

Quantifying the spatial impact of an invasive *Acacia* on ecosystem functioning using remote sensing

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ABSTRACT

Remote sensing technology is increasingly applied to map the occurrence of invasive plant species, yet its use to map their ecological impact remains limited. Furthermore, invader-induced changes beyond the canopy, as well as the environmental context, are rarely considered. This study aimed to assess the impacts of an invasive tree on ecosystem functioning at the landscape scale using remote sensing, taking into account both spatial effects and environmental heterogeneity. Specifically, we investigated a coastal Mediterranean dune ecosystem invaded by the N-fixing tree *Acacia longifolia* (Andrews) Willd. ('*Acacia*'). Four vegetation indices were calculated as proxies of ecosystem functions, and these indices were used to compute functional diversity in terms of spectral Rao's Q for assessing impacts by *Acacia* based on airborne hyperspectral data. Vegetation cover and topographic indices derived from airborne LiDAR (Light Detection and Ranging) were used to account for spatial heterogeneity. For seven sites, we employed Generalized Linear Mixed Models to model the effects of environmental variables and *Acacia*-related variables on proxies of ecosystem functions. Significant impact of the invader was found beyond the invaded area augmenting to 50 % total impact on ecosystem functions. These spatial impacts are particularly prevalent at rather early stages of invasion (~20 % invader cover at landscape level). Consequently, the impact of invaders is underestimated when spatial effects are ignored, but it is overestimated when environmental heterogeneity is neglected. Furthermore, functional diversity decreases due to invasion, though it reaches its maximum at the edges of invader stands, where Rao's Q index captures spectral effects of both the invader and the native vegetation. Thus, we highlight that both 2D and 3D remote sensing data complement each other in remote sensing-driven impact assessments. We envision that advancements in remote sensing of ecosystem structure and functioning in terms of increasing availability of high spectral, spatial and temporal data as well as enhanced methods for data analysis will facilitate tracing the context-dependent and function-specific spatial effects of invasive species especially at early stages of invasion to enable timely management.

1. Introduction

Impact assessments of biological invasions seek to quantify adverse effects of invasive alien species on ecological, economic or social goods at regional levels in order to identify high-impact invaders and to prioritize most harmful species for management (Brundu et al., 2020; Kumschick et al., 2015; Parker et al., 1999; Powell et al., 2013; Pyšek

et al., 2020; Ricciardi et al., 2021; Thiele et al., 2010). In order to assess ecological impacts at larger scales, it is necessary to understand the local effects of invasive species (Blackburn et al., 2014; Hulme et al., 2013; Latombe et al., 2017). This can be done by empirical field studies or by experimental approaches that relate local presence or abundance of the invader to particular ecosystem functions or other goods (Barney et al., 2015; Bernard-Verdier and Hulme, 2019; Lee et al., 2018; Marchante

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et al., 2019; Sofaer et al., 2018; Vilà et al., 2024; Vitousek and Walker, 1989; Yokomizo et al., 2009). Regarding plant species, such studies are usually based on vegetation samples that are either located within invasive stands or in uninvaded and unaffected areas. Hence, effect estimates do rarely (e.g. Gómez-Aparicio and Canham (2008)) consider impacts of the alien species on the surroundings of invasive stands ('spatial impact'). However, disregard of spatial impacts might lead to underestimation of total impact, which may distort rankings of invasive species if they differ in strength and extent of influence on the surroundings.

Quantifying the effects of nitrogen-fixing invasive species on ecosystem processes has gained special attention in invasion ecology for decades (Ehrenfeld, 2010; Scherer-Lorenzen et al., 2007; Vitousek and Walker, 1989). Clear impacts on N cycling have been demonstrated particularly for invasive *Acacia* spp. (Marchante et al., 2019; Rodríguez-Echeverría et al., 2009; Yelenik et al., 2007), which can be regarded as global high impact invaders (Kumschick and Jansen, 2023; Le Maitre et al., 2011; Richardson et al., 2023). It is known that nitrogen fixation of *Acacia* spp. considerably affect nitrogen budgets of adjacent native species (Rascher et al., 2012) especially within a 5–8 m margin outside of their stands (Hellmann et al., 2017). These findings suggest that nitrogen-fixing invasive species may have a significant spatial impact on nitrogen cycling and, consequently, other ecosystem functions, such as photosynthesis and primary productivity, beyond their canopy edges.

In quantitative impact assessments, local effects are projected to the region where the alien species is invasive to provide a measure of total impact. Such impact measures can be calculated by multiplying the average local effect of the invader by the invaded range, i.e. the area that is affected (Parker et al., 1999) although abundance-impact relationship are not necessarily linear (Sofaer et al., 2018; Strayer, 2020; Yokomizo et al., 2009). Clearly, if significant spatial impact is not taken into account, total impact might be underestimated. This might be extremely relevant in case of the invasion by an ecosystem engineer that can profoundly modify ecosystem functioning and, subsequently, cause regime shifts (Kumschick et al., 2015). Thus, it is important to consider areas that are adjacent to invasive stands and to include spatial components, e.g. distance from the invader, into effects models in order to quantify a total impact score of the invader at landscape scale.

Environmental heterogeneity is another important factor to consider when projecting impacts to landscape or regional scales because effects of invasive species are context-dependent and may vary with local conditions, such as topography, habitat type or vegetation structure (Bartz and Kowarik, 2019; Gioria et al., 2023; Hulme et al., 2013; Kumschick et al., 2015; Lee et al., 2018; Pyšek et al., 2012; Sofaer et al., 2018). Not taking into account environmental heterogeneity may lead to substantial bias in impact assessments (Thiele et al., 2011). Hence, environmental covariates should be used in effect models in addition to presence or abundance of the invader and, possibly, variables of invader proximity.

If spatial impacts are to be considered, the underlying data need to be spatially explicit, and scattered samples will not be sufficient. In fact, precise maps of invader occurrence, key environmental variables and state variables of ecosystem functioning that cover large areas are required (Latombe et al., 2017). Obviously, exhaustive field sampling of large areas is not feasible, in particular with regard to the increasing numbers of invasive species (McGeoch et al., 2023; Seebens et al., 2017), but new approaches are needed to support early-warning and surveillance systems to prevent high impacts (Müllerová et al., 2023; Tollington et al., 2017). Remote-sensing technologies, such as airborne hyperspectral imagery and Light Detection and Ranging (LiDAR), have the potential to deliver the required data at regional scale.

Finally, spatial impacts on ecosystem functioning by invasive ecosystem engineers can result in a change of habitat diversity and complexity (Crooks, 2002). However, this effect can be both positive or negative (Crooks, 2002), and subtle invader-induced functional changes might be difficult to decipher (Jarić et al., 2019). While in particular

Acacia species are known to be invaders that simplify habitats (Le Maitre et al., 2011), very little is known on how to capture such impacts using remote sensing. Rocchini et al. (2017) developed a new method to map environmental heterogeneity by remote sensing using a spectrally derived Rao's Q index based on information theory. The underlying concept of the spectral Rao's Q is the Spectral Variation Hypothesis (SVH), which was conceived by Palmer et al. (1999; Palmer et al., 2002) and firstly tested by Gould (2000), as stated in the recent review by Torresani et al., (2024). According to the SVH, spectral variability relates to different facets of biodiversity (Torresani et al., 2024). It was firstly applied to study the biodiversity of plants (Gould 2000, Palmer et al., 2002), e.g., by relating the variability of the Normalized Difference Vegetation Index (NDVI) of a landscape as a proxy for its heterogeneity to plant species richness (Gould 2000). Since then, Torresani et al. (2024) found more than 130 studies using the SVH in remote sensing-based biodiversity assessment, with the majority of studies having been conducted in forest or grassland ecosystems, while coastal ecosystems have received less attention, and only accounted for 5 % of the studies. Beyond assessment of plant species richness, the first studies to assess functional diversity using spectrally derived metrics emerged in 2017 (Torresani et al., 2024) coinciding with the development of the spectrally derived Rao's Q index (Rocchini et al., 2017). In remote sensing approaches, the pixel-based Rao's Q outperforms common biodiversity metrics such as Shannon's entropy H' (Rocchini et al., 2017), it relates to β -diversity as well as functional plant diversity (Rocchini et al., 2018) and it can be parameterized in multidimensional mode to account for both abundance and distance to describe the environmental heterogeneity of a site (Rocchini et al., 2021). However, its application in the context of biological invasions is underexplored. In the aforementioned review regarding the SVH, Torresani et al. (2024) found only one study that examined the potential of the spectral Rao's Q to assess effects of an invasive species on species diversity (Khare et al., 2019). In terms of effects on ecosystem functioning, Gholizadeh et al. (2024) recently demonstrated the positive and linear relationship between remotely-sensed functional diversity and invasive legume cover in a grassland ecosystem. This said, no studies have been found which were conducted in a coastal ecosystem or which used the spectrally derived Rao's Q index to assess the spatial effects of an invasive ecosystem engineer on ecosystem functioning.

In this study, we modelled the impacts of the invasive *Acacia longifolia* on coastal Mediterranean ecosystems using remote sensing data. The aims of our study were:

1. to quantify the spatial impacts of the invader on ecosystem functions (e.g. primary productivity, photosynthesis);
2. to determine the influence of environmental heterogeneity on impact assessment;
3. to assess the effect of the invader on functional diversity.

2. Material and methods

2.1. Study area

The study area was located in Southwest Portugal and comprised a coastal strip of approximately 35 km length for which we chose a subset of seven sites of between 50 and 75 ha (Fig. 1): Fonte do Cortiço (FdCo), Monte Velho (MoVe), Melides (Meli), Pinheiro da Cruz (PdCr), Pinheiro (Pinh), Aberta Nova (AINo), Lagoa da Sancha (LdSa). At these sites, we studied the invasion of *Acacia longifolia* (Andrews) Willd. (in the following being referred to as *Acacia*) into coastal dunes, which are protected under the European NATURA2000 directive (ICNB, 2005) and partly by national legislation (Pinto, 2014). This diverse dune ecosystem comprises a variety of NATURA2000 habitat types such as "Atlantic decalcified fixed dunes" (2150*), "coastal dunes with *Juniperus* spp." (2250*), "dune sclerophyllous scrubs" (2260) or "wooded dunes with *Pinus pinea* and/or *Pinus pinaster* (2270*)" (ICNB, 2005). Priority habitat

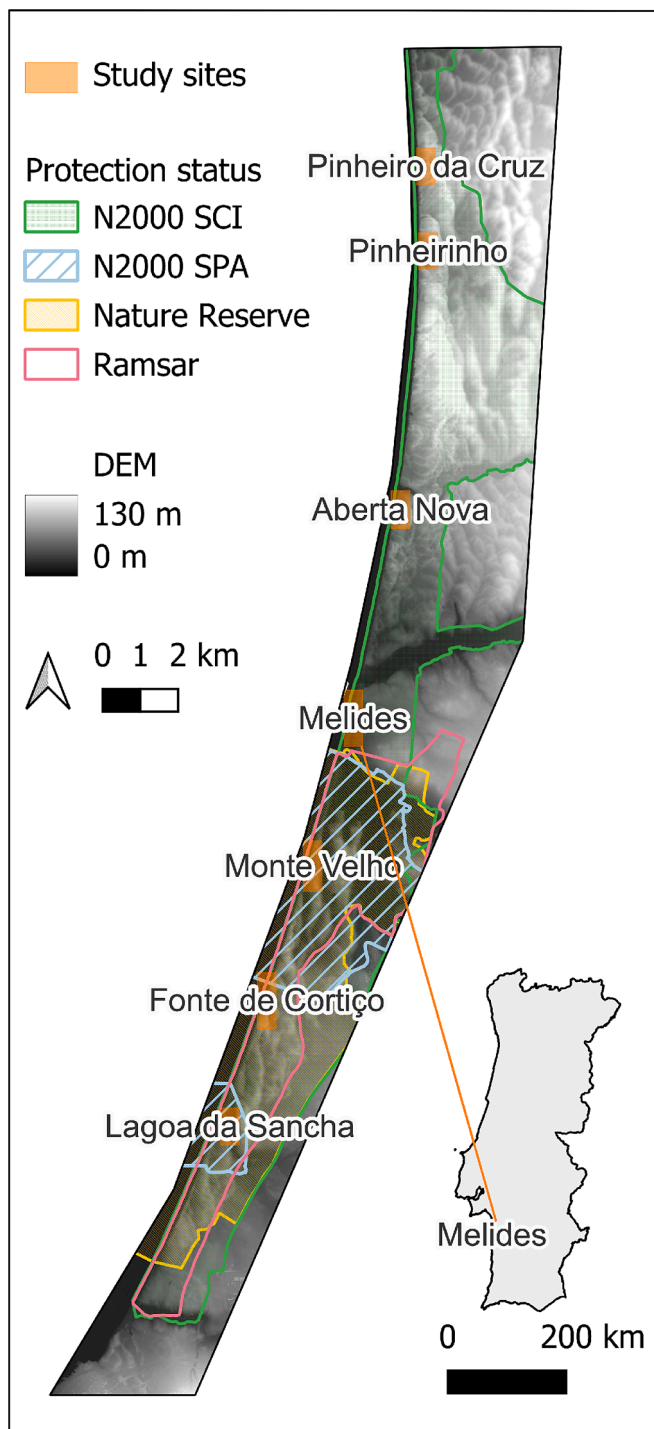


Fig. 1. Map of the studied Mediterranean dune ecosystem in SW Portugal showing the seven study sites with a Digital Elevation Model (Große-Stoltenberg et al., 2018b) in the background. The coastal dunes are part of the Natura 2000 (N2000) network of protected areas in the European Union and are situated in the SCI (Site of Community Importance) ‘Comporta/Galé’. The southern part of the dune ecosystem is further protected by national legislation, the Ramsar wetland convention, and it includes two N2000 Special Protection Areas (SPA).

types according to the NATURA2000 directive are marked with an asterisk (“*”) (ICNB, 2005). Native tall shrubs or trees that co-occur with *Acacia* at the site include *Phillyrea angustifolia* L., *Pinus pinaster* Ait., *Pistacia lentiscus* L., and *Juniperus phoenicea* L.. Examples for medium-size native shrub species are *Cistus salvifolius* L., *Halimium halimifolium*

(L.) Willk., *Lavandula stoechas* L., and *Salvia rosmarinus* Spenn. Typical dwarf shrubs include *Armeria pungens* (Link) Hoffmanns. & Link, *Santolina impressa* Hoffmanns. & Link, *Thymus camphoratus* Hoffmanns. & Link, and *Thymus carnosus* Boiss. (Große-Stoltenberg et al., 2018a). The climate of the study area is Mediterranean with Atlantic influence. For further details on study area and sites including descriptions and analyses of the vegetation see ICNB (2005), Rascher et al. (2011a), Rascher et al. (2011b), Rascher et al. (2012), Hellmann et al. (2011), Hellmann et al. (2016a), Hellmann et al. (2016b), Hellmann et al. (2017), Pinto (2014), Lehmann et al. (2015), Große-Stoltenberg et al. (2016), Große-Stoltenberg et al. (2018a), Große-Stoltenberg et al. (2018b) and Ulm et al. (2017a).

2.2. Study species

Acacia has been introduced to Portugal at the beginning of the 19th century to fix sandy coastal soils (Fernandes, 2012; Marchante et al., 2023). In the study area, it gradually spread out into the herbaceous and scrubby dune vegetation as well as in pine plantations that are abundant at the inland side of the study area (e.g., Große-Stoltenberg et al., 2018b; Rascher et al., 2011a, Rascher et al. 2011b).

The impacts of *Acacia* at the site include the decrease of plant diversity (Hellmann et al., 2011), changing vegetation (Rascher et al., 2011a) and plant community structure (Hellmann et al., 2011; Rascher et al., 2011a), modifying soil properties (Hellmann et al., 2011; Ulm et al., 2017b) and nutrient cycling (Rascher et al., 2012; Ulm et al., 2017a; Ulm et al., 2017b) as well as alterations of water and carbon cycling (Rascher et al., 2011b).

Spatial impacts of *Acacia* on ecosystem functioning in particular have been studied by analysing the spatial distribution of foliar isotopic signatures $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of native plant species growing in vicinity to the invader (Hellmann et al., 2017, 2016a, 2016b; Rascher et al., 2012) to compute so-called “isoscapes” (West et al., 2008). *Acacia* has a spatial effect on N-cycling ($\delta^{15}\text{N}$) (Hellmann et al., 2017, 2016a, 2016b; Rascher et al., 2012) as well as on water use efficiency ($\delta^{13}\text{C}$) of the surrounding vegetation (Hellmann et al., 2016a, Hellmann et al., 2016b). In the case of the $\delta^{15}\text{N}$ isoscapes, airborne LiDAR data, specifically proxies for topography and vegetation structure, have shown to be useful to account for the heterogeneity of the ecosystem and, thus, of the invaders’ spatial impacts on N cycling (Hellmann et al., 2017).

2.3. Remote sensing data

We used airborne remote data on *Acacia* invasion (Große-Stoltenberg et al., 2018b). The hyperspectral (AISA Eagle and Hawk, Spectral Imaging Ltd., Oulu, Finland), LiDAR (Leica ALS50-II, Leica Geosystems AG, Heerbrugg, Switzerland), and true-colour image (Leica RCD105, Leica Geosystems AG, Heerbrugg, Switzerland, Switzerland) data were simultaneously collected on April 8th, 2011, $\pm 2\text{h}$ around solar noon at an altitude of 1350 m. The raw data were processed (see Große-Stoltenberg et al. (2018b) for details), and the pixel size of the hyperspectral data was 2 m x 2 m with a spectral coverage of 400—970 nm and 970—2516 nm, 241 and 245 bands with Full-Width Half-Maximum (FWHM) of 2.20—2.45 nm and 6.3—6.31 nm for the Eagle and Hawk sensor, respectively. The LiDAR data had a point density of 4–5 points/m², and LiDAR-derived products (see below) were also gridded to 2 m x 2 m, so both data sets had the same pixel size. The true colour images with a spatial resolution of 0.2 m were not processed any further, and were used for visual interpretation and visualization.

2.4. Hyperspectral indices as proxies of ecosystem functions

We calculated four vegetation indices related to ecosystem functioning and potential impacts by *Acacia* based on the airborne hyperspectral data. The Near-Infrared Vegetation Index (NIR_v) (Badgley et al., 2017) is sensitive to canopy structure and has been used to scale up gross

primary productivity (GPP) from local to large levels (Badgley et al., 2019). It is based on the Normalized Difference Vegetation Index (Tucker, 1979), and adds further information from the infrared part of the spectrum while having a strong physical basis (Badgley et al., 2017):

$$NIRV = NDVI \times NIR \quad (1)$$

We calculated the NDVI as following, where R_x is the reflectance at the defined wavelength (nm):

$$NDVI = (R_{800} - R_{680}) / (R_{800} + R_{680}), \quad (2)$$

The Modified Chlorophyll Absorption in Reflectance Index (MCARI) is based on the depth of the chlorophyll absorption at 670 nm (Daughtry et al., 2000):

$$MCARI = ((R_{700} - R_{670}) - 0.2 \times (R_{700} - R_{550})) \times (R_{700} / R_{670}). \quad (3)$$

The MCARI is sensitive to both leaf chlorophyll concentrations and background reflectance (Daughtry et al., 2000).

As a proxy for nitrogen, we computed the Normalized Difference Nitrogen Index (Serrano et al., 2002):

$$[\log(1/R_{1510}) - \log(1/R_{1680})] / [\log(1/R_{1510}) + \log(1/R_{1680})] \quad (4)$$

The NDNI uses spectral information from the shortwave infrared part of the electromagnetic spectrum, and it has been developed for shrub vegetation using airborne hyperspectral data in a Mediterranean Ecosystem (Serrano et al., 2002).

To estimate the effect on the water content of vegetation canopies, we used the normalized difference water index (NDWI) (Gao, 1996):

$$(R_{860} - R_{1240}) / (R_{860} + R_{1240}) \quad (5)$$

The NDWI is similar to the NDVI, but instead of using information from the visible part of the spectrum, it uses a water absorption feature of vegetation canopies near 1240 nm (Gao, 1996). The NDWI has been used, for example, to identify drought effects on nutrient availability in Mediterranean grasslands (Cerasoli et al., 2018).

2.5. Spectrally derived Rao's Q index as a proxy for functional diversity

All vegetation indices were selected as input layers to calculate the spectrally derived Rao's Q index (Rocchini et al., 2017) to map the invader's impact on functional diversity. In vegetation science, Rao's quadratic entropy has originally been developed to assess functional diversity based on several traits (Botta-Dukát, 2005). The spectral Rao's Q index has mainly been used together with the NDVI (Khare et al., 2019; Rocchini et al., 2018, 2017; Torresani et al., 2020) or tree height (Torresani et al., 2020) to map species diversity. Here, we assessed the effect of the invader on functional diversity by calculating the parametric spectral Rao's Q entropy (Rocchini et al., 2021) using the *paRao* function from the package *rasterdiv* 0.3–4 (Marcantonio et al., 2024) using R statistical software, version 4.3.3 (R Core Team, 2024). We computed the Rao's Q index in multidimensional mode for all four vegetation indices (NIRv, MCARI, NDNI, NDWI) using Euclidean distance with a spatial moving window of 3x3 pixels so spatial distances between the central pixel and neighbouring pixels in each window (see Rocchini et al., 2024) would be below the spatial range of impact in terms of ¹⁵N-enrichment of up to 6–8 m to *Acacia* canopy as observed in earlier field studies (Hellmann et al., 2017). The alpha parameter was set to infinity to maximise pixel distances and, thus, discrimination potential of the Rao's Q index (Rocchini et al., 2017). Within the *paRao* function, the values for each vegetation index were standardised, i.e. centred on the layer mean and divided by the standard deviation, to ensure similar value ranges for the different vegetation indices, which is

important for calculating distances using Euclidean geometry.

2.6. Data related to *Acacia* invasion

We derived a raster map of presence-absence of *Acacia* from a remote sensing-based detection model (Große-Stoltenberg et al., 2018b). Further, we calculated the horizontal distance and the elevational difference of each raster cell to the nearest stand of *Acacia* with SAGA GIS 8.1 (Conrad et al., 2015). We also allocated the size of the closest *Acacia* stand to each raster cell. For impact modelling, we reduced the dataset to those raster cells that overlapped with 25-m buffers around the *Acacia* stands because previous studies showed that the influence of this invader was virtually zero at this distance (Hellmann et al., 2017).

As distance from *Acacia* is negatively related to impact, we converted distances to proximities by subtraction from the respective maximum values. Regarding horizontal distance, we used 27 m so that the farthest raster cells (max. distance 26.9 m) received a proximity value of 0.1, while cells that were directly adjacent to *Acacia* stands received 25 (given the spatial resolution of 2 m). For cells where *Acacia* was present, we set proximities values to zero (instead of 27) in order to avoid confusion between the statistical effects of invader presence and proximity. To explore the detailed effects on functional diversity, we additionally differentiated between *Acacia* stands ("invasion", distance of zero), the edge of *Acacia* stands ("edge", cells bordering *Acacia* canopy from in- and outside), and the area beyond the edge of *Acacia* canopy ("uninvaded").

Likewise, we calculated elevational proximity values. For this purpose, we coded elevation proximity above and below *Acacia* stands as two separate variables in order to account for possible directional differences. In addition to the original values, we calculated log and square-root transformed elevational distances that we converted to proximities in the same fashion.

2.7. Environmental data

We used vegetation cover and topographic indices to account for spatial heterogeneity of the invaded ecosystems. Vegetation cover was estimated based on LiDAR data with a cut-off of zero, which means that all non-ground points were considered to represent vegetation. Using the airborne LiDAR-derived, smoothed bare-earth DEM (see 2.3 and Große-Stoltenberg et al. (2018b)), we calculated the Topographic Wetness Index (TWI). Further, we calculated a topographic position index (Weiss, 2000) to classify the landform into ridges, slopes, drainages, valleys and plains according to Hellmann et al. (2017).

2.8. Impact modelling

For impact modelling, we discarded all cells that were located within 25 m from the borders of the sites to avoid edge effects due to *Acacia* stands at the outside. All subsequent statistical analyses were conducted in R statistical software, version 3.4.2 (R Core Team, 2017).

We modelled the effects of environmental variables and *Acacia*-related variables on proxies of ecosystem functions with Generalized Linear Mixed Models (GLMM) that contained site ID as random effects. Regarding the fixed effects, we calculated two variants of models: (i) full models that contained all predictors and (ii) basic models that contained only variables related to *Acacia*, but ignored environmental heterogeneity. Pre-analyses with correlograms and Moran's I showed significant spatial auto-correlation in the residuals of preliminary impact models that included all predictors. Thus, as spatial auto-correlation may affect significance tests and estimates of linear models, we included Gaussian spatial correlation structures in the final models (Dormann et al., 2007).

When model residuals did not deviate substantially from the normal distribution, we used *lme* from the package *nlme* 3.1–131 (Pinheiro et al., 2018). This was the case with nitrogen (NDNI) and water (NDWI). The other three target variables, primary productivity (NIRv), indicator

of photosynthesis (MCARI) and functional diversity (Rao's Q), followed a gamma distribution and were modelled with *glimmPQL* from the package MASS 7.3–60.2 (Venables and Ripley 2002). The appropriateness of the gamma distribution was tested with *simulateResiduals* from the package DHARMA 0.4.6 (Hartig 2022).

In all models, we used the identity link which proved to be most suitable. We tested linearity of the relationship between target and predictor variables using *cumres* from the package gof 0.9.1 (Holst 2015). As *cumres* does not work with GLMM, we calculated corresponding models using *lm* or *glm* that included 'site' as a fixed effect, for this purpose. Based on the linearity tests, we identified the best variants of the metric predictor variables (original, log or square root transformed).

The datasets used for modelling comprised between 181,483 and 194,613 raster cells and, thus, were by far too large for models that include spatial correlation structures. For that reason, we divided the datasets into folds of approximately 2000 rows that were stratified by site and *Acacia* presence. Then, we iteratively calculated the same model (regarding predictors and setup etc.) using all of the folds. Finally, we calculated weighted averages of the estimates and their standard errors over all models. Standard errors of the average estimates were calculated according to the following formula:

$$se_t = \frac{\sqrt{\sum_i^N n_i \times s_i^2}}{\sum_i^N n_i} \quad (6)$$

where se_t is the standard error of the average estimate, N is the number of models, n_i is the sample size of model i and s_i is the standard deviation of the estimate in model i (NB: $s_i = se_i \times \sqrt{n_i}$). Based on the average estimates and their standard errors, we calculated t and p -values to assess the significance of predictors for the whole dataset.

We used the average estimates to calculate expected values of the target variables for each raster cell of the dataset. First, we calculated the expected background values using only the estimates of environmental variables plus estimates of the random intercepts of sites (background model). Second, we calculated expected values using the background model plus the effect of presence of *Acacia* (*Acacia*-presence model). Finally, we used all predictors, including the spatial effects of *Acacia* (spatial model). As the values of the water proxy (NDWI) are in the range [-1,1], we scaled its predicted values to the interval [0,1] before summing up over the landscape.

We calculated the impact that occurred within the stands of *Acacia* ('stand impact') as the difference between the expected values of target variables as predicted by the *Acacia*-presence model and the background model for each raster cell. Further, we calculated cell-level impact that occurred outside of the stands ('spatial impact') as the difference between the spatial model and the background model. In addition to these scores of absolute impact, we calculated impact percentages as the ratio of stand or spatial impact to the background value, multiplied by 100.

We measured the total impact of *Acacia* summing up the cell-level impact scores of both *Acacia* presence and the spatial impact over the invaded range. Here, we defined the invaded range as those raster cells that overlapped with the 25-m buffers around invasive stands. We also summed up the background scores over the invaded range to calculate the percentage of increase due to *Acacia* presence and spatial impact. All sums of scores were standardized to 1 ha for comparability.

To assess the influence of invasion stage on the relative strength of stand and spatial impacts, we calculated the sums of impact scores and the number of raster cells occupied by the invader (invader cover) in moving windows of $26 \times 26 \text{ m}^2$ (13×13 cells) over all sites. Thereby, we used stand impact and total impact (spatial model minus background). For graphical presentation, we randomly sampled one hundredth of the moving-window dataset, stratified by site, using *sampleRandom* from the package raster 2.5–8 (Hijmans 2016).

3. Results

3.1. Impacts on ecosystem functions

Presence of *Acacia* significantly increased the values of all proxies of

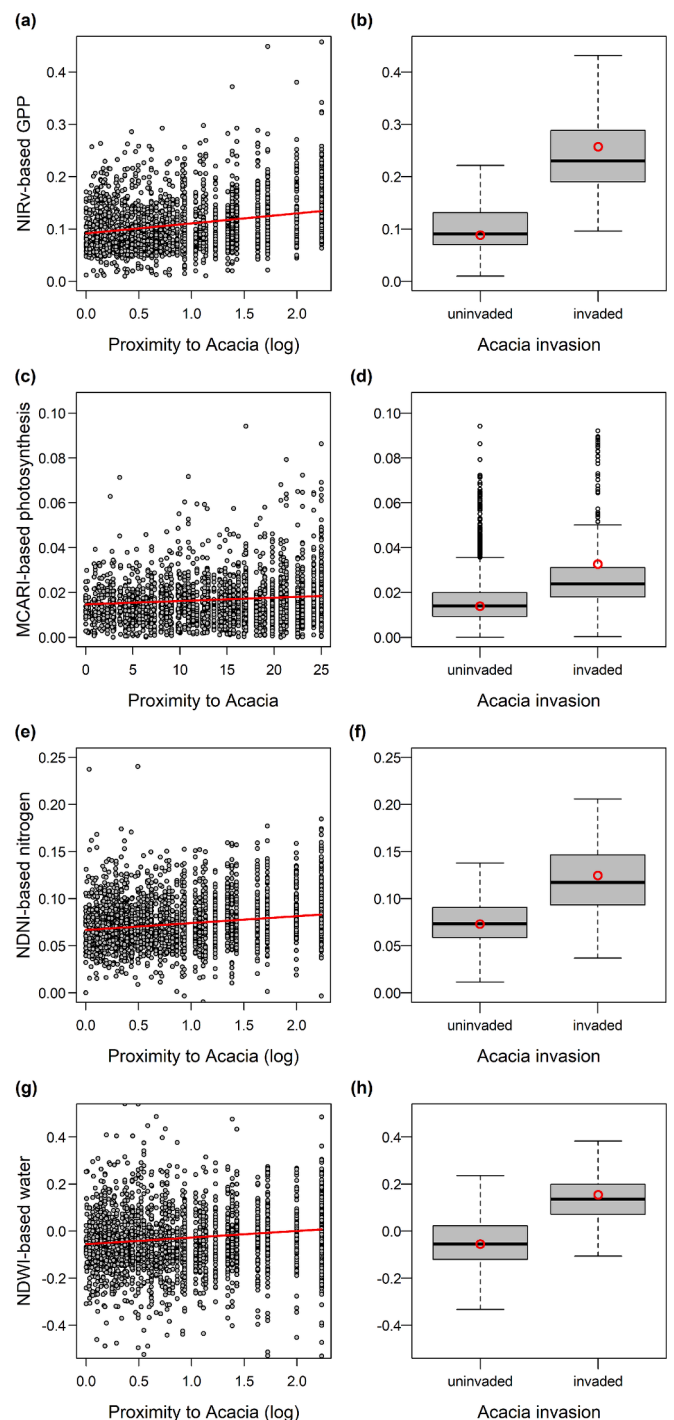


Fig. 2. Local effects of proximity to and presence of *Acacia* on ecosystem functions. Proximity was measured as inverted distance from raster cells classified as *Acacia* (centroid–centroid distance) within a buffer of 27 m, so that cells adjacent to invasive stands received a proximity value of 25 (27–2) and cells at 27 m distance would have a proximity of 0 (27–27). All slopes and differences between boxes were significant at $p < 0.001$. Red circles in boxplots indicate expected values given median values of Topographic Wetness Index and vegetation cover. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

ecosystem functions (Fig. 2; for detailed model summaries see Appendix A1, Tables A1-A10). Proximity of *Acacia* also had significant positive effects on the proxies of ecosystem functions outside of the invasive stands. This was mainly due to horizontal proximity (i.e. inverted distance from *Acacia* stands; Fig. 2). Regarding nitrogen, elevation proximity had small negative effects (Tables A5, A6), which however did not diminish the overall positive effect of proximity of *Acacia*. With respect to water, elevational proximity and stand size had minor negative effects that were overridden by the positive effect of horizontal proximity.

At landscape level, *Acacia* substantially increased the scores of primary productivity, photosynthesis and nitrogen (Fig. 3a-c). Concerning water, the score of the stand impact model (93,007) was within the confidence limits of the background value ($90,675 \pm 1,242$, upper limit: 93,160), while the total impact model was above this range (94,897). Thus, *Acacia* increased the water score significantly indicating a higher vegetation water content adjacent to *Acacia*, but this effect was small (+4.7 % total impact based on the full model; Fig. 3d). Generally, the impacts on ecosystem functions that occurred outside of the stands of *Acacia* (spatial impacts) were as large as or larger than the impacts inside the stands (stand impacts). In particular, the spatial impact on photosynthesis outweighed the stand impact (Fig. 3b). Hence, the impacted area extended far beyond the invasive stands (Fig. 4; Appendix

Figs. A1-A3).

3.2. Environmental heterogeneity

Disregarding environmental heterogeneity had a strong influence on the estimated background values of primary productivity and photosynthesis (Fig. 3a-b). The basic model, without environmental variables, predicted lower background values and, consequently, the relative impacts of *Acacia* increased. Regarding nitrogen and water, the differences between the full and basic models were minor (Fig. 3c-d).

The environmental variables consistently had significant effects on the estimation of background values of ecosystem functions. The most important predictor was vegetation cover that had positive effects on all ecosystem functions (Appendix A1, Tables A1, A3, A5, A7). The Topographic Wetness Index (TWI) had positive effects on nitrogen and water, but negative ones on primary productivity and photosynthesis. However, in all cases the effects of TWI were small. The landforms ‘ridges’ and ‘valleys’ had the highest values of ecosystem proxies, while ‘plains’, ‘slopes’ and ‘drainages’ had lower values, but differences were moderate throughout (Appendix A1, Tables A1, A3, A5, A7).

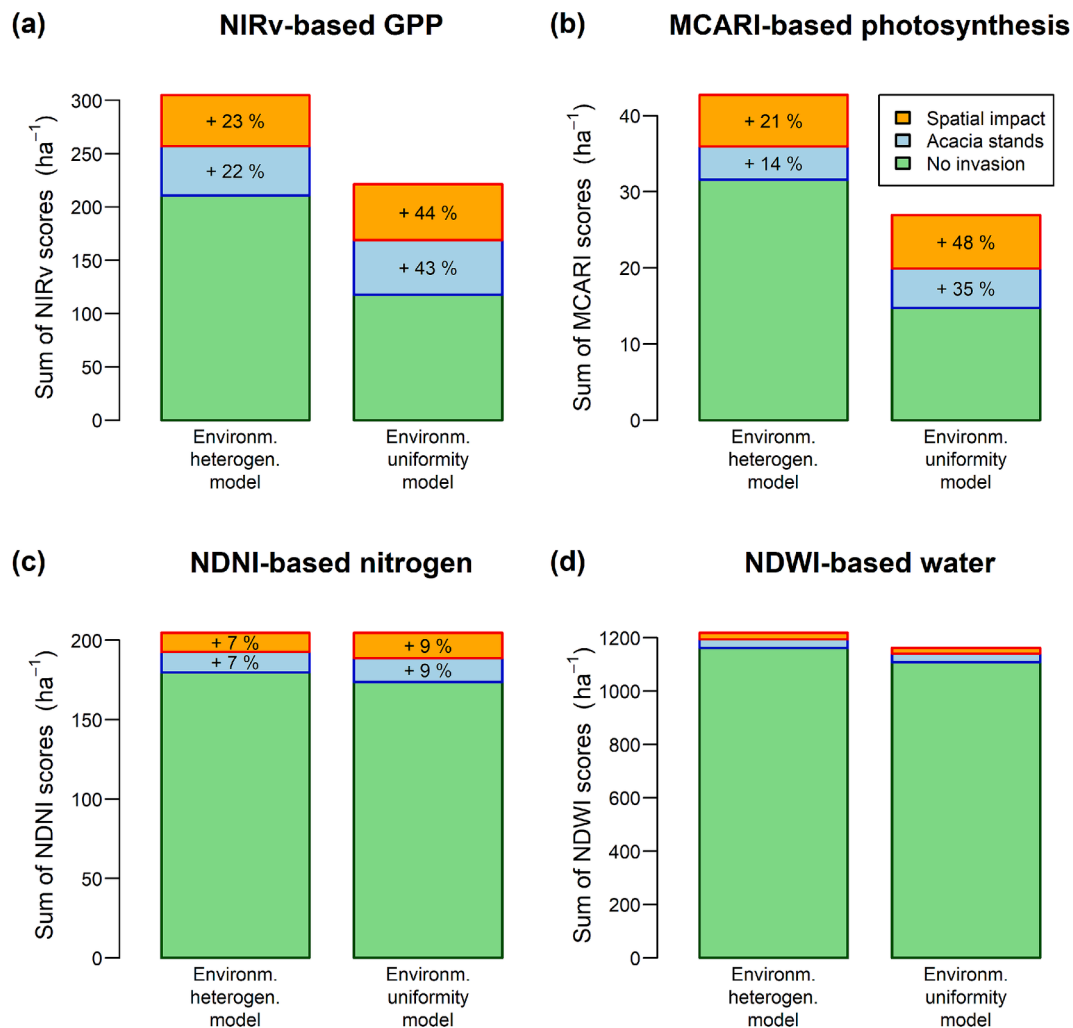


Fig. 3. Impacts of *Acacia* on ecosystem functions of Mediterranean dunes in Portugal at landscape level. The scores are the sums over all raster cells up to 27 m beyond invasive stands of predicted proxy values of ecosystems functions (hyperspectral indices). *Background* scores were estimated based on environmental variables (“Full” model) or based on the intercepts of models disregarding environmental heterogeneity (“Basic” model). *Stand impact* is the added score due to the effect of presence of *Acacia*. *Spatial impact* is the additional impact outside of the invasive stands that was modelled through effects of proximity (horizontal and elevational) and size of the closest stands of *Acacia*.

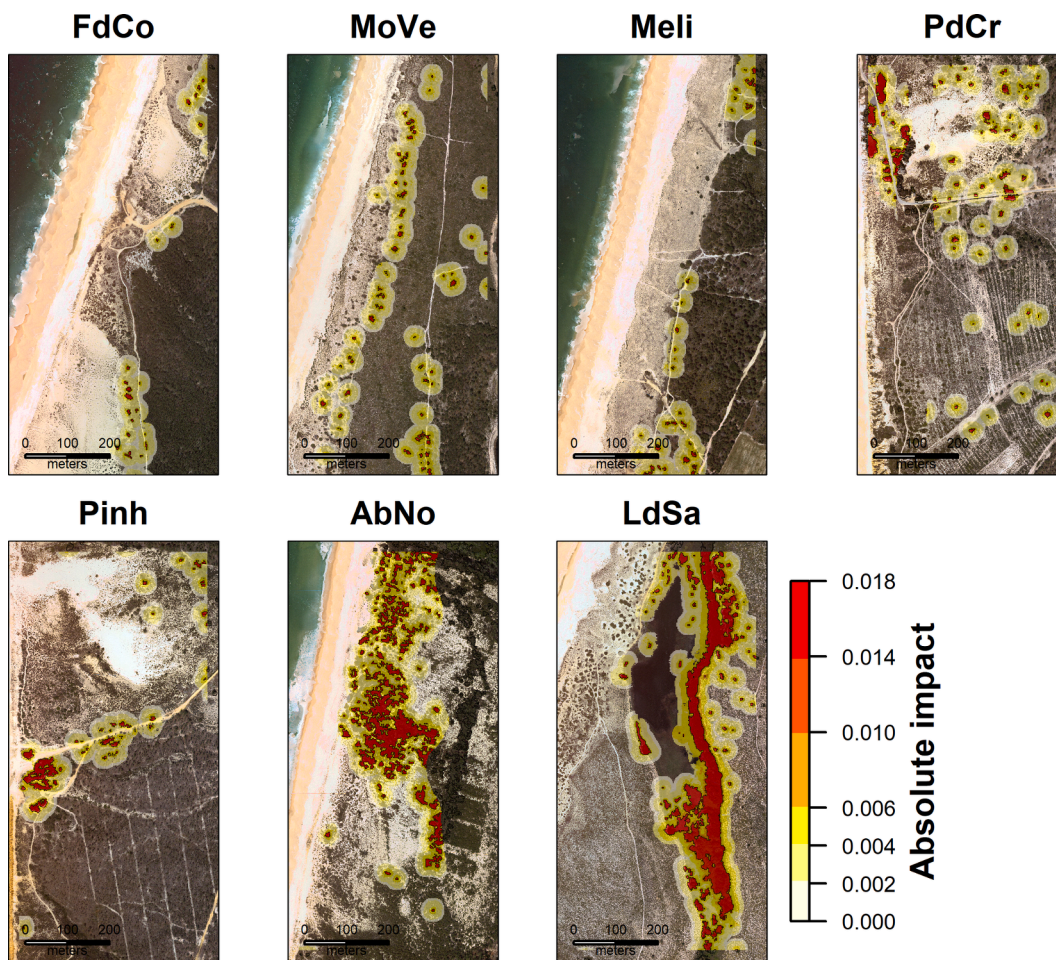


Fig. 4. Maps of impacts of *Acacia* related to photosynthetic activity from our seven study sites from low to high impact. The MCARI vegetation index was derived from hyperspectral data as a proxy of photosynthetic activity. Spatial impacts were modelled up to 27 m around invasive stands. Map backgrounds show aerial images that were taken simultaneously with the hyperspectral images.

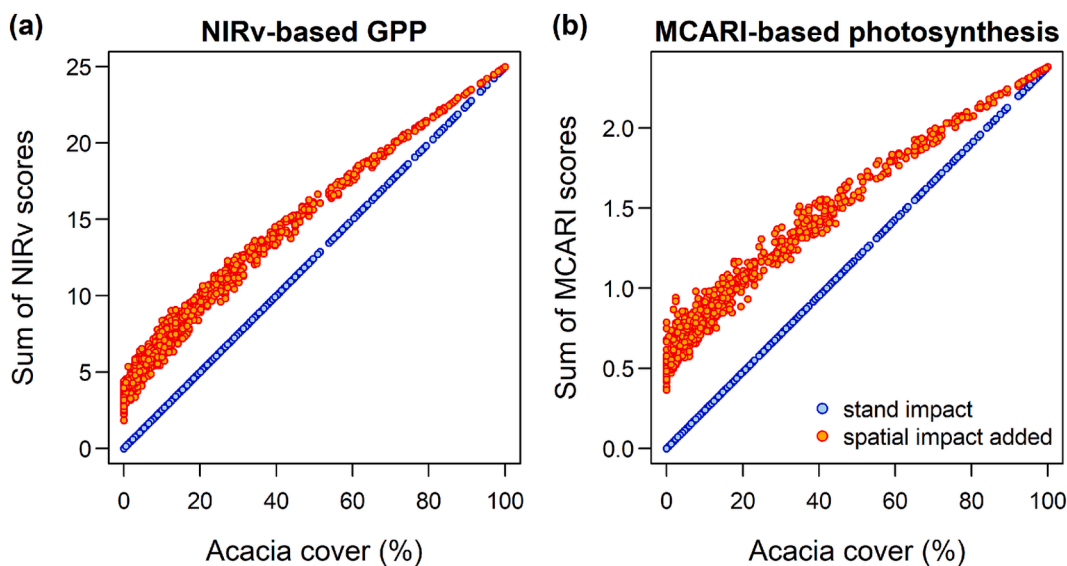


Fig. 5. Sums of impact scores of *Acacia* vs. its cover percentage in moving windows of 26×26 m with respect to (a) the NIRv index as a proxy of gross primary production and (b) MCARI as a proxy of photosynthetic activity. Impact scores were calculated per raster cell as the difference in predicted values of NIRv or MCARI between models that included *Acacia* invasion and background models for uninvaded sites. *Stand impact*: only presence-absence of *Acacia* was used for modelling impacts. *Spatial impact added*: impact models included both presence and proximity of *Acacia*. The difference between ‘stand impact’ and ‘spatial impact added’ equals the spatial impact that occurred outside of the invasive stands.

3.3. Invasion stage

The spatial impact of *Acacia* depended on the stage of invasion expressed as cover percentage of the invader within landscape windows (26×26 m). Regarding primary productivity, the proportion of spatial impact amongst total impact, i.e. the sum of cell-level impact scores of both the *Acacia* presence ('stand impact') and of the spatial impact, increased rapidly from early stage of invasion to up to 20 % invader cover. It then gradually decreased, but still showed positive trends across all cover ranges until the whole area was covered by the invader (Fig. 5a). The same pattern was found for nitrogen and water. However, with respect to photosynthesis, spatial impact was most prevalent at very early stages of invasion (close to 0 % cover) and declined steadily with increasing invader cover (Fig. 5b).

3.4. Functional diversity

Acacia had a spatial impact on functional diversity as the multidimensional Rao's Q index decreased with increasing proximity to the invader (Fig. 6a) in both the basic model and the model including environmental heterogeneity (Appendix A1, Tables A9, A10, Figure A4). Functional diversity was higher in uninvaded areas (native vegetation) compared to *Acacia* canopies where the Rao's Q index reached its minimum (Fig. 6b). However, Rao's Q index reached its maximum in the zone close to *Acacia* (Fig. 6b), and proximity to *Acacia* and 'Edge of *Acacia* stands' had marked positive effects in both models (Appendix A1, Tables A9, A10, Figure A4) indicating functional differences between the invader and the native vegetation.

4. Discussion

The overall aim of this study was to assess the impacts of an invasive tree on ecosystem functioning at the landscape scale using remote sensing. We demonstrate that a) impacts can be mapped by means of hyperspectral vegetation indices and b) that the integration of hyperspectral and LiDAR data improves mapping spatial effects beyond the invasive stands. Our study generated new insights on identifying high impacts at early stages of invasion, considering environmental

heterogeneity in impact assessments at the landscape scale and tracking effects on functional diversity after invasion. These findings enhance our understanding of remote sensing-driven impact assessments of invasive plant species.

4.1. Impact at landscape scale

This study confirms that *Acacia* has substantial effects on ecosystem functioning at landscape scale. Remotely sensed proxies of nitrogen in plant biomass (NDNI), chlorophyll/photosynthesis (MCARI), vegetation water content (NDWI) and primary productivity (NIRv) all increased in invasive stands. These results match those observed in field-based studies. Indeed, *Acacia* enriches invaded ecosystems with nitrogen (Hellmann et al., 2011; Marchante et al., 2019; Ulm et al., 2017b), it changes water cycling (Hellmann et al., 2016b; Rascher et al., 2011b), it shows high vitality productivity indicated by a high growth rate (Hellmann et al., 2011), it increases the Leaf Area Index and it causes densification of the vegetation structure (Rascher et al., 2011a).

Impacts on ecosystem functions are also typical for other invasive *Acacia* spp. (Kumschick and Jansen, 2023; Le Maitre et al., 2023) and other invasive plant species in general (Kumschick et al., 2015; Vilà et al., 2024), and such impacts have occasionally been assessed using remote sensing-based approaches (Müllerová et al., 2023). However, most remote sensing-based studies still focus on mapping invader occurrence (Bolch et al., 2020; Müllerová et al., 2023), and this also applies to well-studied species groups such as invasive *Acacia* spp. (Große-Stoltenberg et al., 2023). At the same time, availability of remote-sensing data as well as capacities for data analysis to study landscape structure and ecosystem functioning and dynamics across scales are increasing (Crowley and Cardille, 2020; Senf, 2022), which led to progress in the field of plant invasions (Müllerová et al., 2023; Saranya et al., 2024). Thus, a solid basis of knowledge and data on plant-invasion impact on ecosystem functioning exists. Together with recent technological progress there is high potential for future research on integrating field-based with remote sensing driven approaches to assess ecological impacts of plant invasions.

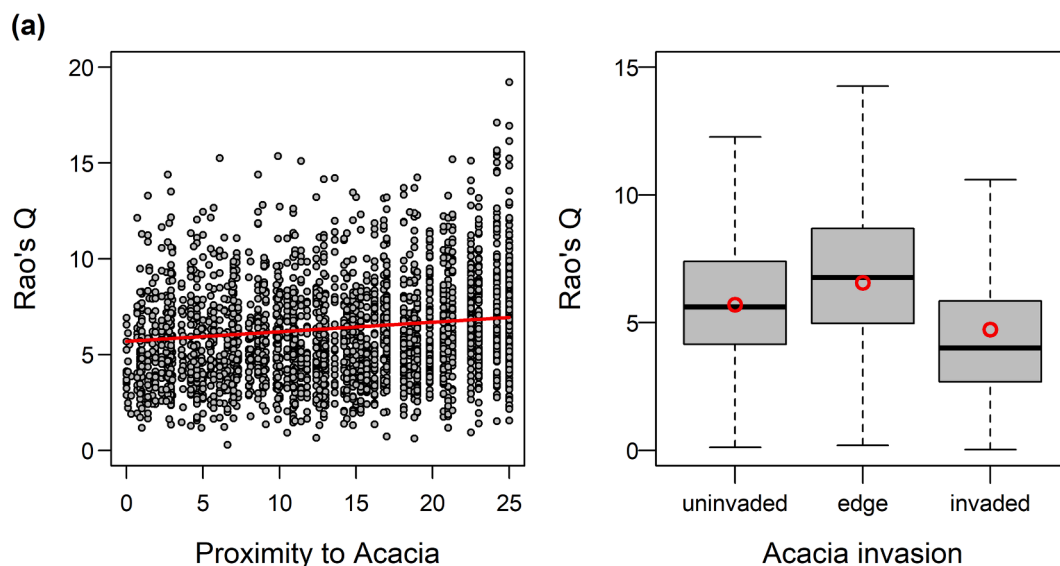


Fig. 6. Local effects of proximity to and presence of *Acacia* on functional diversity in terms of spectrally derived Rao's Q based on the vegetation indices NIRv, MCARI, NDNI and NDWI. (a) Proximity was measured as inverted distance from raster cells classified as *Acacia* (centroid-centroid distance) within a buffer of 27 m, so that cells adjacent to invasive stands received a proximity value of 25 (27–2) and cells at 27 m distance would have a proximity of 0 (27–27). (b) Rao's Q diversity was compared in detail for *Acacia* stands ("invaded"), the area of ± 2 m around the borders of *Acacia* stands ("edge"), and not invaded area ("uninvaded"). All slopes and differences between boxes were significant at $p < 0.001$. Red circles in boxplots indicate expected median values of Topographic Wetness Index and vegetation cover.

4.2. Spatial impacts beyond invader canopy

In this study, the impacts of *Acacia* can be traced outside of the stands of the invader, and their spatial dimension differs. Even though absolute impacts are substantially lower outside of the stands compared to inside, the sum of spatial impacts is considerable. These spatial impacts do not increase linearly with progressing invasion, but are particularly prevalent in rather early stages (~20 % invader cover at landscape level). Therefore, impact assessments of the studied *Acacia*, and likely also other *Acacia* species (Le Maitre et al., 2023) or nitrogen-fixing invaders, such as *Morella faya* (Ait.) Wilbur and *Ulex europaeus* L., that belong to the 100 of the world's worst invasive species (Lowe et al., 2000; Luque et al., 2014), will markedly underestimate impacts especially at early stages of invasion if spatial effects (see also Cuddington and Hastings (2004)) are neglected.

In addition, *Acacia* creates homogeneous stands, which are functionally less diverse than the native vegetation, and stark functional differences occur at the edge of *Acacia* canopies. This is in line with earlier research showing the functional diversity of the studied system and the distinct traits of invasive *Acacia* spp. compared to the native tall shrubs and trees (Große-Stoltenberg et al., 2018a) and the tendency of *Acacia* to form dense, monospecific thickets (Große-Stoltenberg et al., 2018b; Rascher et al., 2011a). Recent progress in remote sensing technology allows examining plant-plant interactions at both fine scale and large extents (Chen et al., 2022), and offers a large but untapped potential to analyse invader-ecosystem interactions (Werner et al., 2024). We argue that this technological progress facilitates to identify or to screen for such functional changes at the neighbourhood scale, which are difficult to decipher otherwise (Goyal and Sharma, 2019; Jarić et al., 2019). For example, the availability of remote sensing data with high spectral and spatial resolution is increasing (Crowley and Cardille, 2020), which facilitates trait-based approaches to examine invasion impacts (Niphadkar and Nagendra, 2016; Saranya et al., 2024) such as alterations of forest canopy chemistry (e.g., Ewald et al., 2018). Future directions include trait retrieval using hybrid approaches combining machine learning with physical models (Berger et al., 2020) as well as multi-trait retrieval using deep learning (Cherif et al., 2023) in the context of impact assessments (Werner et al., 2024). Regarding remote sensing of belowground impacts (e.g., Rakotoarivony et al., 2024), invasive species might change (Lekberg et al., 2013) or be limited by (Pringle et al., 2009) mycorrhizal traits. First studies show that such traits can be derived from hyperspectral data (Sousa et al., 2021; Jantzen et al., 2023), which could be an avenue for future research. Thus, a broad range of tools and methods are at hand, which combined could enhance the understanding of invader-ecosystem interactions (Werner et al., 2024).

While we present a showcase for the spatial dimension of impact, the temporal aspect of remote sensing-based impact assessments could be a future research direction. For example, resource use and competition, e.g., increased water use under drought conditions (Rascher et al., 2011b), are important parameters that guide invasion management (Kumschick et al., 2015). Remotely sensed land surface phenology might not only be helpful to produce precise distribution maps (Lake et al., 2022), but could be used to study changes of resource use (Dronova and Taddeo, 2022). Therefore, we envision that advancements in remote sensing together with spatial (and temporal) modelling will facilitate tracing the spatial effects of invasive species on ecosystem functioning including functional homogenisation and, by doing so, improve insights into abundance-impact relationships and support early detection of different types and magnitudes of ecological impacts at broad spatial extents.

4.3. The role of environmental heterogeneity

While neglecting spatial effects leads to underestimation of impact, neglecting environmental heterogeneity may lead to overestimation of invader impact. Here, the effects of environmental heterogeneity on

ecosystem functioning, especially regarding landforms, were mostly constant, but slight differences occurred between the studied proxies, emphasizing that effects of heterogeneity on ecological impacts can be function-specific. In fact, context-dependency is still a major challenge in invasion research (Ricciardi et al., 2021). Indeed, spatial environmental heterogeneity in terms of topography is a strong driver of species richness (Stein et al., 2014), and it shapes vegetation structure, e.g., in dune ecosystems (Sewerniak and Jankowski, 2017). Regarding impact modelling, spatial heterogeneity caused by “patchy” processes, such as disturbances or land use, may entail spatial auto-correlation in the data when working on contiguous landscape sections, such as aerial images. To safeguard valid impact estimates, spatial auto-correlation should be considered in the models, e.g., using spatial auto-correlation structures (Dormann et al., 2007). Airborne LiDAR remote sensing is a powerful tool to characterize topographical heterogeneity and vegetation patterns in coastal dunes with high spatial detail and broad coverage, and LiDAR-derived proxies of ecosystem functioning agree well with proxies derived from optical sensors and field measurements (Yousefi Lalimi et al., 2017). Regarding ecological impacts of invasive plant species, LiDAR-derived proxies of environmental heterogeneity are well suited to map invader impacts, e.g., regarding N-fixation, across sites (Hellmann et al., 2017). The toolbox to characterize the 3D structure of ecosystems is rapidly evolving (Valbuena et al., 2020), and there is large potential to study plant-plant interactions (Chen et al., 2022) including effects of invasive species on ecosystem structural variability (Barenblitt et al., 2024) using 3D data. Therefore, the spatial environmental heterogeneity matrix is an important habitat characteristic that shapes ecological impacts of invasive species, and 3D remote sensing offers new opportunities to characterize heterogeneity at multiple scales in a standardized way, which is extremely useful to advance in the field of context-dependency of plant invasion impact.

4.4. Perspective on upscaling to satellite-based observations

In this study we presented a proof-of-concept for mapping spatial impacts of an invasive tree species on ecosystem functioning in a Mediterranean dune ecosystem considering landscape heterogeneity. To do so, we used single-time airborne hyperspectral and LiDAR data with high spatial resolution that was acquired in spring during the greening up phase (Große-Stoltenberg et al., 2018b). Upscaling this approach using satellite data would be desirable as it would provide the means to screen for plant invasion impacts over large spatial extents as a prerequisite for understanding invasion processes (Werner et al., 2024), for a continuous monitoring (Müllerová et al., 2023) and to guide management in a spatially explicit way (Saranya et al., 2024). However, challenges integrating remote sensing information with in-situ observations apply (Cavender-Bares et al., 2022). The core challenge is to select a sensor or sensor-combination that captures data at appropriate spatial, spectral and temporal scales to examine the respective impact caused by the invader (Werner et al., 2024). This mirrors the challenges when inferring biodiversity metrics from remote sensing data to test the transferability of the SVH (see Torresani et al., 2024). Clearly, as a first step the local process of invader – ecosystem-interaction need to be understood as a precondition for upscaling using remote sensing (Gholizadeh et al., 2024; Werner et al., 2024, this study). In our example, the spatial effect of *Acacia* on functional properties of the surrounding native vegetation was first identified using in-situ measurements of stable isotopes (Rascher et al., 2012; Hellmann et al., 2016a; Hellmann et al., 2016b). Then, spatial heterogeneity of the landscape was derived from airborne LiDAR point clouds gridded to fine resolution and integrated in spatial models to account for environmental context (Hellmann et al., 2017). Finally, hyperspectral vegetation indices related to the identified impacts from in-situ measurements covering the VNIR-SWIR part of the electromagnetic spectrum were computed at fine spatial resolution and combined in the Rao's Q index to map context-dependant-spatial effects across large spatial extents (this

study). Our findings and approach might be upscalable to satellite data but with some caveats. First, stand impact might be identifiable at sub-pixel level of medium-resolution remote sensing data with a pixel size of 30 m (Große-Stoltenberg et al., 2018b), and such corresponding multi-temporal satellite data with high temporal resolution is freely available (Crowley and Cardille 2020), so even scaling across time could be tested. Second, spatial impacts in terms of ^{15}N -enrichment were observed in a distance up to 6–8 m to *Acacia* canopy (Hellmann et al. 2017), and the airborne data, i.e. hyperspectral vegetation indices as well as the Rao's Q index, were computed at 2 m resolution, which was sufficient to map the spatial impacts using remote sensing. Such data is, with limitations in terms of spectral coverage, available from commercial providers and has successfully been applied to map invasive plant species in complex landscapes (Lake et al., 2022), and might be considered in this context. However, it would be an open question if high temporal, but lower spatial resolution (3 m) and spectral coverage (VNIR) Planetscope imagery (Lake et al., 2022) would be able to capture the fine-scale effects in close vicinity to invader canopy, or if low temporal, but higher spatial resolution and spectral coverage Worldview data (Lake et al., 2022) would be necessary and/or sufficient. Therefore, using such data not only for mapping but also for spatial impact assessments could be a future avenue of research. Third, spatial heterogeneity in our example was computed based on airborne point-cloud data gridded with a grain size of 2 m (Hellmann et al., 2017, this study), and a high spatial resolution is likely to be required in this complex Mediterranean dune ecosystem. While availability of 3D information derived from satellites is increasing, their spatial resolution is coarser compared to airborne data (Valbuena et al., 2020). It would need to be tested to which degree which type of 3D metric (e.g., topographical parameters, proxies of vegetation structure) could be upscaled in spatial impact models to still capture the spatial heterogeneity that shapes the invader-ecosystem under study. If no airborne 3D data is available, drone-based LiDAR or photogrammetry (Müllerová et al., 2023) could be used for testing upscaling, and high-resolution spaceborne synthetic aperture radar (Shennan and Crabbe, 2024) could be a promising alternative for large scale mapping of spatial heterogeneity in the context of plant invasions. In conclusion, first proofs-of-concept to link in-situ observations of spatial impacts of invasive plants species on ecosystem functioning to remotely-sensed information have been developed. Analogue to the SVH (Torresani et al., 2024), challenges in terms of transferability and upscaling likely apply, but a variety of sensor technologies and modelling approaches exist to support future research.

5. Conclusion

The invasive tree *Acacia longifolia* is able to alter ecosystem functioning, and we mapped its impacts by means of hyperspectral indices related to nitrogen in plant biomass, chlorophyll/photosynthesis, vegetation water content and primary productivity even beyond invasive stands by integrating airborne LiDAR in our spatial impact models. By doing so, we showcase that both 2D and 3D remote sensing data complement each other in remote sensing-driven impact assessments. Further, we illustrate that the spatial dimensions differ between impacts, and that while the total score of these spatial impacts was low, the sum of spatial impacts beyond invader canopy was substantial. Moreover, spatial impacts did not increase linearly with progressing invasion, but were relatively high when invader cover was still relatively low (~20 % cover at landscape level). In addition, we showed that while neglecting spatial effects could lead to underestimation of impact, neglecting environmental heterogeneity would have led to overestimation of invader impact. Therefore, we emphasize that both spatial effects and environmental heterogeneity, e.g. derived from airborne LiDAR data, need to be considered to neither under- nor overestimate ecological impacts of invasion, and that such effects are function-specific. Finally, *Acacia* creates homogeneous stands, which are functionally less diverse than the native vegetation, and stark functional differences occur at the

edge of *Acacia* canopies, which we mapped using the spectral version of the Rao's Q index based on the aforementioned impacts. That being the case, we argue that remotely sensed proxies of functional diversity allow for identifying both pronounced functional differences at the interface between the invader canopy and the native vegetation, and invader-induced functional homogenisation of the landscape. Together, mapping these spatial effects provides data to guide management, e.g., to derive thresholds for intervention, while accounting for environmental heterogeneity informs the context-dependency of ecological impacts. Challenges apply to upscale the approach to satellite-based observations, but it could be a promising avenue of research due to progress in sensor technology and analytical methods.

CRediT authorship contribution statement

André Große-Stoltenberg: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Christiane Werner:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization. **Christine Hellmann:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Jens Oldeland:** Writing – review & editing, Writing – original draft, Funding acquisition, Formal analysis. **Jan Thiele:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Authors' contributions statement

AGS and JT conceived the ideas and designed methodology; AGS and JO processed the data, JT analysed the data with inputs from AGS; AGS led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2024.112928>.

Data availability

Data will be made available on request.

References

- Badgley, G., Field, C.B., Berry, J.A., 2017. Canopy near-infrared reflectance and terrestrial photosynthesis. *Sci. Adv.* 3, e1602244. <https://doi.org/10.1126/sciadv.1602244>.
- Badgley, G., Anderegg, L.D.L., Berry, J.A., Field, C.B., 2019. Terrestrial gross primary production: Using NIRV to scale from site to globe. *Glob. Change Biol.* 25, 3731–3740. <https://doi.org/10.1111/gcb.14729>.
- Barenblitt, A., Fatoyinbo, L., Thomas, N., Stovall, A., de Sousa, C., Nwobi, C., Duncanson, L., 2024. Invasion in the Niger Delta: remote sensing of mangrove conversion to invasive *Nypa fruticans* from 2015 to 2020. *Remote Sens. Ecol. Conserv.* 10, 5–23. <https://doi.org/10.1002/rse2.353>.
- Barney, J.N., Tekiel, D.R., Barrios-García, M.N., Dimarco, R.D., Hufbauer, R.A., Leipzig-Scott, P., Nunez, M.A., Pauchard, A., Pyšek, P., Vítková, M., et al., 2015. Global Invader Impact Network (GIIN): toward standardized evaluation of the ecological impacts of invasive plants. *Ecol. Evol.* 5, 2878–2889. <https://doi.org/10.1002/ece3.1551>.
- Bartz, R., Kowarik, I., 2019. Assessing the environmental impacts of invasive alien plants: a review of assessment approaches. *Neobiota* 43, 69–99. <https://doi.org/10.3897/neobiota.43.30122>.
- Berger, K., Verrelst, J., Féret, J.B., Hank, T., Wocher, M., Mauser, W., Camps-Valls, G., 2020. Retrieval of aboveground crop nitrogen content with a hybrid machine learning method. *Int. J. Appl. Earth Obs. Geoinf.* 92, 102174. <https://doi.org/10.1016/j.jag.2020.102174>.
- Bernard-Verdier, M., Hulme, P.E., 2019. Alien plants can be associated with a decrease in local and regional native richness even when at low abundance. *J. Ecol.* 107, 1343–1354. <https://doi.org/10.1111/1365-2745.13124>.
- Blackburn, T.M., Essl, F., Evans, T., Hulme, P.E., Jeschke, J.M., Kühn, I., Kumschick, S., Marková, Z., Mrugała, A., Nentwig, W., Pergl, J., Pyšek, P., Rabitsch, W., Ricciardi, A., Richardson, D.M., Sendek, A., Vila, M., Wilson, J.R.U., Winter, M., Genovesi, P., Bacher, S., 2014. A unified classification of alien species based on the magnitude of their environmental impacts. *PLOS Biol.* 12, e1001850. <https://doi.org/10.1371/journal.pbio.1001850>.
- Bolch, E.A., Santos, M.J., Ade, C., Khanna, S., Basinger, N.T., Reader, M.O., Hestir, E.L., 2020. Remote Detection of Invasive Alien Species. In: Cavender-Bares, J., Gamon, J. A., Townsend, P.A. (Eds.), *Remote Sensing of Plant Biodiversity*. Springer International Publishing, Cham, pp. 267–307. https://doi.org/10.1007/978-3-030-33157-3_12.
- Botta-Dukát, Z., 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *J. Veg. Sci.* 16, 533–540. <https://doi.org/10.1111/j.1654-1103.2005.tb02393.x>.
- Brundu, G., Pauchard, A., Pyšek, P., Pergl, J., Bindewald, A.M., Brunori, A., Canavan, S., Campagnaro, T., Celesti-Grappo, L., Dechoum, M. de S., Dufour-Dror, J.-M., Essl, F., Flory, S.L., Genovesi, P., Guarino, F., Guangzhe, L., Hulme, P.E., Jäger, H., Kettle, C. J., Krumm, F., Langdon, B., Lapin, K., Lozano, V., Le Roux, J.J., Novoa, A., Nuñez, M. A., Porté, A.J., Silva, J.S., Schaffner, U., Sitzia, T., Tanner, R., Tshidada, N., Vítková, M., Westergren, M., Wilson, J.R.U., Richardson, D.M., 2020. Global guidelines for the sustainable use of non-native trees to prevent tree invasions and mitigate their negative impacts. *Neobiota* 61, 65–116. <https://doi.org/10.3897/neobiota.61.58380>.
- Cavender-Bares, J., Schneider, F.D., Santos, M.J., Armstrong, A., Carnaval, A., Dahlin, K. M., Fatoyinbo, L., Hurr, G.C., Schimel, D., Townsend, P.A., Ustin, S.L., Wang, Z., Wilson, A. M., 2022. Integrating remote sensing with ecology and evolution to advance biodiversity conservation. *Nat. Ecol. Evol.* 6, 506–519. <https://doi.org/10.1038/s41559-022-01702-5>.
- Cerasoli, S., Campagnolo, M., Faria, J., Nogueira, C., Caldeira, M., da, C., 2018. On estimating the gross primary productivity of Mediterranean grasslands under different fertilization regimes using vegetation indices and hyperspectral reflectance. *Biogeosciences* 15, 5455–5471. <https://doi.org/10.5194/bg-15-5455-2018>.
- Chen, B.J.W., Teng, S.N., Zheng, G., Cui, L., Li, S., Staal, A., Eitel, J.U.H., Crowther, T.W., Berdugo, M., Mo, L., Ma, H., Bialic-Murphy, L., Zohner, C.M., Maynard, D.S., Averill, C., Zhang, J., He, Q., Evers, J.B., Anten, N.P.R., Yizhaq, H., Stavi, I., Argaman, E., Basson, U., Xu, Z., Zhang, M.-J., Niu, K., Liu, Q.-X., Xu, C., 2022. Inferring plant–plant interactions using remote sensing. *J. Ecol.* 110, 2268–2287. <https://doi.org/10.1111/1365-2745.13980>.
- Cherif, E., Feilhauer, H., Berger, K., Dao, P.D., Ewald, M., Hank, T.B., He, Y., Kovach, K. R., Lu, B., Townsend, P.A., Kattenborn, T., 2023. From spectra to plant functional traits: transferable multi-trait models from heterogeneous and sparse data. *Remote Sens. Environ.* 292, 113580. <https://doi.org/10.1016/j.rse.2023.113580>.
- Conrad, O., Bechtel, B., Bock, M., Dietrich, H., Fischer, E., Gerlitz, L., Wehberg, J., Wichmann, V., Böhner, J., 2015. System for Automated Geoscientific Analyses (SAGA) v. 2.1.4. *Geosci. Model Dev.* 8, 1991–2007. <https://doi.org/10.5194/gmd-8-1991-2015>.
- Crooks, J.A., 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos* 97, 153–166. <https://doi.org/10.1034/j.1600-0706.2002.970201.x>.
- Crowley, M.A., Cardille, J.A., 2020. Remote sensing's recent and future contributions to landscape ecology. *Curr. Landsc. Ecol. Rep.* 5, 45–57. <https://doi.org/10.1007/s40823-020-00054-9>.
- Cuddington, K., Hastings, A., 2004. Invasive engineers. *Ecol. Model.* 178, 335–347. <https://doi.org/10.1016/j.ecolmodel.2004.03.010>.
- Daughtry, C.S.T., Walthall, C.L., Kim, M.S., De Colstoun, E.B., McMurtrey, J.E., 2000. Estimating corn leaf chlorophyll concentration from leaf and canopy reflectance. *Remote Sens. Environ.* 74, 229–239. [https://doi.org/10.1016/S0034-4257\(00\)00113-9](https://doi.org/10.1016/S0034-4257(00)00113-9).
- Dormann, C.F., McPherson, J.M., Araujo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kuehn, I., Ohlemueller, R., Peres-Neto, P.R., Reineking, B., Schroeder, B., Schurr, F.M., Wilson, R., 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30, 609–628. <https://doi.org/10.1111/j.2007.0906-7590.05171.x>.
- Dronova, I., Taddeo, S., 2022. Remote sensing of phenology: Towards the comprehensive indicators of plant community dynamics from species to regional scales. *J. Ecol.* 110, 1460–1484. <https://doi.org/10.1111/1365-2745.13897>.
- Ehrenfeld, J.G., 2010. Ecosystem consequences of biological invasions. *Annu. Rev. Ecol. Evol. Syst.* 41, 59–80. <https://doi.org/10.1146/annurev-ecolsys-102209-144650>.
- Ewald, M., Skowronek, S., Aerts, R., Dolos, K., Lenoir, J., Nicolas, M., Warrie, N., Hattab, T., Feilhauer, H., Honnay, O., Garzón-López, C.X., Decocq, G., Van de Kerchove, R., Somers, B., Rocchini, D., Schmidlein, S., 2018. Analyzing remotely sensed structural and chemical canopy traits of a forest invaded by *Prunus serotina* over multiple spatial scales. *Biol. Invasions* 20, 2257–2271. <https://doi.org/10.1007/s10530-018-1700-9>.
- Fernandes, M.M., 2012. Acácias e geografia histórica: rotas de um percurso global (parte1). *Cadernos do curso de doutoramento em Geografia* 4, 23–40.
- Gao, B., 1996. NDWI—A normalized difference water index for remote sensing of vegetation liquid water from space. *Remote Sens. Environ.* 58, 257–266. [https://doi.org/10.1016/S0034-4257\(96\)00667-3](https://doi.org/10.1016/S0034-4257(96)00667-3).
- Gholizadeh, H., Rakotoarivony, M.N.A., Hassani, K., Johnson, K.G., Hamilton, R.G., Fuhlendorf, S.D., Schneider, F.D., Bachelot, B., 2024. Advancing our understanding of plant diversity-biological invasion relationships using imaging spectroscopy. *Rem. Sens. Environ.* 304, 114028. <https://doi.org/10.1016/j.rse.2024.114028>.
- Gioria, M., Hulme, P.E., Richardson, D.M., Pyšek, P., 2023. Why are invasive plants successful? *Annu. Rev. Plant Biol.* 74, 635–670. <https://doi.org/10.1146/annurev-arplant-070522-071021>.
- Gómez-Aparicio, L., Canham, C.D., 2008. Neighborhood models of the effects of invasive tree species on ecosystem processes. *Ecol. Monogr.* 78, 69–86. <https://doi.org/10.1890/06-2036.1>.
- Gould, W., 2000. Remote sensing of vegetation, plant species richness, and regional biodiversity hotspots. *Ecol. Appl.* 10, 1861–1870. [https://doi.org/10.1890/1051-0761\(2000\)010\[1861:RSOVPS\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[1861:RSOVPS]2.0.CO;2).
- Goyal, N., Sharma, G.P., 2019. Unveiling cryptic ecological functions: prospects in plant invasions. *Trop. Ecol.* 60, 1–5. <https://doi.org/10.1007/s42965-019-00002-7>.
- Große-Stoltenberg, A., Lizarazo, I., Brundu, G., Paiva Gonçalves, V., Prado Osco, L., Masemola, C., Müllerová, J., Werner, C., Kotze, I., Oldeland, J., 2023. Remote sensing of invasive wattles: state of the art and future perspectives., in: Richardson, D.M., Le Roux, J.J., Marchante, E. (Eds.), *Wattles – Australian Acacia Species around the World*. CAB International, Wallingford, UK, pp. 474–496. <https://doi.org/10.1079/9781800622197.0029>.
- Große-Stoltenberg, A., Hellmann, C., Werner, C., Oldeland, J., Thiele, J., 2016. Evaluation of continuous VNIR-SWIR spectra versus narrowband hyperspectral indices to discriminate the invasive *Acacia longifolia* within a Mediterranean dune ecosystem. *Remote Sens.* 8, 334. <https://doi.org/10.3390/rs8040334>.
- Große-Stoltenberg, A., Hellmann, C., Thiele, J., Oldeland, J., Werner, C., 2018a. Invasive acacias differ from native dune species in the hyperspectral/biochemical trait space. *J. Veg. Sci.* 29, 325–335. <https://doi.org/10.1111/jvs.12608>.
- Große-Stoltenberg, A., Hellmann, C., Thiele, J., Werner, C., Oldeland, J., 2018b. Early detection of GPP-related regime shifts after plant invasion by integrating imaging spectroscopy with airborne LiDAR. *Remote Sens. Environ.* 209, 780–792. <https://doi.org/10.1016/j.rse.2018.02.038>.
- Hartig, F., 2022. DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.6, <https://github.com/florianhartig/dharma>.
- Hellmann, C., Sutter, R., Rascher, K.G., Máguas, C., Correia, O., Werner, C., 2011. Impact of an exotic N2-fixing *Acacia* on composition and N status of a native Mediterranean community. *Acta Oecol.* 37, 43–50. <https://doi.org/10.1016/j.actao.2010.11.005>.
- Hellmann, C., Rascher, K.G., Oldeland, J., Werner, C., 2016a. Isoscapes resolve species-specific spatial patterns in plant–plant interactions in an invaded Mediterranean dune ecosystem. *Tree Physiol.* 36, 1460–1470. <https://doi.org/10.1093/treephys/tpw075>.
- Hellmann, C., Werner, C., Oldeland, J., 2016b. A spatially explicit dual-isotope approach to map regions of plant–plant interaction after exotic plant invasion. *PLoS ONE* 11, e0159403. <https://doi.org/10.1371/journal.pone.0159403>.
- Hellmann, C., Große-Stoltenberg, A., Thiele, J., Oldeland, J., Werner, C., 2017. Heterogeneous environments shape invader impacts: integrating environmental, structural and functional effects by isoscapes and remote sensing. *Sci. Rep.* 7, 4118. <https://doi.org/10.1038/s41598-017-04480-4>.
- Hijmans, R., 2016. raster: Geographic Data Analysis and Modeling. R package version 3.6-30, <https://raster.org/raster>.
- Holst, K.K., 2015. Model Diagnostics Based on Cumulative Residuals: The R-package gof. arXiv e1507.0117.
- Hulme, P.E., Pyšek, P., Jarošík, V., Pergl, J., Schaffner, U., Vilà, M., 2013. Bias and error in understanding plant invasion impacts. *Trends Ecol. Evol.* 28, 212–218. <https://doi.org/10.1016/j.tree.2012.10.010>.
- ICNB, 2005. Sítio Comporta/Galé, Plano sectorial da Rede Natura 2000. Instituto da Conservação da Natureza e da Biodiversidade, Lisbon, Portugal.
- Jantzen, J.R., Laliberté, E., Carteron, A., Beauchamp-Rioux, R., Blanchard, F., Crofts, A. L., Girard, A., Hacker, P.W., Pardo, J., Schweiger, A.K., Demers-Thibeault, S., Coops, N.C., Kalaska, M., Vellend, M., Bruneau, A., 2023. Evolutionary history explains foliar spectral differences between arbuscular and ectomycorrhizal plant species. *New Phytol.* 238, 2651–2667. <https://doi.org/10.1111/nph.18902>.

- Jarić, I., Heger, T., Castro Monzon, F., Jeschke, J.M., Kowarik, I., McConkey, K.R., Pyšek, P., Sagouis, A., Essl, F., 2019. Crypticity in biological invasions. *Trends Ecol. Evol.* 34, 291–302. <https://doi.org/10.1016/j.tree.2018.12.008>.
- Khare, S., Latifi, H., Rossi, S., 2019. Forest beta-diversity analysis by remote sensing: how scale and sensors affect the Rao's Q index. *Ecol. Indic.* 106, 105520. <https://doi.org/10.1016/j.ecolind.2019.105520>.
- Kumschick, S., Jansen, C., 2023. Evidence-Based Impact Assessment for Naturalized and Invasive Australian *Acacia* Species, in: Richardson, D.M., Roux, J.J.L., Marchante, E. (Eds.), *Wattles – Australian Acacia Species around the World*. CABI, Wallingford, UK, pp. 359–381. <https://doi.org/10.1079/9781800622197.0023>.
- Kumschick, S., Gaertner, M., Vila, M., Essl, F., Jeschke, J.M., Pyšek, P., Ricciardi, A., Bacher, S., Blackburn, T.M., Dick, J.T.A., Evans, T., Hulme, P.E., Kuhn, I., Mruga, A., Pergl, J., Rabitsch, W., Richardson, D.M., Sendek, A., Winter, M., 2015. Ecological impacts of alien species: quantification, scope, caveats, and recommendations. *BioScience* 65, 55–63. Doi: 10.1093/biosci/biu193.
- Lake, T.A., Briscoe Runquist, R.D., Moeller, D.A., 2022. Deep learning detects invasive plant species across complex landscapes using Worldview-2 and PlanetScope satellite imagery. *Remote Sens. Ecol. Conserv.* 8, 875–889. <https://doi.org/10.1002/rse2.288>.
- Latombe, G., Pyšek, P., Jeschke, J.M., Blackburn, T.M., Bacher, S., Capinha, C., Costello, M.J., Fernández, M., Gregory, R.D., Hobern, D., Hui, C., Jetz, W., Kumschick, S., McGrannachan, C., Pergl, J., Roy, H.E., Scalera, R., Squires, Z.E., Wilson, J.R.U., Winter, M., Genovesi, P., McGeoch, M.A., 2017. A vision for global monitoring of biological invasions. *Biol. Conserv.* 213, 295–308. <https://doi.org/10.1016/j.biocon.2016.06.013>.
- Le Maitre, D.C., Máguas, C., Ulm, F., Marchante, H., 2023. Ecological Impacts and Changes in Ecosystem Services and Disservices Mediated by Invasive Australian *Acacia* Species, in: Richardson, D.M., Roux, J.J.L., Marchante, E. (Eds.), *Wattles – Australian Acacia Species around the World*. CABI, Wallingford, UK, pp. 342–358. <https://doi.org/10.1079/9781800622197.0022>.
- Le Maitre, D.C., Gaertner, M., Marchante, E., Ens, E.-J., Holmes, P.M., Pauchard, A., O'Farrell, P.J., Rogers, A.M., Blanchard, R., Bignaut, J., Richardson, D.M., 2011. Impacts of invasive Australian acacias: implications for management and restoration: Australian acacias: linking impacts and restoration. *Divers. Distrib.* 17, 1015–1029. <https://doi.org/10.1111/j.1472-4642.2011.00816.x>.
- Lee, M.R., Flory, S.L., Phillips, R.P., Wright, J.P., 2018. Site conditions are more important than abundance for explaining plant invasion impacts on soil nitrogen cycling. *Ecosphere* 9, e02454. <https://doi.org/10.1002/ecs2.2454>.
- Lehmann, J.R.K., Große-Stoltenberg, A., Römer, M., Oldeland, J., 2015. Field Spectroscopy in the VNIR-SWIR Region to Discriminate between Mediterranean Native Plants and Exotic-Invasive Shrubs Based on Leaf Tannin Content. *Remote Sens.* 7, 1225–1241. <https://doi.org/10.3390/rs70201225>.
- Lekberg Y., Gibbons S.M., Rosendahl S., Ramsey P.W., 2013. Severe plant invasions can increase mycorrhizal fungal abundance and diversity. *ISME J.* 7, 1424–1433. <https://doi.org/10.1038/ismej.2013.41>.
- Lowe, S., Browne, M., Boudjelas, S., De Poorter, M., 2000. 100 of the World's Worst Invasive Alien Species: A Selection From The Global Invasive Species Database. The Invasive Species Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN). <https://doi.org/10.1525/9780520948433-159>.
- Luque, G.M., Bellard, C., Bertelsmeier, C., Bonnauud, E., Genovesi, P., Simberloff, D., Courchamp, F., 2014. The 100th of the world's worst invasive alien species. *Biol. Invasions* 16, 981–985. <https://doi.org/10.1007/s10530-013-0561-5>.
- Marcantonio, M., Iannacito, M., Marchetto, E., Thouverai, E., Torresani, M., Re, D.D., Tattoni, C., Bacaro, G., Vicario, S., Ricotta, C., Rocchini, D., 2024. rasterdiv: Diversity Indices for Numerical Matrices.
- Marchante, E., Gouveia, A.C., Brundu, G., Marchante, H., 2023. Australian *Acacia* Species in Europe, in: Richardson, D.M., Roux, J.J.L., Marchante, E. (Eds.), *Wattles – Australian Acacia Species around the World*. CABI, Wallingford, UK, pp. 148–166. <https://doi.org/10.1079/9781800622197.0010>.
- Marchante, E., Marchante, H., Freitas, H., Kjeller, A., Struwe, S., 2019. Decomposition of an N-fixing invasive plant compared with a native species: consequences for ecosystem. *Appl. Soil Ecol.* 138, 19–31. <https://doi.org/10.1016/j.apsoil.2019.02.016>.
- McGeoch, M.A., Buba, Y., Arlé, E., Belmaker, J., Clarke, D.A., Jetz, W., Li, R., Seebens, H., Essl, F., Groom, Q., García-Berthou, E., Lenzner, B., Meyer, C., Vicente, J.R., Wilson, J.R.U., Winter, M., 2023. Invasion trends: an interpretable measure of change is needed to support policy targets. *Conserv. Lett.* 16, e12981. <https://doi.org/10.1111/conl.12981>.
- Müllerová, J., Brundu, G., Große-Stoltenberg, A., Kattenborn, T., Richardson, D.M., 2023. Pattern to process, research to practice: remote sensing of plant invasions. *Biol. Invasions* 25, 3651–3676. <https://doi.org/10.1007/s10530-023-03150-z>.
- Nipadkar, M., Nagendra, H., 2016. Remote sensing of invasive plants: incorporating functional traits into the picture. *Int. J. Remote Sens.* 37, 3074–3085. <https://doi.org/10.1080/01431161.2016.1193795>.
- Palmer, M.W., Earls, P.G., Hoagland, B.W., White, P.S., Wohlgenuth, T., 2002. Quantitative tools for perfecting species lists. *Environmetrics* 13, 121–137. <https://doi.org/10.1002/env.516>.
- Palmer, M.W., Wohlgenuth, T., Earls, P.G., Arévalo, J., Thompson, S.D., 1999. Opportunities for long-term ecological research at the tallgrass prairie preserve, Oklahoma. K. Lajtha, K. Vanderbilt (Eds.), *Cooperation in Long Term Ecological Research in Central and Eastern Europe: Proceedings of ILTER Regional Workshop, Budapest, Hungary* (2000), pp. 123–128.
- Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., Von Holle, B., Moyle, P.B., Byers, J.E., Goldwasser, L., 1999. Impact: toward a Framework for Understanding the Ecological Effects of Invaders. *Biol. Invasions* 1, 3–19. <https://doi.org/10.1023/A:1010034312781>.
- Pinheiro, J., Bates, D., R Core Team, 2018. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-131, <https://CRAN.R-project.org/package=nlme>.
- Pinto, M.J., 2014. Guia das plantas e dos ecossistemas da Reserva Natural das Lagoas de Santo André e da Sancha. Instituto da Conservação da Natureza e das Florestas (ICNF), Lisbon, Portugal.
- Powell, K.I., Chase, J.M., Knight, T.M., 2013. Invasive plants have scale-dependent effects on diversity by altering species-area relationships. *Science* 339, 316–318. <https://doi.org/10.1126/science.1226817>.
- Pringle, A., Bever, J.D., Gardes, M., Parrent, J.L., Rillig, M.C., Klironomos, J.N., 2009. Mycorrhizal symbioses and plant invasions. *Annu. Rev. Ecol. Evol. Syst.* 40, 699–715. <https://doi.org/10.1146/annurev.ecolsys.39.110707.173454>.
- Pyšek, P., Jarošík, V., Hulme, P.E., Pergl, J., Hejda, M., Schaffner, U., Vilà, M., 2012. A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Glob. Change Biol.* 18, 1725–1737. <https://doi.org/10.1111/j.1365-2486.2011.02636.x>.
- Pyšek, P., Hulme, P.E., Simberloff, D., Bacher, S., Blackburn, T.M., Carlton, J.T., Dawson, W., Essl, F., Foxcroft, L.C., Genovesi, P., 2020. Scientists' warning on invasive alien species. *Biol. Rev.* 95, 1511–1534. <https://doi.org/10.1111/brv.12627>.
- R Core Team, 2017. R: A language and environment for statistical computing. Version 3.4.2. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- R Core Team, 2024. R: A language and environment for statistical computing. Version 4.3.3. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Rakotoarivony, M.N.A., Gholizadeh, H., Hassani, K., McMahan, S., Struble, E., Fuhlendorf, S., Hamilton, R., Bachelot, B., 2024. Using imaging spectroscopy to assess the impacts of invasive plants on aboveground and belowground characteristics. *Gisci. Remote Sens.* 61, 2399388. <https://doi.org/10.1080/15481603.2024.2399388>.
- Rascher, K.G., Große-Stoltenberg, A., Máguas, C., Meira-Neto, J.A.A., Werner, C., 2011a. *Acacia longifolia* invasion impacts vegetation structure and regeneration dynamics in open dunes and pine forests. *Biol. Invasions* 13, 1099–1113. <https://doi.org/10.1007/s10530-011-9949-2>.
- Rascher, K.G., Große-Stoltenberg, A., Máguas, C., Werner, C., 2011b. Understory Invasion by *Acacia longifolia* Alters the Water Balance and Carbon Gain of a Mediterranean Pine Forest. *Ecosystems* 14, 904–919. <https://doi.org/10.1007/s10021-011-9453-7>.
- Rascher, K.G., Hellmann, C., Máguas, C., Werner, C., 2012. Community scale ¹⁵N isoscapes: tracing the spatial impact of an exotic N₂-fixing invader. *Ecol. Lett.* 15, 484–491. <https://doi.org/10.1111/j.1461-0248.2012.01761.x>.
- Ricciardi, A., Iacarella, J.C., Aldridge, J.C., Blackburn, T.M., Carlton, J.T., Catford, J.A., Dick, J.T.A., Hulme, P.E., Jeschke, J.M., Liebhold, A.M., 2021. Four priority areas to advance invasion science in the face of rapid environmental change. *Environ. Rev.* 29, 119–141. <https://doi.org/10.1139/er-2020-0088>.
- Richardson, D.M., Marchante, E., Le Roux, J.J., 2023. Australian *Acacia* Species Around the World: Historical, Social, Evolutionary and Ecological Insights into One of the Planet's Most Widespread Plant Genera, in: Richardson, D.M., Roux, J.J.L., Marchante, E. (Eds.), *Wattles – Australian Acacia Species around the World*. CABI, Wallingford, UK, pp. 1–26. <https://doi.org/10.1079/9781800622197.0001>.
- Rocchini, D., Marcantonio, M., Ricotta, C., 2017. Measuring Rao's Q diversity index from remote sensing: an open source solution. *Ecol. Indic.* 72, 234–238. <https://doi.org/10.1016/j.ecolind.2016.07.039>.
- Rocchini, D., Luque, S., Pettorelli, N., Bastin, L., Doktor, D., Faedi, N., Feilhauer, H., Féret, J.-B., Foody, G.M., Gavish, Y., Godinho, S., Kunin, W.E., Lausch, A., Leitão, P. J., Marcantonio, M., Neteler, M., Ricotta, C., Schmidtlein, S., Vihervaara, P., Wegmann, M., Nagendra, H., 2018. Measuring β -diversity by remote sensing: a challenge for biodiversity monitoring. *Methods Ecol. Evol.* 9, 1787–1798. <https://doi.org/10.1111/2041-210X.12941>.
- Rocchini, D., Marcantonio, M., Da Re, D., Bacaro, G., Feoli, E., Foody, G.M., Furrer, R., Harrigan, R.J., Kleijn, D., Iannacito, M., Lenoir, J., Lin, M., Malavasi, M., Marchetto, E., Meyer, R.S., Moudry, V., Schneider, F.D., Šimová, P., Thornhill, A.H., Thouverai, E., Vicario, S., Wayne, R.K., Ricotta, C., 2021. From zero to infinity: minimum to maximum diversity of the planet by spatio-parametric Rao's quadratic entropy. *Glob. Ecol. Biogeogr.* 30, 1153–1162. <https://doi.org/10.1111/geb.13270>.
- Rocchini, D., Torresani, M., Ricotta, C., 2024. On the mathematical properties of spatial Rao's Q to compute ecosystem heterogeneity. *Theor. Ecol.* 17, 247–254. <https://doi.org/10.1007/s12080-024-00587-3>.
- Rodríguez-Echeverría, S., Crisóstomo, J.A., Nabais, C., Freitas, H., 2009. Belowground mutualists and the invasive ability of *Acacia longifolia* in coastal dunes of Portugal. *Biol. Invasions* 11, 651–661. <https://doi.org/10.1007/s10530-008-9280-8>.
- Saranya, K.R.L., Satish, K.V., Reddy, C.S., 2024. Remote sensing enabled essential biodiversity variables for invasive alien species management: towards the development of spatial decision support system. *Biol. Invasions* 26, 943–951. <https://doi.org/10.1007/s10530-023-03240-y>.
- Scherer-Lorenzen, M., Venterink, H.O., Buschmann, H., 2007. Nitrogen Enrichment and Plant Invasions: the Importance of Nitrogen-Fixing Plants and Anthropogenic Eutrophication, in: Nentwig, W. (Ed.), *Biological Invasions, Ecological Studies*. Springer, Berlin, Heidelberg, pp. 163–180. https://doi.org/10.1007/978-3-540-36920-2_10.
- Seebens, H., Blackburn, T.M., Dyer, E.E., Genovesi, P., Hulme, P.E., Jeschke, J.M., Pagad, S., Pyšek, P., Winter, M., Arianoutsou, M., Bacher, S., Blasius, B., Brundu, G., Capinha, C., Celesti-Grapo, L., Dawson, W., Dullinger, S., Fuentes, N., Jäger, H.,

- Kartesz, J., Kenis, M., Kreft, H., Kühn, I., Lenzner, B., Liebhold, A., Mosen, A., Moser, D., Nishino, M., Pearman, D., Pergl, J., Rabitsch, W., Rojas-Sandoval, J., Roques, A., Rorke, S., Rossinelli, S., Roy, H.E., Scalera, R., Schindler, S., Stajerová, K., Tokarska-Guzik, B., van Kleunen, M., Walker, K., Weigelt, P., Yamanaka, T., Essl, F., 2017. No saturation in the accumulation of alien species worldwide. *Nat. Commun.* 8, 14435. <https://doi.org/10.1038/ncomms14435>.
- Senf, C., 2022. Seeing the system from above: the use and potential of remote sensing for studying ecosystem dynamics. *Ecosystems* 25, 1719–1737. <https://doi.org/10.1007/s10021-022-00777-2>.
- Serrano, L., Peñuelas, J., Ustin, S.L., 2002. Remote sensing of nitrogen and lignin in Mediterranean vegetation from AVIRIS data: decomposing biochemical from structural signals. *Remote Sens. Environ.* 81, 355–364. [https://doi.org/10.1016/S0034-4257\(02\)00011-1](https://doi.org/10.1016/S0034-4257(02)00011-1).
- Sewerniak, P., Jankowski, M., 2017. Topographically-controlled site conditions drive vegetation pattern on inland dunes in Poland. *Acta Oecol.* 82, 52–60. <https://doi.org/10.1016/j.actao.2017.06.003>.
- Shennan, G., Crabbe, R., 2024. A review of spaceborne synthetic aperture radar for invasive alien plant research. *Remote Sens. Appl.: Soc. Environ.* 36, 101358. <https://doi.org/10.1016/j.rsase.2024.101358>.
- Sofaer, H.R., Jarnevich, C.S., Pearse, I.S., 2018. The relationship between invader abundance and impact. *Ecosphere* 9, e02415. <https://doi.org/10.1002/ecs2.2415>.
- Sousa D., Fisher J.B., Galvan F.R., Pavlick, R.P., Cordell, S., Giambelluca, T.W., Giardina, C.P., Gilbert, G.S., Imran-Narahari, F., Litton, C.M., Lutz, J.A., North, M.P., Orwig, D.A., Ostertag, R., Sack, L., Philipps, R.P., 2021. Tree canopies reflect mycorrhizal composition. *Geophys. Res. Lett.*, 48, e2021GL092764. <https://doi.org/10.1029/2021GL092764>.
- Stein, A., Gerstner, K., Kreft, H., 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecol. Lett.* 17, 866–880. <https://doi.org/10.1111/ele.12277>.
- Strayer, D.L., 2020. Non-native species have multiple abundance–impact curves. *Ecol. Evol.* 10, 6833–6843. <https://doi.org/10.1002/ece3.6364>.
- Thiele, J., Kollmann, J., Markussen, B., Otte, A., 2010. Impact assessment revisited: improving the theoretical basis for management of invasive alien species. *Biol. Invasions* 12, 2025–2035. <https://doi.org/10.1007/s10530-009-9605-2>.
- Thiele, J., Isermann, M., Kollmann, J., Otte, A., 2011. Impact scores of invasive plants are biased by disregard of environmental co-variation and non-linearity. *NeoBiota* 10, 65–79. <https://doi.org/10.3897/neobiota.10.1191>.
- Tollington, S., Turbé, A., Rabitsch, W., Groombridge, J.J., Scalera, R., Essl, F., Schwartz, A., 2017. Making the EU Legislation on Invasive Species a Conservation Success. *Conserv. Lett.* 10, 112–120. <https://doi.org/10.1111/conl.12214>.
- Torresani, M., Rocchini, D., Sonnenschein, R., Zebisch, M., Hauffe, H.C., Heym, M., Pretzsch, H., Tonon, G., 2020. Height variation hypothesis: a new approach for estimating forest species diversity with CHM LiDAR data. *Ecol. Indic.* 117, 106520. <https://doi.org/10.1016/j.ecolind.2020.106520>.
- Torresani, M., Rossi, C., Perrone, M., Hauser, L.T., Féret, J.B., Moudrý, V., Simova, P., Ricotta, C., Foody, G.M., Kacic, P., Feilhauer, H., Malavasi, M., Tognetti, R., Rocchini, D., 2024. Reviewing the Spectral Variation Hypothesis: twenty years in the tumultuous sea of biodiversity estimation by remote sensing. *Ecol. Inform.* 82, 102702. <https://doi.org/10.1016/j.ecoinf.2024.102702>.
- Tucker, C.J., 1979. Red and photographic infrared linear combinations for monitoring vegetation. *Remote Sens. Environ.* 8, 127–150. [https://doi.org/10.1016/0034-4257\(79\)90013-0](https://doi.org/10.1016/0034-4257(79)90013-0).
- Ulm, F., Hellmann, C., Cruz, C., Máguas, C., 2017a. N/P imbalance as a key driver for the invasion of oligotrophic dune systems by a woody legume. *Oikos* 126. <https://doi.org/10.1111/oik.03810>.
- Ulm, F., Jacinto, J., Cruz, C., Máguas, C., 2017b. How to outgrow your native neighbour? Belowground changes under native shrubs at an early stage of invasion. *Land Degrad. Dev.* 28, 2380–2388. <https://doi.org/10.1002/ldr.2768>.
- Valbuena, R., O'Connor, B., Zellweger, F., Simonson, W., Vihervaara, P., Maltamo, M., Silva, C.A., Almeida, D.R.A., Danks, F., Morsdorf, F., Chirici, G., Lucas, R., Coomes, D.A., Coops, N.C., 2020. Standardizing ecosystem morphological traits from 3D information sources. *Trends Ecol. Evol.* 35, 656–667. <https://doi.org/10.1016/j.tree.2020.03.006>.
- Venables, W.N., Ripley, B.D., 2002. *Modern Applied Statistics with S*, fourth ed. Springer, New York. <https://doi.org/10.1007/978-0-387-21706-2>.
- Vilà, M., Trillo, A., Castro-Díez, P., Gallardo, B., Bacher, S., 2024. Field studies of the ecological impacts of invasive plants in Europe. *NeoBiota* 90, 139–159. <https://doi.org/10.3897/neobiota.90.112368>.
- Vitousek, P.M., Walker, L.R., 1989. Biological Invasion by *Myrica faya* in Hawai'i: plant demography, nitrogen fixation, ecosystem effects. *Ecol. Monogr.* 59, 247–265. <https://doi.org/10.2307/1942601>.
- Weiss, A.D., 2000. Topographic position and landforms analysis, in: Poster Presentation. Presented at the ESRI user conference, San Diego, CA.
- Werner, C., Hellmann, C., Große-Stoltenberg, A., 2024. An integrative framework to assess the spatio-temporal impact of plant invasion on ecosystem functioning. *NeoBiota* 94, 225–242. <https://doi.org/10.3897/neobiota.94.126714>.
- West, J.B., Sobek, A., Ehleringer, J.R., 2008. A simplified GIS approach to modeling global leaf water isoscapes. *PLoS One* 3, e2447. <https://doi.org/10.1371/journal.pone.0002447>.
- Yelenik, S.G., Stock, W.D., Richardson, D.M., 2007. Functional group identity does not predict invader impacts: differential effects of nitrogen-fixing exotic plants on ecosystem function. *Biol. Invasions* 9, 117–125. <https://doi.org/10.1007/s10530-006-0008-3>.
- Yokomizo, H., Possingham, H.P., Thomas, M.B., Buckley, Y.M., 2009. Managing the impact of invasive species: the value of knowing the density–impact curve. *Ecol. Appl.* 19, 376–386. <https://doi.org/10.1890/08-0442.1>.
- Yousefi Lalimi, F., Silvestri, S., Moore, L.J., Marani, M., 2017. Coupled topographic and vegetation patterns in coastal dunes: Remote sensing observations and ecomorphodynamic implications. *J. Geophys. Res. Biogeosciences* 122, 119–130. <https://doi.org/10.1002/2016JG003540>.