

Assessing eco-physiological patterns of *Ailanthus altissima* (Mill.) Swingle and differences with native vegetation using Copernicus satellite data on a Mediterranean Island

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ABSTRACT

Biological invasions, one of the most pervasive components of global change, can cause irreversible alterations in the composition and functioning of ecosystems. This includes changes of eco-physiological traits of plant communities. Satellite remote sensing provides the means to map surrogates of ecosystem composition and functioning such as eco-physiological traits over large spatial extents. In this study, Sentinel-2 and Sentinel-3 Copernicus satellite data resampled to 20 m² spatial resolution was used to characterize the annual cycle of spectral eco-physiological traits in 176 patches invaded by *Ailanthus altissima* (Mill.) Swingle in Sardinia (Italy) and in their corresponding and surrounding non-invaded areas. The overall aim was to examine if and how eco-physiological traits differed between *A. altissima* and native vegetation classes. A set of spectral eco-physiological indices proxies related to leaf chlorophyll and carotenoid content (Chlorophyll Vegetation Index – CVI, Structure Intensive Pigment Index 3 – SIPI3), productivity and canopy biomass (Enhanced Vegetation Index – EVI, Leaf Area Index – LAI), leaf water content (Normalized Multi-band Drought Index – NMDI, Moisture Stress Index – MSI), daily evapotranspiration (ET), and soil features (Coloration Index – CI) were calculated. The monthly trends of these indices in invaded patches and the seasonal differences between invaded and non-invaded cells were analyzed using linear mixed models (LMMs). One-way Analysis of Variance (ANOVA), and Estimated Marginal Means (EMMs) were used to test the differences between invaded and non-invaded cells. Our results highlighted the effectiveness of Sentinel-2 and -3 data in capturing the temporal trends of spectral eco-physiological traits. Most significant differences between invaded and non-invaded cells were observed during summer, with invaded cells featuring higher productivity, canopy biomass, and leaf water content, while leaf carotenoid content and bare soil cover was lower. Overall, our findings based on satellite-based remote sensing analysis provide further evidence of the competitive advantages *A. altissima* has over native vegetation, particularly in summer, when vegetation in Mediterranean-type ecosystems faces an intense drought stress. Such spatially explicit information facilitates the identification and selection of field sites for proximal measurements of the alterations and potential impacts attributed to *A. altissima* invasion.

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1. Introduction

Biological invasions are considered one of the main components of global change, altering biodiversity, ecosystem services, environmental quality and conservation status of native communities (Seebens et al., 2017, 2021; Roy et al., 2023; Castro-Díez et al., 2019). Invasive non-native species can irreversibly modify native ecosystem composition and functioning (e.g. primary productivity, nutrient cycles; Vilà et al., 2011; Bartz and Kowarik, 2019; Rai and Singh, 2020). Invasion success depends on both the invasibility of native communities due to fragmentation, over-exploitation and urbanization (Bellard et al., 2016; Chytrý et al., 2008; Liu et al., 2023; Pyšek et al., 2010) and the eco-physiological traits of non-native species (Gallagher et al., 2014; Sapsford et al., 2020; Sobuj et al., 2024; Werner et al., 2024). Competitive advantages of invasive non-native species can be attributed to, inter alia, high photosynthetic activity, rapid growth, and high phenotypic plasticity (Mathakutha et al., 2019; Pyšek and Richardson, 2007; Wani and Shah, 2020).

The development of tools to investigate eco-physiological traits (the adaptations of plants imposed by their physiology and how they respond to environmental conditions and changes, sensu Beyschlag and Ryel, 2007) that can promote invasive plant spread is a crucial challenge in the understanding of the interactions between non-native and native plants (e.g. competition) and to better define management and control strategies at different scales, from global to local levels (Pyšek et al., 2020). Differences in eco-physiological traits between vegetation dominated by invasive non-native or native plants are commonly analyzed through costly and labor-intensive field and laboratory research that focuses on one or a few eco-physiological traits, and that explore single date and specific areas (Ackerly et al., 2000; Bartz and Kowarik, 2019; Rai and Singh, 2020; Werner et al., 2024).

Remote sensing collects data at diverse temporal and spatial scales in a standardized and replicable way, which can be exploited to produce vegetation maps (Gómez et al., 2016; Pandey et al., 2021; Punalekar et al., 2024), e.g. for detecting and monitoring invasive non-native plants (García et al., 2024; Lourenço et al., 2021; Rakgoale and Ngetar, 2024; Royimani et al., 2019). The recent advancement of remote sensing data in terms of availability and free access to high resolution imagery, derived by different platforms (e.g. satellite, aerial) and instruments (i.e. Red-Green-Blue – RGB, multispectral, hyperspectral, Synthetic Aperture Radar, and thermal) has enhanced their use for ecological studies (Cavender-Bares et al., 2020; Reddy, 2021), including non-native plant invasions (Müllerová et al., 2023; Pádua et al., 2022; Vaz et al., 2018; Villalobos Perna et al., 2023; Werner et al., 2024). Furthermore, or more specifically, remote sensing data captures a wide range of ecosystem properties related to ecosystem composition and function in a spatially and temporally explicit way, which can be used as surrogates for environmental monitoring purposes (Crowley and Cardille, 2020; Foody, 2007; Senf, 2022), e.g. in ecological studies related to biodiversity (Rocchini et al., 2015; Torresani et al., 2024), productivity (Zhang et al., 2024), phenology (Perrone et al., 2024), and eco-physiological traits (Lausch et al., 2016). Distinct spectral responses and, thus, different ecological characteristics of native and invasive vegetation (Große-Stoltenberg et al., 2025; Lombardi et al., 2023; Long et al., 2024; Marzioletti et al., 2021; Niphadkar and Nagendra, 2016; Perrone et al., 2023) could be exploited to investigate ecosystem changes after invasion.

A broad range of eco-physiological traits, such as photosynthesis rate, phenology and productivity, leaf size, chlorophyll and carotenoid leaf content, evapotranspiration and some abiotic properties of the soil (e.g., organic soil content), that are intricately linked to biotic processes, can be estimated from remote sensing data (Homolová et al., 2013), e.g. by computing spectral indices and via statistical modelling (Hinojo-Hinojo and Goulden, 2020; Houborg et al., 2015). However, the analysis of differences in remotely sensed spectral eco-physiological traits on invaded vegetation and native (non-invaded) vegetation deserves

further attention (Niphadkar and Nagendra, 2016; Werner et al., 2024) as it is focused on a limited number of non-native plants such as *Acacia longifolia* (Andrews) Willd. (Große-Stoltenberg et al., 2018a, 2018b; Hellmann et al., 2017), *Rosa rugosa* Thunb. (Helsen et al., 2020), *Impatiens glandulifera* Royle, *Solidago gigantea* Aiton (Van Cleemput et al., 2020), and *Sporobolus alterniflorus* (Loisel.) P.M. Peterson & Saarela (Ren et al., 2021).

Ailanthus altissima (Mill.) Swingle (Simaroubaceae) is one of the most widespread invasive non-native tree species worldwide. *Ailanthus altissima* is listed in the European Union (EU) in a dedicated regulation (EU Regulation no. 1143/2014) according to which EU Member States are obliged to implement management and control measures (e.g. early-warning and surveillance systems), to develop action plans of rapid eradication and prevention and to define long-term mitigation and monitoring approaches (European Commission, 2019). *Ailanthus altissima* tends to thrive in regions with Mediterranean and temperate climates, and in areas highly disturbed by human activities such as urban areas, agricultural areas, but also in semi-natural habitats (e.g. open shrublands) and wetlands (Kowarik and Säumel, 2007; Lazzaro et al., 2020; Mayoral et al., 2018).

Numerous studies based on field sampling and laboratory experiments have highlighted the changes of eco-physiological traits caused by the invasion of *A. altissima* into Mediterranean ecosystems habitats (e.g. Brooks et al., 2021; Constan-Nava et al., 2015; Gómez-Aparicio and Canham, 2008; Lawrence et al., 1991; Mayoral et al., 2018; Medina-Villar et al., 2016; Moos et al., 2019; Motard et al., 2015; Terzi et al., 2021). However, studies applying remote sensing techniques to estimate changes in eco-physiological traits caused by the invasion of *A. altissima* are lacking.

In previous studies related to *A. altissima* invasion, the use of remote sensing has mainly focused on early detection and mapping (Likó et al., 2024; Naharki et al., 2024; Tarantino et al., 2019), and on modelling current and future habitat suitability (Baker et al., 2023; de Groot et al., 2024). Meanwhile, the spectral eco-physiological traits of vegetation invaded by *A. altissima* using remote sensing data in Mediterranean natural vegetation have been overlooked. Identifying the alterations in spectral eco-physiological traits caused by *A. altissima* invasion and localizing the most affected areas in space and time can improve the management through targeted actions to limit and contrast its alterations during the field campaigns (Saranya et al., 2024).

Considering the above, we propose a methodological approach to analyze the spectral eco-physiological traits of native vegetation dominated by the invasive *A. altissima* and compare the differences with non-invaded native vegetation on a Mediterranean island (Sardinia) using free remote sensing data for an entire phenological cycle (2021–2022). The research, based on multispectral (Sentinel-2), and thermal (Sentinel-3) remote sensing imagery, addressed the following questions: (i) does multi-temporal satellite imagery allow for identifying and describing monthly trends of spectral eco-physiological traits in native vegetation highly invaded by *A. altissima*? (ii) are there seasonal differences in spectral eco-physiological traits between native vegetation and invaded vegetation? (iii) how do the seasonal variations of spectral eco-physiological traits differ between native vegetation and invaded vegetation?

This approach meets the urgent need to produce an applied methodological tool easily reproducible and capable of analyzing the eco-physiological traits of non-native plants during the seasons and to better understand the competitive advantage of *A. altissima* on native communities, to develop effective management strategies to contrast non-native invasive species of Union concern as required by EU Regulation no. 1143/2014.

2. Materials and methods

2.1. Study area and target species

The study was carried out in Sardinia (Italy), the second largest island in the Mediterranean (24,089 km²; Fig. 1A). Sardinia is characterized by a mosaic of diverse geology and by topographic landscapes with a moderate altitudinal range (from 0 to 1834 m above sea level; Punta la Marmora, Gennargentu massif). The bioclimate is typically Mediterranean, and is characterized by long, hot-dry summers (mean maximum summer temperature: 28.1–31.6 °C, mean cumulate summer precipitation: 46.0 mm) and relatively rainy and mild winters (mean minimum winter temperature: 4.2–5.8 °C, mean cumulate winter precipitation: 236.0 mm, Canu et al., 2015). Sardinia is a biodiversity hotspot with a high rate of endemism (Fois et al., 2022). It hosts 341 endemic plants of the Tyrrhenian islands and 195 local species of endemism, most of which are included in the IUCN red list (Fois et al., 2022).

Sardinian vegetation is characterized by a cultural agro-silvo-pastoral landscape composed of a mosaic of wooded pastures alternating with shrublands, garrigues and meadows (Fig. 1B, Bacchetta et al., 2009). Similar to other regions in the Mediterranean, Sardinia's cultural landscapes are undergoing significant changes due to the abandonment of traditional agricultural and pastoral activities (Balestrieri and Ganciu, 2018). Natural forests in Sardinia are mainly composed of evergreen sclerophyllous species such as *Quercus ilex* L. and *Q. suber* L. often transformed into pastures with sparse trees. Deciduous formations of *Q. pubescens* s.l. are also present. Shrub vegetation, named Mediterranean maquis, is characterized by *Pistacia lentiscus* L., *Arbutus unedo* L., *Erica* sp. pl., *Juniperus* sp. pl., *Myrtus communis* L. *Olea europaea* L., *Phillyrea* sp. pl..

Ailanthus altissima is a fast-growing deciduous tree with high reproduction and sprouting capacity, native to Southeast Asia. This non-native tree species was intentionally introduced in the 18th century in Europe and Italy, with multiple applications as an ornamental, for landscape restoration, erosion control, and for breeding a silkworm to produce a silk substitute (Kowarik and Säumel, 2007; Swingle, 1916). The phenological cycle occupied by *A. altissima* is different from the native vegetation with a longer vegetative period that starts earlier (mid-April) and finishes later (end-October). *Ailanthus altissima* tends to form dense monospecific patches, thereby causing loss of native plant

diversity (Montecchiari et al., 2020; Terzi et al., 2021; Vilà et al., 2006). It is also able to alter soil physicochemical and nutrient parameters (Constán-Nava et al., 2015; Medina-Villar et al., 2016), and it can change hydrological processes and water availability (Sadeghi et al., 2017), which can result in modifications of ecosystem structure (Kowarik and Säumel, 2007; Sladonja et al., 2015). In addition, it may influence ecosystem biomass and productivity through allelopathic effects (Medina-Villar et al., 2017).

The high capacity of *A. altissima* to invade a wide variety of habitats and landscapes is due to its biological and ecological properties (Sladonja et al., 2015). In fact, besides a fast growth and high reproductive and sprouting rates, *A. altissima* has eco-physiological traits, such as the production of allelopathic compounds, that facilitate the invasion process (Gómez-Aparicio and Canham, 2008). It is well adapted to high temperatures and it can survive in a wide range of climatic conditions and tolerates long drought periods (Constán-Nava et al., 2015). Indeed, *A. altissima* has several adaptations against water stress in different plant organs. It may develop a very extensive root system that optimizes water uptake from the soil, and a stomata regulation mechanism reducing leaf water evapotranspiration (Kowarik and Säumel, 2007). Under intense solar radiation, *A. altissima* shows an enhanced light-use efficiency and photosynthetic activity (Sedej et al., 2021).

Additionally, as in other Mediterranean areas, human pressure has facilitated *A. altissima* invasion in Sardinia, where it is found mostly in urban areas and along roads, from where it easily spreads to abandoned agricultural areas (olive groves and vineyards), but also to Mediterranean maquis and seminatural vegetation habitats (Camarda and Brundu, 2021).

2.2. *Ailanthus altissima* and native vegetation mapping

A total of 1513 *A. altissima* georeferenced occurrences (Fig. 1B) were collected between 2003 and 2024 through field campaigns (895 occurrences, Brundu et al., 2003), with periodical resurveys of the invaded sites and, more recently (2022–2024), using citizen science data from the dedicated iNaturalist project “*Ailanthus altissima* Sardinia” (619 occurrences, <https://www.inaturalist.org/projects/ailanthus-altissima-sardinia> - accessed on the 24th April 2023). These occurrences were the starting point to produce a digital map of *A. altissima* patches located in natural and seminatural habitats with an extension detectable by remote sensing (Fig. 2A). Therefore, *A. altissima* occurrences located in towns

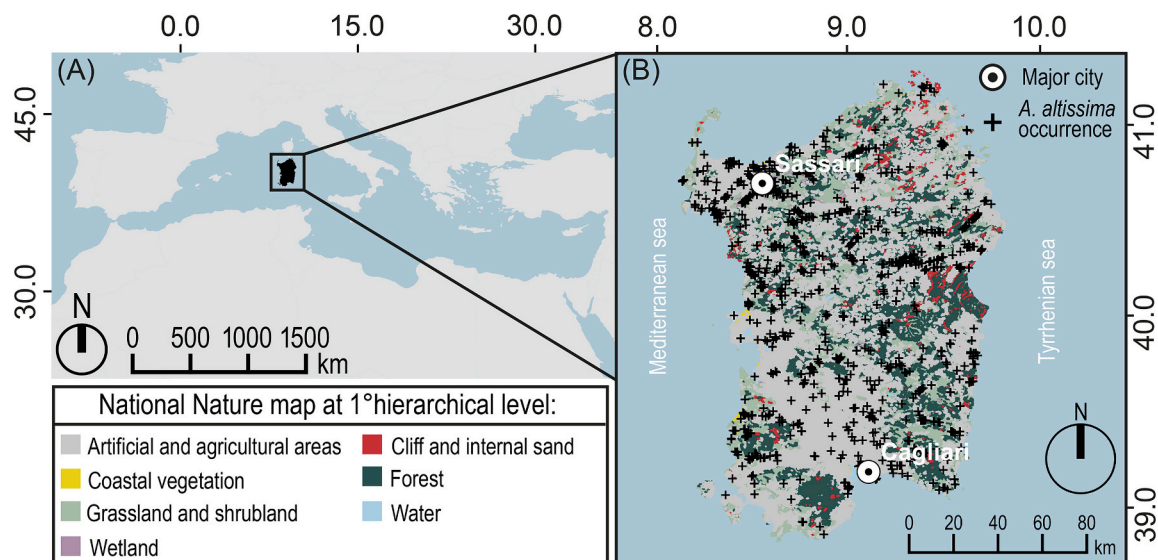


Fig. 1. In black (A) the geographic location of the study area (Sardinia, reference system: World Geodetic System 1984, EPSG 4326) in the Mediterranean basin. (B) Map of Sardinia island, displaying the distribution of *A. altissima* occurrences (black crosses) plotted on the habitat types of the “Carta della Natura” at its first hierarchical level (Camarda et al., 2015).

and in artificial areas as well as single trees or clones with limited extension (i.e. covering and area below 2 m²) were excluded from the analysis (Fig. 2A). The *A. altissima* patches were digitalized and marked with an identification number (ID) through visual photo-interpretation of Google Earth RGB orthophotos and 360-degree images of the Google Street View (Fig. 2A, Kotowska et al., 2021) in QGIS (QGIS 3.28, QGIS.org, 2023). The analyzed orthophotos were visualized in QGIS 3.28 using the “HCMGIS” ver. 23.7.19 plugin (Quach, 2023) and included the most recent satellite and aerial orthophotos of the time frame 2019–2023 (<1 m spatial resolution) available for free in Google Earth provided by the companies AIRBUS, Inc. and Maxar Technologies. The corresponding Google Street View images were directly opened in QGIS 3.28 using the “StreetView” ver. 3.2 plugin (Saccon, 2020). The accuracy assessment of the digital map of *A. altissima* patches was based on 272 ground control points collected in March 2024. A set of accuracy

metrics including overall accuracy, producer accuracy, user accuracy, and Cohen’s Kappa statistics were calculated through an error matrix (Fig. 2A Congalton and Green, 2019).

For characterizing the native vegetation in the invaded habitats, we used the “Carta della Natura” map (hereafter National Nature Map), whose vegetation classes correspond to the second hierarchical level of CORINE biotopes at 1:50,000 scale with native vegetation patches identified by an ID (Camarda et al., 2015).

2.3. Satellite imagery selection

Monthly time series of freely available Sentinel-2A/2B (hereafter S2) and Sentinel-3 (hereafter S3) images were downloaded from the repository of Sentinel imagery of the European Space Agency (ESA), the Copernicus Data Space Ecosystem (<https://browser.dataspace.copernicus.eu/>

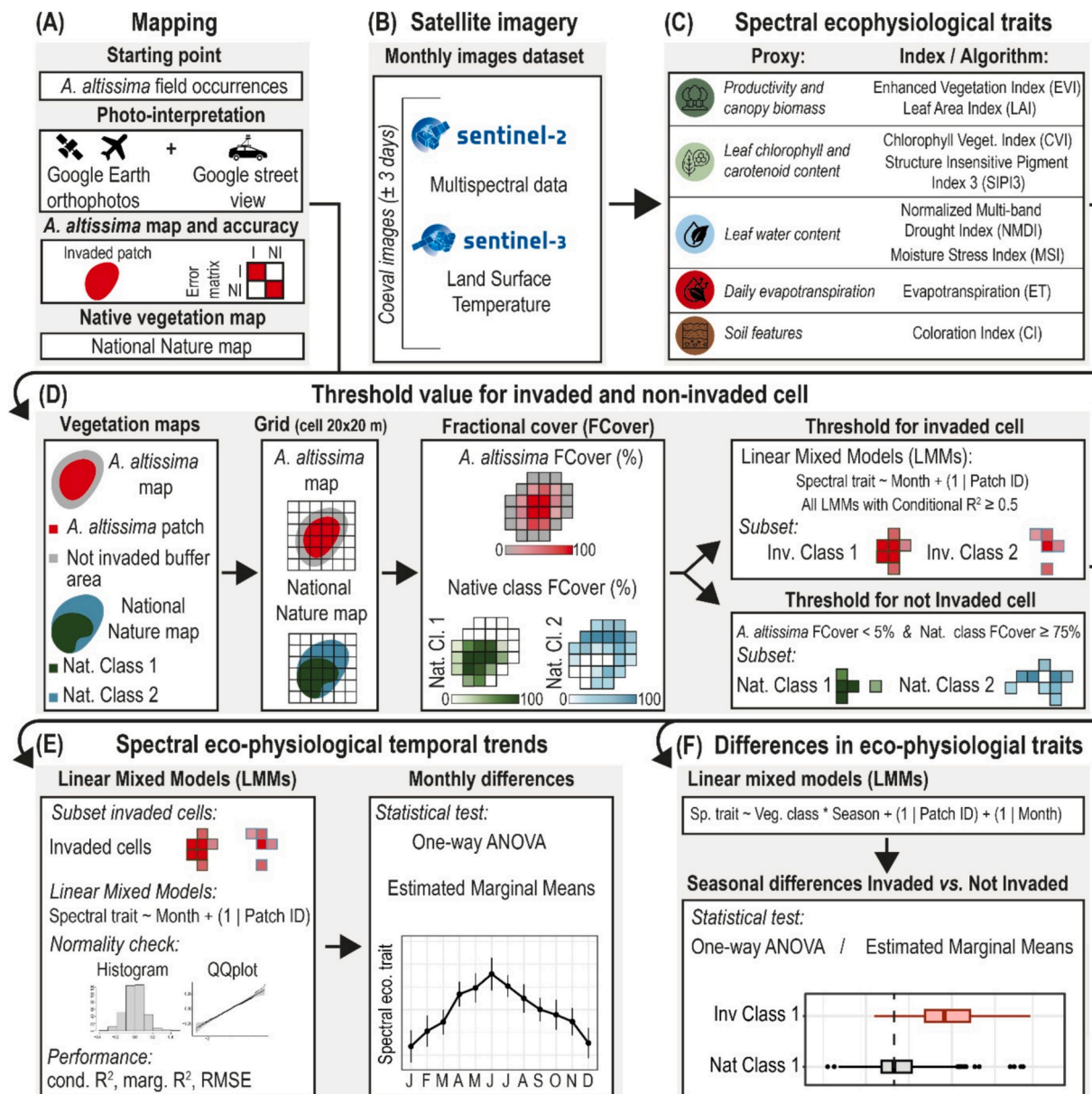


Fig. 2. Schematic overview of the methodology used to analyze the temporal trends of spectral eco-physiological traits of *A. altissima* invaded areas and to test seasonal variability on invaded and non-invaded native vegetation. (A) *Ailanthus altissima* and native vegetation mapping, (B) Satellite imagery selection, (C) Spectral eco-physiological trait measuring, (D) Spectral eco-physiological traits extracting, (E) Spectral eco-physiological temporal trends in invaded cells, (F) Seasonal spectral eco-physiological differences between invaded and non-invaded cells. All steps above described and computed in tools of SNAP, QGIS, and the R language code are reported in Table S4.

nicus.eu, Fig. 2B), covering an entire phenological cycle (November 2021 – October 2022). The S2 satellites (S2A, S2B) are equipped with a multispectral instrument with 13 bands registering data in visible, near-infrared, and short-wave infrared sectors of the electromagnetic spectrum, with high and medium spatial resolutions (10, 20, and 60 m, Table 1), and a revisit frequency of five days at the equator (Drusch et al., 2012). As the study area is included in six tiles of the S2 tiling grid (i.e. T32TML, T32TNL, T32TMK, T32TNK, T32SMJ, T32SNJ, Fig. 2A), we downloaded monthly S2 images for each tile (i.e. 12 images per each of one of the 6 tiles, 12×6) for a total of 72 imageries, at the second processing level (level-2A) atmospherically corrected to surface reflectance by ESA using the Sen2cor processor (Luis et al., 2019) with low cloud coverage ($< 6\%$, except for six images, Table S1). The few remaining cloud-affected pixels were removed from each S2 image using ESA's Sentinel-2 toolbox—ESA Sentinel Application Platform v. 9.0 (SNAP, 2022).

The S3 satellites (S3A, S3B) with time frequency almost daily at the Equator, are equipped with multiple sensing instruments, particularly the Microwave Radiometer, Synthetic Aperture Radar Altimeter, Ocean and Land Colour Instrument, and Sea and Land Surface Temperature Radiometer (SLSTR, Donlon et al., 2012). The SLSTR sensor includes nine bands, of which six cover the visible and near infrared part of the electromagnetic spectrum (bands S1 to S6), and the other three cover the thermal infrared part of the spectrum range, namely S7 (wavelengths 3742 ± 398 nm), S8 (wavelengths $10,854 \pm 776$ nm), and S9 (wavelengths $12,022.50 \pm 905$ nm). The combination of the three thermal bands was used to estimate the Land Surface Temperature (LST) with a resolution of 1000 m at the second processing level (level-2) (Donlon et al., 2012). We downloaded 30 SLSTR images produced by S3 satellites that are nearly contemporary (± 3 days) of S2 images at the second processing level (Table S2). The time of passage of downloaded S3A/S3B was between 09:00 and 10:15 a.m. over the island of Sardinia.

2.4. Calculation of spectral eco-physiological traits

To investigate differences between invaded and non-invaded areas in terms of (a) productivity and canopy biomass, (b) leaf chlorophyll and carotenoid content (e.g. photosynthetic activity), (c) leaf water content, (d) daily evapotranspiration and (e) soil features (e.g. bare surfaces and organic content), a set of spectral eco-physiological traits were calculated for each month, avoiding multicollinearity (Variance Inflation Factor < 5 , Table S3, Fig. 2C).

Calculation of spectral eco-physiological traits required combining information from spectral bands with a cell size of 10 m^2 (B, G, R, NIR) with bands with a cell size of 20 m^2 (RE₇₀₅, RE₇₄₀, RE₇₈₃, RE₈₆₅, SWIR₁₆₁₀, SWIR₂₁₉₀; Table 2). Thus, all S2 bands were resampled to 20 m^2 spatial resolution using the Nearest Neighbor algorithm in SNAP (SNAP, 2022).

Proxies of productivity and canopy biomass were derived from S2

Table 1

Sentinel-2 bands characteristics: original band name (Band), name, acronym, wavelengths, and original spatial resolution.

Band	Name	Acronym	Wavelengths (nm)	Original spatial resolution (m)
B2	Blue	B	490 ± 65	10
B3	Green	G	560 ± 35	10
B4	Red	R	665 ± 30	10
B5	Red Edge 705	RE ₇₀₅	705 ± 15	20
B6	Red Edge 740	RE ₇₄₀	740 ± 15	20
B7	Red Edge 783	RE ₇₈₃	783 ± 20	20
B8	Near Infrared	NIR	842 ± 115	10
B8A	Red Edge 865	RE ₈₆₅	865 ± 22	20
B11	Short-wave infrared 1610	SWIR ₁₆₁₀	1610 ± 20	20
B12	Short-wave infrared 2190	SWIR ₂₁₉₀	2190 ± 20	20

data by computing the Enhanced Vegetation Index (EVI) and the Leaf Area Index (LAI, Table 2). EVI is a particularly efficient spectral index to quantify canopy biomass, reducing soil and atmospheric effects (Huete et al., 2002). The EVI ranges from 0 (very low canopy biomass and productivity) to 1 (high biomass and productivity). LAI, defined as half the area of photosynthetically active elements per unit of horizontal ground area, is a dimensionless biophysical parameter that relates to several plant/vegetation physiological parameters such as productivity, photosynthetic activity, evaporation, transpiration, and carbon flux (Asner et al., 2003). We calculated LAI using the “Biophysical processor Sentinel-2” tool in SNAP that applies an artificial neural network algorithm and requires eight input variables (Sentinel-2 bands: G, R, RE₇₀₅, RE₇₄₀, RE₇₈₃, RE₈₆₅, SWIR₁₆₁₀, SWIR₂₁₉₀), as well as viewing zenith, solar zenith and the relative azimuth angles. LAI values range from 0 to 10 and increasing LAI values depict increasing canopy density. Further details can be found in Weiss and Baret (2016).

Proxies for leaf chlorophyll and carotenoid content were derived from S2 data by computing the Chlorophyll Vegetation Index (CVI) and the Structure Intensive Pigment Index 3 (SIPI3, Table 2). The CVI is highly sensitive to leaf chlorophyll content, and thus estimate pigment content by combining NIR/green ratio normalized by the red/green ratio to minimize vegetation structural effects (Vincini et al., 2008). The SIPI3 quantifies the ratio between carotenoids and photosynthetic pigments, with higher values indicating higher content of carotenoid pigments and increased leaf stress (Peñuelas et al., 1995).

Leaf water content proxies were computed based on two spectral indices that integrate the short wave infrared (SWIR) bands, namely the Normalized Multi-band Drought Index (NMDI) and the Moisture Stress

Table 2

Spectral proxies of eco-physiological traits derived from Sentinel-2 and 3 satellite data: acronyms, full name, formulas and algorithms, and references. The spectral eco-physiological traits are grouped by their role as proxy of different ecosystem functions (e.g. productivity and canopy biomass, leaf chlorophyll and carotenoid content, leaf water content, daily evapotranspiration, and soil features).

Acronym	Name	Formula and Algorithm	Reference
Productivity and canopy biomass			
EVI	Enhanced Vegetation Index	$2.5 \times \frac{\text{NIR} - \text{R}}{(\text{NIR} + 6 \times \text{R} - 7.5 \times \text{B}) + 1}$	Huete et al., 2002
LAI	Leaf Area Index	Artificial Neural Network	Weiss and Baret, 2016
Leaf chlorophyll and carotenoid content			
CVI	Chlorophyll Vegetation Index	$\frac{\text{NIR} \times \text{R}}{\text{G} \times \text{G}}$	Vincini et al., 2008
SIPI3	Structure intensive pigment index 3	$\frac{\text{NIR} - \text{B}}{\text{NIR} - \text{R}}$	Peñuelas et al., 1995
Leaf water content			
NMDI	Normalized multi-band drought index	$\frac{\text{RE}_{865} - (\text{SWIR}_{1610} - \text{SWIR}_{2190})}{\text{RE}_{865} + (\text{SWIR}_{1610} - \text{SWIR}_{2190})}$	Wang and Qu, 2007
MSI	Moisture stress index	$\frac{\text{SWIR}_{1610}}{\text{NIR}}$	Hunt Jr. and Rock, 1989
Daily evapotranspiration			
ET	Evapotranspiration	Sen-Et algorithm	Guzinski et al., 2020
Soil features			
CI	Coloration index	$\frac{\text{R} - \text{G}}{\text{R} + \text{G}}$	Mathieu et al., 1998

Index (MSI, Table 2). The NMDI combines two SWIR bands (SWIR₁₆₁₀, SWIR₂₁₉₀), and is a good indicator of water content in vegetation and soil (high, NMDI values $\approx$ high moisture; Wang and Qu, 2007). MSI instead is related to drought stress and high MSI values correspond to low leaf water content (Hunt Jr. and Rock, 1989).

A proxy of daily evapotranspiration was modeled using the open source “Sentinels for Evapotranspiration” tool (Sen-ET) available as a plugin for the SNAP toolbox (Guzinski et al., 2020). Sen-ET estimates Evapotranspiration (ET) by combining S2 bands resampled to 20 m² (see Table 1), LST derived by S3 data sharpened with S2 images and the digital elevation model (SRTM 1 s) with 20 m² cell size, meteorological data from the European Centre for Medium-Range Weather Forecasts in particular (ECMWF) the reanalysis 5 (ERA-5) dataset (downloaded from the Copernicus Climate Change Service: <https://cds.climate.copernicus.eu/#/home>), and the Land Cover map of 2015 with 100 m spatial resolution (downloaded from the Copernicus Land Monitoring Service: <https://land.copernicus.eu/en/products/global-dynamic-land-cover>), coeval with National Nature Map. For further details, see Guzinski et al. (2020).

Finally, proxies for soil features, such as bare soil and organic matter content, were estimated using Coloration Index (CI, Table 2). CI is a spectral index that depicts bare soil presence, organic carbon content, nutrients and texture, combining the R and G band from the visible part of the electromagnetic spectrum (Mathieu et al., 1998).

2.5. Threshold value for invaded and non-invaded cell

A buffer of 20 m was created around each *A. altissima* patch to include non-invaded areas composed of the same native vegetation classes invaded by *A. altissima* (Fig. 2D). Then, a grid with 20 m² sized cells, co-registered with S2 images, was overlaid onto the *A. altissima* patches and the surrounding buffers (Fig. 2D). For each 20 m² cell of this grid, the fractional cover of *A. altissima* and the native vegetation classes, respectively, was calculated as relative percentage cover (Fig. 2D). Then, in each cell, the values of spectral eco-physiological traits (Table 2) were extracted. After, we reduced the number of cells by considering two different thresholds to differentiate non-invaded cells from invaded cells. The mixed cells (a cell composed of no single dominant vegetation class) were excluded from the analysis. Non-invaded or scarcely invaded cells were considered when *A. altissima* fractional cover was lower than 5 % and the fractional cover of one native vegetation class was greater than or equal to 75 %. These cells are hereinafter called “non-invaded”, followed by the name of the native dominant vegetation class. Non-invaded cells are dominated by a single native vegetation class and *A. altissima* has a very low cover or it is absent (≤ 5 %). After, we conducted a sensitivity analysis to determine the fractional cover threshold at which native vegetation can be considered invaded by *A. altissima*. We considered all the cells with a fractional cover of an *A. altissima* patch greater than or equal to 1 %. Before running the sensitive analysis, we removed outliers (identify_outliers of the R package ‘rstatix’ ver. 0.7.2; Kassambara, 2023a), i.e. cells with values greater than the sum of the third quartile (Q3) and 1.5 times the interquartile range (Q3 – Q1) or lower than the subtraction of first quartile (Q1) and 1.5 times the interquartile range (Eq. (1)).

$$\text{Outlier} \geq Q3 + 1.5 \cdot (Q3 - Q1) \text{ OR } \text{Outlier} \leq Q1 - 1.5 \cdot (Q3 - Q1) \quad (1)$$

The sensitivity analysis was performed in three steps, as follows:

1. *Iterative LMMs*: for each spectral eco-physiological trait, we computed separate linear mixed-effects models (LMMs) considering different fractional cover thresholds ranging from 1 % to 100 % (interval of 1 %). We used as fixed effect the monthly values of each spectral eco-physiological trait. An *A. altissima* patch ID was included as a random factor to account for the temporal repeated measure in each patch (see Table 2, Fig. 2E, Eq. (2)).

$$\text{Spectral eco-physiological trait} \sim \text{Month} + (1 | \text{Patch ID}) \quad (2)$$

2. *Performance calculation*: to assess the performance of each fractional cover threshold, we estimated the conditional R² for each LMM and compared them across thresholds for each spectral eco-physiological trait.
3. *Threshold definition*: to identify the minimum threshold of *A. altissima* fractional cover at which native vegetation can be considered invaded, we selected the threshold at which models had a conditional R² value greater than or equal to 0.5 for all spectral eco-physiological traits (Chicco et al., 2021; Hair et al., 2011). Hereinafter, these cells were called “invaded cell” followed by the name of the native vegetation class.

2.6. Temporal trends of spectral eco-physiological traits in the cells invaded by *A. altissima*

To analyze the potential of Sentinel data to depict temporal variability in spectral eco-physiological traits of *A. altissima*, we used the LMMs (Eq. (2)) on invaded cells to assess the differences in spectral eco-physiological traits between months. The monthly differences were estimated using one-way ANOVA and the function *emmeans* of ‘emmeans’ R package ver. 1.8.7 with Bonferroni adjustment to compute estimated marginal means (EMMs) in each LMM (Lenth, 2023).

In each LMM, the normality of the residuals was checked by visual inspection of QQ plots and the histogram of residuals using the *ggqplot* function of ‘ggpubr’ R package ver. 0.6 (Kassambara, 2023b). To evaluate the goodness-of-fit of each LMM, we estimated the root mean square error (RMSE) and the explained variance of the fitting model considering both conditional and marginal R² values. Marginal R² quantifies the explained variance considering only the fixed effects, while conditional R² considers both fixed and random effects (Nakagawa and Schielzeth, 2013). All LMMs were calculated using the *lmer* function of ‘lme4’ R Package ver. 1.-35.1 (Bates et al., 2015) and *model_performance* of ‘performance’ R Package ver. 0.11.0 (Lüdtke et al., 2021).

2.7. Seasonal spectral eco-physiological differences between invaded and non-invaded cells

To assess the differences in spectral eco-physiological traits between invaded and non-invaded cells, we compared their seasonal variations using LMMs (Fig. 2F). Specifically, we tested on each spectral eco-physiological trait the effects of vegetation classes, season, and their interaction (vegetation classes $\times$ season). To account for the repeated measure within and across seasons we included as random effects the month and the ID of *A. altissima* and native vegetation patches. The significant seasonal differences were estimated by one-way ANOVA and post hoc test EMMs with Bonferroni adjustment on the LMMs’ results (Fig. 2F, Eq. (3)).

$$\text{Spectral eco-physiological parameter} \sim \text{Vegetation class} \cdot \text{Season} + (1 | \text{Patch ID}) + (1 | \text{Month}) \quad (3)$$

Before the computation of LMMs, we removed the outlier values, as described above (see Eq. (1)), for each native vegetation class. Finally, the normality of the residuals was checked by visual inspection of QQ plots and histogram of residuals.

3. Results

3.1. Accuracy of the *A. altissima* map and assignment of the native vegetation classes

The map of *A. altissima* yielded high accuracies with overall accuracy and Cohen's Kappa greater than 95.00 % and 0.90, respectively (Table S5). The sensitivity analysis allowed to establish 75 % as the fractional cover threshold for which all LMMs reached moderate or higher goodness of fit ($R^2 > 0.5$, Fig. S1). Subsequently, 24,469 cells resulted as invaded and non-invaded by *A. altissima* in native vegetation. These cells corresponded to 20 CORINE biotopes of the “National Nature Map”, referring to six vegetation classes at the second hierarchical level (Table 3). The most frequent cells belonged to the classes of Mediterranean Sub-nitrophilous Grassland (MSG), Agricultural Herbaceous Areas (AHA), and Agricultural Woody Areas (AWA) followed by the cells of Evergreen Woody Vegetation (EWV), Deciduous Woody Vegetation (DWV), and Mediterranean Maquis (MMA, see Table 3, Fig. S2). The cells dominated by *A. altissima* (INV) were the least frequent with only 390 cells (Table 3, Fig. S2).

3.2. Temporal trends of spectral eco-physiological traits in cells invaded by *A. altissima*

Overall, monthly trends of spectral eco-physiological traits in the cells invaded by *A. altissima* were significantly captured by Sentinel data

Table 3

Native vegetation classes (CORINE biotopes at the second hierarchical level) in invaded patches and surrounding buffer, their relative acronyms, description, CORINE biotypes codes that they include and, number of 20 m² cells.

Acronym	Vegetation class	Description	CORINE biotypes	Cells
INV	<i>A. altissima</i> invasion	Natural and seminatural vegetation dominated by <i>A. altissima</i>	–	390
MMA	Mediterranean Maquis	Evergreen Mediterranean shrubs and matorral dominated by <i>Pistacia lentiscus</i> , <i>Phillyrea latifolia</i> , <i>Arbutus unedo</i> , and <i>Erica arborea</i> .	32.11, 32.12, 32.211, 32.23, 32.4	1211
MSG	Mediterranean Sub-nitrophilous Grassland	Grasslands formed by temporary rest (1–2 years) of crops with more common as <i>Bromus</i> sp.pl., <i>Avena</i> sp.pl., and <i>Vulpia</i> sp.pl.	34.81	7013
DWV	Deciduous Woody Vegetation	Forest dominated by deciduous trees as <i>Quercus pubescens</i> s.l.	41.72, 41.732	1498
EWV	Evergreen Woody Vegetation	Forest dominated by evergreen trees such as <i>Quercus ilex</i> , <i>Q. suber</i> , and <i>Ceratonia siliqua</i> .	45.1, 45.21, 45.317	1937
AHA	Agricultural Herbaceous Areas	Intensive and extensive herbaceous crops of cereal, paddy, vegetable, and pasture.	82.1, 82.3	6480
AWA	Agricultural Woody Areas	Intensive and extensive woody crops of olive groves, vineyards, and pasture areas	83.11, 83.15, 83.16, 83.21, 83.31, 84.6	5940

with conditional R^2 values ranging from 0.523 for CVI to 0.782 for LAI, and with low RMSE values in the LMMs (Fig. 3, Table 4, Fig. S3).

The use of the patch ID as random effect increased the performance of each LMM with a mean increment between conditional R^2 and marginal R^2 equal to 0.008 ± 0.005 (Table 4). Furthermore, the results of one-way ANOVA and the monthly variation estimated by EMMs confirmed the significant variability of spectral eco-physiological traits in invaded cells (see Table S6, Fig. S4 – S11).

The measured monthly trends of spectral eco-physiological traits showed clear ecological patterns of invaded cells in semi-natural landscapes (Fig. 3). For instance, the monthly trends in EVI and LAI traits highlighted high productivity and canopy biomass from April to October, corresponding to the growing season of *A. altissima* in Sardinia (Fig. 3). The CVI trait exhibited an increase in leaf chlorophyll content in April, followed by a decrease in October, while carotenoid content (SIPI3) displayed a decrease in April and an increase in October (Fig. 3). However, the CVI values during winter (December, January, February) showed high heterogeneity, likely due to the presence of bare soil in these months. Leaf water content started increasing before the growing season, and by February, NMDI values showed a continuous increase until October (Fig. 3). In contrast, the moisture stress (MSI spectral trait) remained minimal between April and October (Fig. 3). Additionally, the daily evapotranspiration trend indicated increased evapotranspiration (ET) between April and October, with a peak in May (Fig. 3). Finally, the soil characteristics described by CI exhibited a similar but opposite trend compared to EVI and LAI parameters, with a decrease in bare soil from April to October and an increase in organic content in the soil during the winter months (Fig. 3).

3.3. Seasonal spectral eco-physiological differences between invaded and non-invaded cells

The spectral eco-physiological traits significantly varied across invaded and non-invaded cells (Table 5, Figs. 4, 5, Fig. S12 – S17). In particular, the performance of LMMs calculated to assess the seasonal differences of spectral eco-physiological traits between invaded and non-invaded cells showed a range of conditional R^2 values from good model fits in EVI of Agricultural Woody Areas (AWA, cond. R^2 equal to 0.223) to very high value in ET of Deciduous Woody Vegetation (DWV, cond. R^2 equal to 0.880, Table 5). On average, the higher LMM performances were verified in DWV class with conditional R^2 always greater than 0.400 in all spectral parameters, and low RMSE values, while AHA evidenced the lower LMM performances with conditional R^2 values always below 0.550 (Table 5). Two random effects (Patch ID, Months) considerably improved the performance of LMMs, as demonstrated by the differences between marginal R^2 and conditional R^2 (Table 5).

The spectral eco-physiological traits of the invaded cells exhibited significant seasonal differences compared to the same vegetation classes of non-invaded cells. Indeed, the one-way ANOVA and EMMs comparisons evidenced significant seasonal differences of spectral eco-physiological traits (Figs. 4, 5, Table S7 – S12, Fig. S18 – S23). In summer, these differences were more pronounced, as highlighted by the higher productivity and canopy biomass in invaded cells (e.g. EVI and LAI values; Fig. 5). Concerning leaf chlorophyll and carotenoid content, SIPI3 summer values were significantly lower in the invaded cells, except for the EWV class, while CVI values were higher only in the DWV class (Fig. 5). In invaded cells, the summer leaf water content resulted higher (high values of NMDI) as moisture stress resulted lower (low values of MSI) for EWV and AWA classes. Moreover, daily evapotranspiration (ET) resulted lower on MSG and DWV classes in invaded cells compared to non-invaded cells (Fig. 5). Finally, invaded cells showed in summer higher bare soil presence and soil organic content in the MMA class, and lower CI for MSG, DWV, and AHA classes (Fig. 5).

Regarding the other seasons (i.e., spring, winter, autumn), the spectral eco-physiological traits of invaded cells were significantly different mainly in winter for some vegetation classes (Figs. 4, 5). During

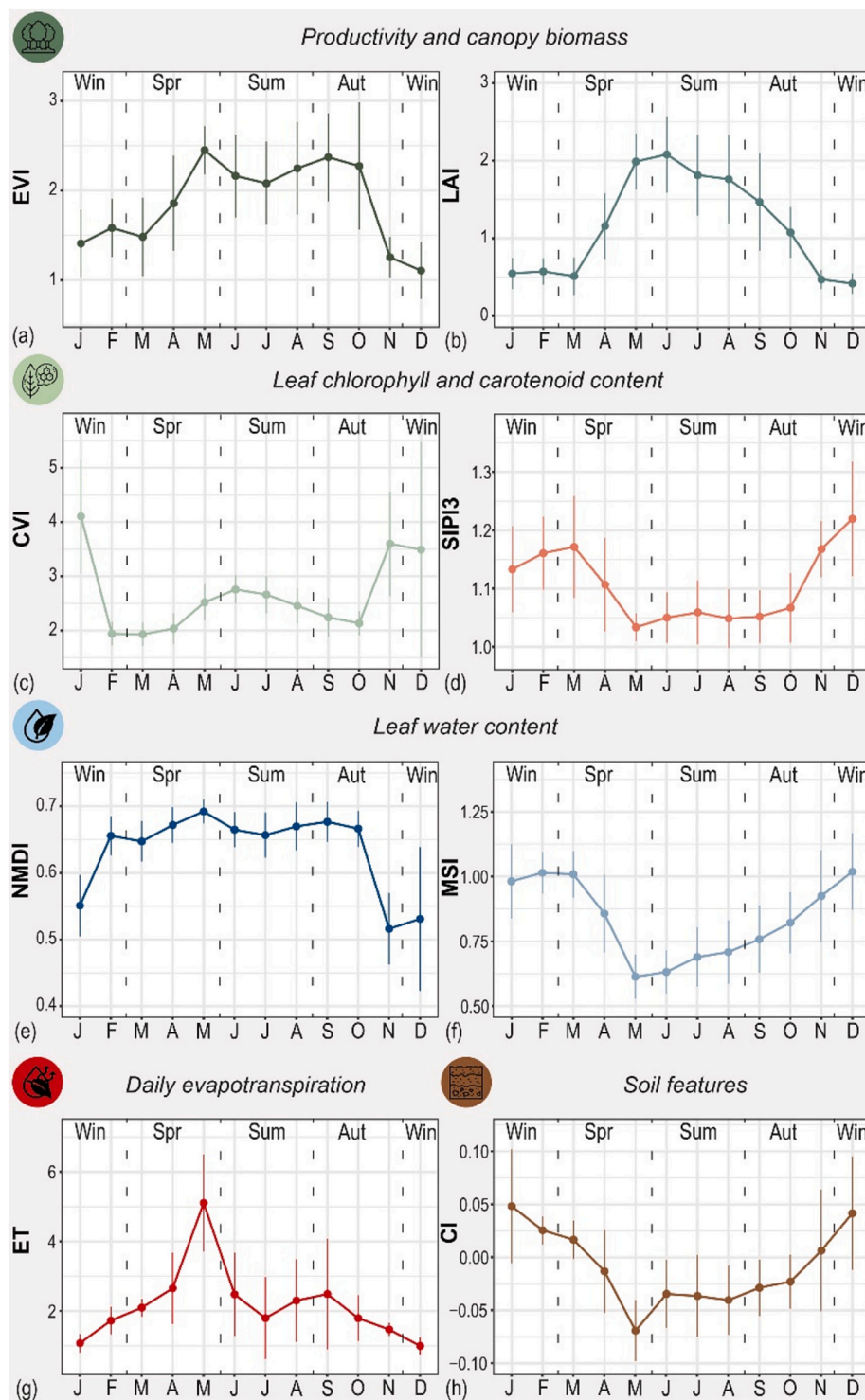


Fig. 3. Monthly average of spectral eco-physiological traits in invaded cells for productivity and canopy biomass (a, b), for leaf chlorophyll and carotenoid content (c, d), for leaf water content (e, f), for daily evapotranspiration (g), and for soil features (h).

winter, invaded cells evidenced higher moisture stress (higher MSI values) in MMA, EWV, and AWA vegetation classes (Fig. 4) and higher bare soil values in MSG and in AWA classes (Fig. 4). Furthermore, invaded cells showed higher carotenoid content (SIPI3) in MMA class, as well as lower leaf area index (LAI) values in the same class (Fig. 4). The spectral eco-physiological traits recorded during spring and autumn showed a weak difference caused by *A. altissima* invasion. Differences were observed only in the MSI and SIPI3 traits for the MSG, EWV, and MMA classes (Figs. 4, 5).

4. Discussion

In this study, we assessed the potential of combining multi-temporal multispectral (S2) and thermal (S3) satellite data from the Copernicus program to characterize monthly trends of spectral eco-physiological traits of the invasive non-native tree *A. altissima* and to compare the seasonal spectral eco-physiological traits between invaded and non-invaded vegetation in Sardinia. The combination of S2 and S3 data has proven particularly effective in characterizing the monthly trends of

Table 4

Summary of linear mixed models in the invaded cells considering the monthly trends in spectral eco-physiological traits proxies of: productivity and canopy biomass, leaf chlorophyll and carotenoid content, leaf water content, daily evapotranspiration, and soil features (see Table 2 for spectral eco-physiological traits description).

Spectral traits	Conditional R ²	Marginal R ²	RMSE
Productivity and canopy biomass			
EVI	0.666	0.660	0.096
LAI	0.782	0.704	0.335
Leaf chlorophyll and carotenoid content			
CVI	0.523	0.478	0.677
SIPI3	0.628	0.497	0.047
Leaf water content			
NMDI	0.730	0.672	0.035
MSI	0.651	0.506	0.108
Daily evapotranspiration			
ET	0.671	0.627	0.738
Soil features			
CI	0.544	0.424	0.033

invaded vegetation. Furthermore, the seasonal patterns of the invasive tree differed significantly from those of the native vegetation, especially during the drought period in summer that is typical for Mediterranean ecosystems. Spectral eco-physiological traits of *A. altissima* in summer indicated higher productivity, canopy biomass, and leaf water content, but lower leaf carotenoid content and bare soil cover compared to native vegetation classes.

4.1. Advantages of multispectral (S2) and thermal (S3) imagery combination

The workflow developed in this study exemplifies a great potential for integrating different types of free and open-source satellite data from different platforms to detect seasonal effects of one of the most widespread invasive non-native tree species over large areas in Mediterranean ecosystems characterized by very intense summer droughts, such as in Sardinia. Our results confirmed the effectiveness of free remote sensing data such as S2 and S3 imagery to monitor the alterations caused

by non-native trees at regional and local scales, and the combination of S2 and S3 data supply an effective tool to assess the invasion dynamic of *A. altissima* (Ahmed et al., 2022; Arasumani et al., 2021a). The effectiveness of remote sensing data was expected, as it had been previously proved on other invasive non-native trees that alter the eco-physiological traits of native vegetation (Große-Stoltenberg et al., 2018a, 2018b; Hellmann et al., 2017; Ren et al., 2021; Van Cleemput et al., 2020). The high spatial, spectral, and temporal resolutions of S2 and S3 enabled a detailed characterization of the eco-physiological trends of *A. altissima* and its alterations on native vegetation within highly fragmented Mediterranean landscapes. The findings confirm that the monitor of invasion is a scale-dependent process, and 20 m² resolution is effective for monitoring the invasion of *A. altissima* (Müllerová et al., 2023).

As remarked in several studies (Arasumani et al., 2021b; Rocchini et al., 2015b; Saranya et al., 2024; Werner et al., 2024), the use of multi-temporal remote sensing imagery with adequate spatial resolution enables the comprehension of the invasion process, improving the planning of management actions. The combination of S2 and S3 allowed the temporal assessment of alterations caused by *A. altissima* invasion, identifying seasonal vulnerability in different Mediterranean ecosystems. This helps prioritize management efforts and allocate resources effectively. Indeed, in the Mediterranean, in the planning of management actions to contrast *A. altissima* invasion, the effects of the summer season with warm and drought periods on the invasion process and in particular on competition with native vegetation should be considered. Consequently, the peak of the growth period during summer, as evinced by drought resistance, high productivity, and high photosynthetic efficiency, could mean it might be an opportune season to undertake management and mitigation actions against the invasion (EPPO, 2020).

Furthermore, LMMs are powerful statistical approaches to detect effects of invasive plants species on ecosystem functioning using remote sensing (Große-Stoltenberg et al., 2025; Hellmann et al., 2017; Van Cleemput et al., 2020; Werner et al., 2024). In this study, we demonstrated that LMMs proved a high effectiveness at estimating the alteration of evapotranspiration, combining LST S3 and multispectral S2 data. This result proves the reliability of Sen-Et plugin for non-native tree as *A. altissima* (Guzinski et al., 2023; Guzinski and Nieto, 2019).

4.2. *Ailanthus altissima* invasion alters spectral eco-physiological traits of native vegetation

The success of a non-native tree and its level of invasibility depend

Table 5

Summary of linear mixed models for seasonal differences in spectral eco-physiological traits between invaded and non-invaded cells (see Table 3 for vegetation description). Comparisons of spectral eco-physiological traits depicting productivity and canopy biomass, leaf chlorophyll and carotenoid content, leaf water content, daily evapotranspiration, and soil features (see Table 2 for the complete description of spectral eco-physiological traits).

Veg. class	Performance	Productivity and canopy biomass		Leaf chlorophyll and carotenoid content		Leaf water content		Daily evapotranspiration	Soil features
		EVI	LAI	CVI	SIPI3	NMDI	MSI	ET	CI
MMA	Cond. R ²	0.288	0.556	0.693	0.367	0.626	0.430	0.702	0.296
	Marg. R ²	0.114	0.113	0.107	0.039	0.043	0.031	0.238	0.019
	RMSE	0.126	0.446	0.779	0.080	0.040	0.144	0.673	0.054
MSG	Cond. R ²	0.298	0.506	0.542	0.435	0.648	0.432	0.755	0.332
	Marg. R ²	0.183	0.232	0.143	0.249	0.169	0.181	0.258	0.169
	RMSE	0.143	0.469	0.631	0.200	0.050	0.184	0.656	0.057
DWV	Cond. R ²	0.472	0.716	0.575	0.407	0.690	0.692	0.880	0.637
	Marg. R ²	0.146	0.169	0.175	0.103	0.213	0.136	0.312	0.252
	RMSE	0.129	0.365	0.738	0.165	0.054	0.131	0.541	0.037
EWV	Cond. R ²	0.291	0.470	0.545	0.242	0.671	0.271	0.739	0.362
	Marg. R ²	0.109	0.114	0.154	0.096	0.080	0.041	0.362	0.048
	RMSE	0.122	0.451	0.936	0.086	0.042	0.139	0.821	0.053
AHA	Cond. R ²	0.225	0.369	0.463	0.345	0.491	0.365	0.522	0.281
	Marg. R ²	0.107	0.144	0.123	0.206	0.108	0.132	0.223	0.096
	RMSE	0.157	0.559	0.687	0.192	0.057	0.183	0.847	0.069
AWA	Cond. R ²	0.223	0.369	0.574	0.466	0.649	0.420	0.661	0.355
	Marg. R ²	0.139	0.153	0.124	0.245	0.111	0.195	0.291	0.163
	RMSE	0.134	0.461	0.631	0.169	0.047	0.174	0.729	0.059

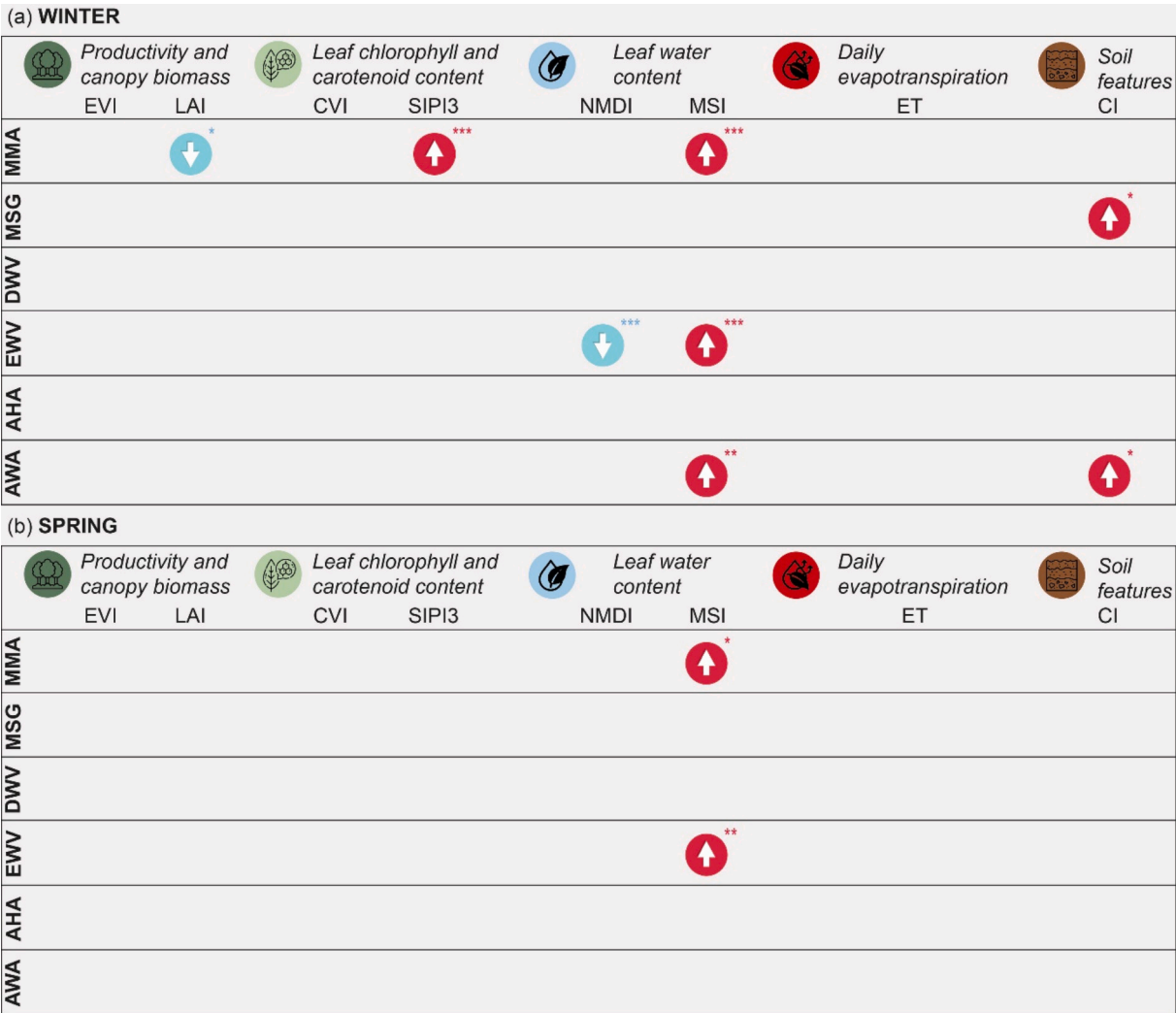


Fig. 4. Differences in spectral eco-physiological traits between invaded and non-invaded cells across Winter and Spring. Red arrows indicate spectral eco-physiological traits with significantly greater values in invaded cells, while sky blue arrows indicate spectral eco-physiological traits with significantly lower values. *p*-value: * < 0.05; ** < 0.01; *** < 0.001. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

on its ability to modify the ecosystem it is invading to its advantage (Daly et al., 2023; Jeschke et al., 2014; Kuebbing and Nuñez, 2016). A critical step in facilitating this transformation involves the alteration of eco-physiological traits within the invaded ecosystem (Boardman et al., 2022; Liu et al., 2019). *A. altissima* invasion determined high alterations of eco-physiological traits across Sardinia. Indeed, we detected differences in the eco-physiological seasonal responses between invaded and non-invaded cells. These findings are consistent with previous research conducted in laboratory settings or in the field (e.g. Knüsel et al., 2019; Pepe et al., 2022; Petruzzellis et al., 2018; Sedej et al., 2021; Trifilò et al., 2004). Therefore, spectral eco-physiological traits have a large potential to provide a valid support for studying and monitoring the alterations occurring in vegetation affected by invasive non-native tree species (Müllerová et al., 2023; Werner et al., 2024) such as *A. altissima*. In our study, the spectral eco-physiological traits indicated high productivity and biomass as well as elevated leaf water content during hot-dry months (e.g. from late spring to early autumn) typical of the Mediterranean climate. This trend may probably be related to well-known drought resistance strategies adopted by *A. altissima* as described by field and laboratory analysis (Pepe et al., 2022; Petruzzellis et al., 2018). This includes the extended root system of *A. altissima* that facilitates water uptake and other adaptations through reduced hydraulic

conductance during drought periods (Trifilò et al., 2004), its efficient water transport system (Knüsel et al., 2015; Knüsel et al., 2019), and its optimized stomata closure (Petruzzellis et al., 2018). These adaptive mechanisms are in line with the spectral properties we derived from remote sensing data analysis, which emphasizes the potential of multi-temporal satellite data to characterize invasive non-native plants in terms of ecosystem functioning.

Another interesting aspect of the temporal trend of spectral eco-physiological traits is related to the large leaf area of *A. altissima* (high values of satellite-derived LAI) during the drought period (from May to September), highlighting its growth potential and efficient resource preservation mechanisms during this limited period of precipitation (Lake and Leishman, 2004; Leishman et al., 2007). Furthermore, the LAI values in invaded cells were higher compared to non-invaded cells during very intense drought periods during summer. These drought periods are characteristic for Mediterranean ecosystems, and photosynthetic activity of the native vegetation is typically reduced (Gouveia et al., 2017). The adaptation of *A. altissima* to long drought periods is its ability to maintain very low evapotranspiration levels (Pepe et al., 2022). This could enhance the competitive capacity of *A. altissima*, thereby exacerbating the water stress to which native vegetation is exposed (Galmés et al., 2007). We found significantly lower

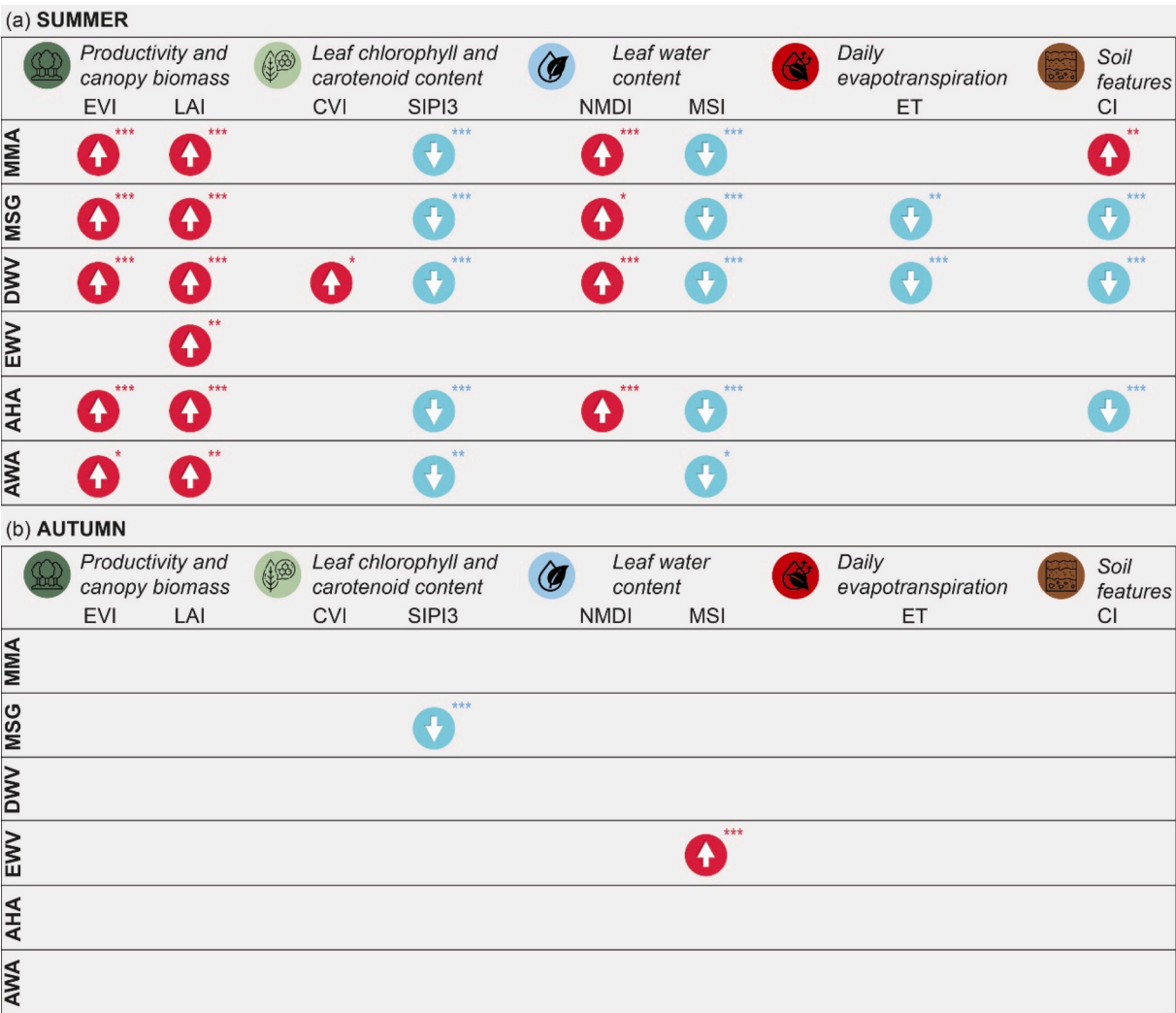


Fig. 5. Differences in spectral eco-physiological traits between invaded and non-invaded cells across Autumn and Summer. Red arrows indicate spectral eco-physiological traits with significantly greater values in invaded cells, while sky blue arrows indicate spectral eco-physiological traits with significantly lower values. *p*-value: * < 0.05; ** < 0.01; *** < 0.001. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

evapotranspiration values during summer in invaded cells. Such differences become particularly evident when comparing the summer evapotranspiration values of invaded cells and of non-invaded cells in Mediterranean sub-nitrophilous grassland and in deciduous woody vegetation. Moreover, these differences are accompanied also by summer differences for spectral leaf water content proxies (NMDI, MSI indices; Trifilò et al., 2004; Petruzzellis et al., 2018; Yin et al., 2021).

These effective water use mechanisms, due to a very efficient root system (Trifilò et al., 2004) and leaf adaptations (Petruzzellis et al., 2018), could prevent canopy stress during summer drought with high solar irradiation. This is highlighted by summer differences in leaf chlorophyll and carotenoid content between invaded and non-invaded cells. In particular, the lower values of SIPI3 index (i.e. the ratio between carotenoid chlorophyll) of *A. altissima* suggest that this invasive non-native tree does not reduce photosynthetic activity during the summer season (Granata et al., 2020).

The evidenced drought resistance as well as the high productivity and photosynthetic efficiency of *A. altissima* could be indicators of enhanced invasive potential and they pose a significant threat to Mediterranean vegetation, especially in the context of future climate change (Trájer et al., 2016), which is expected to bring higher temperatures, decreased precipitations, and increased aridity to the Mediterranean

region (Carvalho et al., 2022).

Another indication of the competitive advantage of *A. altissima* in Mediterranean areas is given by the lower bare soil values observed in the summer season compared to other native vegetation classes (i.e. MSG, DWV, AHA classes). This is likely related to its higher productivity and tendency to form dense mono-specific stands (Isler et al., 2023).

To summarize, *A. altissima* invasion in Sardinia alters eco-physiological traits, with higher productivity, drought resistance, and efficient resource use during dry summers. These traits, estimated by a remote sensing approach, enhance its invasive potential and threaten Mediterranean ecosystems, especially under climate change.

4.3. Limitations of the research and way forward

Our results demonstrate that the workflow developed in this study holds significant potential for analyzing the spectral eco-physiological traits of *A. altissima* and its competitive advantage over native vegetation. However, the workflow also reveals common methodological limitations. Firstly, it can be effectively applied only to those non-native species which form dense and quite large monospecific patches that can be monitored using spatial resolution data with a cell size of 20 m² resulting from the combination of S2 and S3 imagery. Consequently, this

approach allows us to estimate the alterations of eco-physiological traits only in advanced stages of invasion. The use of satellite data with finer spatial resolution for both multispectral data (e.g. constellations such as PlanetScope, WorldView, SkySat, etc.; Marzialelli et al., 2022) and thermal imagery (e.g. new satellite constellations such as HotSat-1; SatVu, 2025) could enable to capture alterations of eco-physiological traits even at early stages of invasion. These are, however, currently only partially available in the open domain (only for research purposes). Unmanned Aerial Vehicles (UAVs) provide very fine multispectral and thermal data for the detection of a wide range of non-native plant species, from herbaceous plants to trees in all stages of invasion. However, their effective application necessitates a meticulously designed work plan tailored to specific sampling periods and spatial constraints (Bolch et al., 2020). These limitations can be addressed through advanced upscaling techniques that integrate UAV-based data with satellite imagery, enabling broader spatial and temporal coverage (Gupta et al., 2024; Kattenborn et al., 2019; Marzialelli et al., 2022).

In addition, the spectral coverage of multispectral S2 imagery only allows to capture a limited number of spectral eco-physiological traits, while the use of hyperspectral sensors (Dao et al., 2021; Labonté et al., 2020; Skowronek et al., 2017) could be exploited in overcoming these limitations. These limitations varied widely depending both on indices/algorithms and on vegetation types (Xue and Su, 2017). Previous studies demonstrated that the LAI calculated by “Biophysical processor Sentinel-2” tool in SNAP showed from moderate to high concordance with LAI calculated in situ (Kganyago et al., 2020; Pasqualotto et al., 2019). Furthermore, previous studies proved that EVI evidences high resistance for saturation (Gao et al., 2023), CVI shows high sensitivity for chlorophyll concentration (Gao et al., 2024), MSI is highly effective to assess the state of leaf water content (Srinet et al., 2019; Watt et al., 2021), and CI is particularly efficient to represent bare soil and organic matter content (Bachauoui et al., 2014). Moreover, the Sen-Et plugin is a robust surrogate of ET when the ET is quantified on pixel composed of single and homogenous vegetation types (Burchard-Levine et al., 2021). These results confirmed the importance of using these spectral eco-physiological traits to analyze their seasonal differences between native and invaded vegetation using S2 and S3 imagery. On the contrary, SIPI3 highlights swift saturation of their values making it difficult to discriminate vegetation types in dense forests (Gao et al., 2024). In addition to this, NMDI does not distinguish the effects of drought on soil or on vegetation in areas with moderate vegetation coverage, confirming the importance of analyzing only areas with high values of fractional cover (Wang and Qu, 2007).

In the future, the growing availability of high-resolution RS data through free cloud-based platforms (e.g. Google Earth Engine datasets; Yang et al., 2022), combined with advancements in high-performance algorithms and tools (e.g. super-resolution techniques; Dong et al., 2016), will provide innovative approaches for analyzing the eco-physiological traits of non-native plants across all life forms and invasion stages (introduction, establishment and spread). These developments will also enhance understanding of their competitive advantages over native vegetation.

Despite these limitations, the proposed methodological approach exhibits substantial efficacy and robustness in pinpointing the spectral eco-physiological traits that promote the invasion of *A. altissima*. It could be applied to other invasive non-native plants to explore the eco-physiological traits that induce competitive advantage on native communities as our workflow is based on freely available remote sensing data and free and open-source software. In future studies, this approach could be developed further by using multispectral, thermal and hyperspectral imagery with enhanced spatial resolution and by exploiting advanced methods of trait retrieval.

5. Conclusions

This study developed an innovative methodological approach based

on free remote sensing data (i.e. Sentinel-2 and Sentinel-3) to identify and to describe the temporal trend of spectral eco-physiological traits in 20 m² sized cells invaded by *A. altissima* on the Mediterranean island of Sardinia. Furthermore, this methodological approach based on remote sensing allowed us to estimate the seasonal differences in spectral eco-physiological traits between invaded and non-invaded cells across the vegetation classes affected by *A. altissima* invasion in Sardinia. The seasonal differences in spectral eco-physiological traits captured the competitive advantage of *A. altissima* on Mediterranean native vegetation in the course of the seasons. This methodological approach, even with a few limitations mainly due to coarse resolutions of Sentinel data, is certainly an effective approach to directly monitoring the invaded areas on a large scale and the traits promoting the spread of *A. altissima* as required by EU Regulation no. 1143/2014. This remote sensing approach highlighted that *A. altissima* exhibits high productivity, biomass, and leaf water content, with low drought stress during summer, confirming its drought resistance. Furthermore, the larger leaf area of *A. altissima* during the summer drought period suggests a higher growth potential, giving it a competitive advantage. Finally, lower evapotranspiration rates of *A. altissima* compared to native vegetation demonstrate its water-saving mechanisms, crucial for climate change adaptation. Such remote sensing approaches could support management activities by giving insights into functional aspects of *A. altissima* invasion.

Therefore, the methodological approach proposed can be a very effective tool for localizing the areas with the most intense alterations in eco-physiological traits and also to highlight sites where to conduct field measurements to limit, contain and monitor these alterations caused by *A. altissima*. The use of free available remote sensing data with broad spatio-temporal coverage together with open source software ensures transferability to other sites and to other invasive plant species that alter ecosystem functioning.

CRedit authorship contribution statement

Flavio Marzialelli: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Vanessa Lozano:** Writing – review & editing, Writing – original draft, Validation, Supervision, Investigation, Data curation. **André Große-Stoltenberg:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Maria Laura Carranza:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Formal analysis. **Michele Innangi:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis. **Greta La Bella:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis. **Simonetta Bagella:** Writing – review & editing, Data curation. **Giovanni Riveccio:** Writing – review & editing, Data curation. **Gianluigi Bacchetta:** Writing – review & editing, Data curation. **Lina Podda:** Writing – review & editing, Data curation. **Giuseppe Brundu:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, 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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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecoinf.2025.103080>.

Data availability

The data utilized for the analysis were obtained from open-access resources. The occurrence data of *Ailanthus altissima* were sourced from a dataset of field campaigns from 2023 to 2024 (available on request) and a dedicated iNaturalist project “*Ailanthus altissima* Sardinia” (<https://www.inaturalist.org/projects/ailanthus-altissima-sardinia>). The Sentinel-2 and Sentinel-3 imagery were download by repository of Sentinel imagery of the European Space Agency (ESA), the Copernicus Data Space Ecosystem (<https://browser.dataspace.copernicus.eu>). The “Carta della Natura” map for Sardinia region was obtained by Istituto Superiore per la Protezione e la Ricerca Ambientale (ISPRA, <https://www.isprambiente.gov.it/it/servizi/sistema-carta-della-natura-cartografia/carta-della-natura-alla-scala-1-50.000/sardegna>). The meteorological data from the European Centre for Medium-Range Weather Forecasts in particular ECMWF reanalysis 5 (ERA-5) dataset were downloaded from the Copernicus Climate Change Service (<https://cds.climate.copernicus.eu/#/home>). The Land Cover map of 2015 with 100 m of spatial resolution was downloaded from the Copernicus Land Monitoring Service (<https://land.copernicus.eu/en/products/global-dynamic-land-cover>).

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