structural variables related primarily to landscape composition (and secondly, to configuration), however it also emphasized a good predictive ability for remote sensing variables related to vegetation dynamics and functioning (9, 12, 24). Additionally, this technique provided insights into which specific aspects of annual vegetation dynamics linked to timing/phenology, seasonality fluctuations and/or primary productivity mostly affects species distribution or diversity patterns for different groups. Overall, our results stress the importance of considering landscape attributes related to landscape function, composition and configuration to explain diversity patterns at the local scale. However, for some indicators, such as the species richness of endemic plants or the species richness of granivorous birds, vegetation indices derived from high temporal resolution RS data may in fact provide better predictive results. High-temporal RS data of vegetation dynamics also showed promising results for assessing potential impacts of fire on biodiversity, as well as, potential recovery towards pre-fire conditions. Although more testing is required, this may suggest that RS-based vegetation indices may contribute for effectively mapping and monitoring a large array of biodiversity indicators over large areas due to their synoptic and high-temporal resolution (10, 11, 25).

Based on multi-temporal data, our methodological approach allowed exploring the effects of short-term environmental variations on the spatiotemporal dynamics of habitat suitability. This is especially useful since these fluctuations may pose additional threats to species with already high extinction risk. Habitat suitability time-series can also provide useful inputs for systematic

conservation planning, allowed assessing and ranking suitable habitat areas according to their relative stability in time. Functional indicators of vegetation dynamics could provide early warnings of tipping changes in ecosystem state and processes (26) affecting habitat suitability and general biodiversity indicators, well before assessments based on structural landscape metrics calculated from LUC maps. Even at a local scale, functional indicators of vegetation dynamics may provide useful data for biodiversity monitoring in combination with habitat suitability/diversity models. This may be especially interesting if landscape dynamics is prone to frequent and various types of disturbances (e.g., frequent fires or LUC changes) not easily measured by low frequency-update LUC data products provided by environmental/conservation agencies.

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