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Assessing the effect of *Tamarix* spp. invasion on ecosystem function using optical traits and hyperspectral remote sensing



Sustainable Development – *Environmental Change and Ecosystems*

Master's Thesis

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ABSTRACT

Invasive species are a significant economic and ecological threat, which is growing with climate change, land use change, and increasing global trade and travel. Hyperspectral remote sensing can be used to estimate the increasing ecosystem impacts of invasions, enabling early detection and prompt management. Plants traits, measurable characteristics connected to plant growth, survival and reproduction, have been linked to both invasiveness and ecosystem service provision. Optical traits, those measurable with spectroscopy, were used to assess the effects of invasion on native ecosystem functional trait values. We investigate invasion-induced trait replacement on the landscape scale in the Sonoran Desert, Arizona, US, by assessing if optical traits can be differentiated between invasive tamarisk (*Tamarix* spp.) and native palo verde (*Parkinsonia* spp.).

Field data and predictive algorithms of species presence were combined with handheld and airborne spectroscopy to measure trait values of each species and test whether they varied significantly by species. *Tamarix* spp. was consistently differentiable from *Parkinsonia* spp. at reflectances below 1350 nm, and in the short-wave infrared (>1940 nm). Given this spectral separability, vegetation indices were then used to measure each trait. *Tamarix* spp. showed significantly higher vegetation index values for all measured traits, namely chlorophyll, leaf area, water content, lignin-cellulose, and salinity tolerance, although less strongly for water content.

Indicators were constructed using principal component analysis to combine and weight the most robust indices for each trait. *Tamarix* spp. was significantly associated with every indicator of invasiveness and the summed invasiveness score for the ground-truthed data and the combined species presence map using both algorithms. However, the Mixture Tuned Matched Filtering classification showed *Parkinsonia* spp. to have significantly higher invasive trait scores.

Finally, indicators were mapped to illustrate trait hotspots, using total invasiveness score maps, and using indicators as RGB bands. Highest invasive trait values tended to correlate with larger patches of vegetation. The difference between the species, however, was not as strong as expected – vegetation sparseness and drought conditions may have reduced reflectance and trait values. Therefore we can only make general, directional assessments of the impact of invasion on optical traits and in turn ecosystem effects. However, the study demonstrates a transferable method with the potential to track non-species specific invasion effects in native populations, using traits that can be linked to ecosystem processes and services, providing another tool in the management of invasives.

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ABBREVIATIONS

See tables in the methods section for indices and their abbreviations.

ASD	Analytical Spectrum Devices
AVIRIS	Airborne Visible/Infrared Imaging Spectrometer
CSTARS	Centre for Spatial Technologies and Remote Sensing
CWC	Canopy Water Content
DOS	Dark Object Subtraction
EDRR	Early Detection and Rapid Response
ENVI	ENvironment for Visualization of Images
EWT	Equivalent Water Thickness
FLAASH	Fast Line-of-Sight Atmospheric Analysis of Hypercubes
IAS	Invasive Alien Species
LAI	Leaf Area Index
MLC	Maximum Likelihood Classification
MNF	Minimum Noise Fraction
MTMF	Mixed Tuned Matched Filtering
NIR	Near Infrared
PCA	Principal Component Analysis
REIP	Red Edge Inflective Position
ROI	Region Of Interest
RS	Remote Sensing
RWC	Relative Water Content
SAM	Spectral Angle Mapping
SWIR	ShortWave InfraRed
VIS	VISible Light
YPG	Yuma Proving Ground

INTRODUCTION

As we enter the sixth mass extinction, biodiversity loss continues to accelerate (Chapin III et al., 2000; Millennium Ecosystem Assessment, 2005). This loss degrades both the resilience of ecosystems to disturbance, as well as the functioning of provisioning, regulating and supporting ecosystem services vital to human wellbeing (Folke et al., 2004). Invasive alien species (IAS) are non-native species with a rapid spread potential that can negatively affect, ecologically, environmentally or economically the habitats into which they have been introduced (Masters & Norgrove, 2010). Identified as one of the main drivers of global biodiversity loss, IAS are therefore a significant and growing problem (Masters & Norgrove, 2010); with the current rate and diversity of invasions, driven by global change, being unprecedented in the fossil record (Ricciardi, 2007).

INCREASING INVASIONS

Several factors have accelerated the problem of IAS. Some non-native species can establish and become invasive with sufficient propagule pressure, that is, the number and frequency of introductions. The increasing spread of introductions over a wide range of areas makes it more likely that suitable conditions for establishment will be found (Simberloff, 2009). Natural self-introduction or colonisation, for example via wind or animal transport, occurs slowly (Theoharides & Dukes, 2007). In contrast, human-mediated introduction, both deliberate and unintentional, can be much more rapid, and is increasing (Hulme, 2009), non-native introductions in Europe for example growing exponentially since the 1850s (Pyšek et al., 2009). Corridors such as roads, tracks and waterways dramatically enhance the likelihood of invasion (Mortensen et al., 2009), such infrastructure is rapidly expanding, exposing wilderness areas, particularly in emerging economies, to IAS (Masters & Norgrove, 2010). Combined with the continued expansion of tourism, air transport, and worldwide trade, propagule pressure and invasion is heightening dramatically (Hulme, 2015).

Increasing global change, in terms of climate, nutrient cycles, and land use, aggravates the problem of IAS (Dukes & Mooney, 1999). Related changes in temperature, water availability and CO₂ concentration can stress ecosystems and increase the chances of successful invasion (Simberloff, 2000). Climate change will potentially:

1. Change transport and introduction mechanisms of non-natives
2. Lead to the establishment of new IAS
3. Change the distribution and impacts of existing IAS
4. Change the effectiveness of control strategies

(from Hellmann et al., 2008)

Global change also makes invasions even more unpredictable. While in some regions, invasion risk may decline and recovery potential increase (Allen & Bradley, 2016), the species range shifts caused by climatic and land use changes will create new invasion hotspots around the world (Bellard et al., 2013; Bradley et al., 2010). These range shifts will also make the differentiation of harmful invasion and natural range expansion or colonisation more difficult, and with it the tracking of IAS over space and time (Walther et al., 2009). Global changes lead generally to the increasing prevalence and impact of invasions (Bradley et al., 2010); the very impacts of IAS can then feedback into further global change, for example, through the alteration of the carbon balance of an ecosystem.

INCREASING IMPACTS

But what makes IAS so problematic? Lacking the co-evolved local competitors, parasites and pathogens that would naturally regulate their numbers, and potentially able to exploit resources natives cannot, IAS can thrive (Colautti et al., 2004; Torchin et al., 2003; Wolfe, 2002). IAS can then outcompete native flora for limited water, sunlight and nutrient resources, displacing and threatening local populations with extinction (Mooney & Cleland, 2001). Species which may have provided important habitats for local biota can be lost (Belnap et al., 2014).

The common traits of invasive plants: rapid growth, strong dispersal mechanisms, and wide tolerances, make them predisposed to such environmental change, and allow them to capitalise on any disturbances that follow (Bradley, et al., 2010; Dukes & Mooney, 1999). Increased nutrient availability, for example from nitrogen deposition, also favours IAS over local plants adapted to resource poor soils (Dukes & Mooney, 1999).

While invasions can cause local and global biodiversity loss, this direct effect is often difficult to separate from the numerous other associated ecosystem impacts (Gurevitch & Padilla, 2004). The invasion of, or impact upon, ecosystem engineers (species with a significant role in the physical structure and processes of an ecosystem) will have wide-ranging effects (Baiser et al., 2008). Local environmental conditions can be changed or degraded, from the allelopathic effects of individual species (Herrera et al., 2016), to carbon and nutrient cycling (Jackson et al., 2002; Liao et al., 2008), to wider changes to water tables, local climatic conditions, and fire regimes (Brooks et al., 2004; Pimental et al., 2002). Furthermore, hybridisation with local plants, in general, reduces total genetic material stocks and increases extinction risk of rare taxa (Ayres et al., 1999; Mooney & Cleland, 2001; Todesco et al., 2016). Around 42% of threatened or endangered species are at risk primarily because of invasive species (Pimentel et al., 2005).

Certainly, not all invasions are equal, even involving the same IAS, given the differences in local environmental and ecological conditions (Gurevitch & Padilla, 2004). IAS do not always lead to local extinctions; invasive plants, particularly, can increase species richness in the short-term on the sub-regional scale (Sax et al., 2002; Sax & Gaines, 2008). In the long-term the situation is even more uncertain: plant extinctions related to invasion can have time lags of hundreds of years, which can create an unforeseen 'extinction debt' for the future (Sax & Gaines, 2008; Tilman, et al., 1994). As Gurevitch & Padilla (2004) highlight, there is a lack of evidence for widespread extinction following plant invasion, and the focus upon aliens, rather than, for example, the maintenance of ecosystem services, can be unhelpful.

Ecosystem services are the services and products of ecological systems directly and indirectly critical to both human welfare and Earth's life support system (Costanza et al., 1997). Economic effects of IAS can also be high: from production loss in agriculture and forestry, decreasing recreational and tourist revenues, to mitigation and recovery costs (Pimentel et al., 2005; Simberloff, 2000). Direct costs of invasive species and their management in the US alone reach around \$120 billion per year, excluding the degradation of ecosystem services (Pimentel et al., 2005); globally costs exceed those of natural disasters (Ricciardi et al., 2011). Conversely, IAS can also have positive effects on these services – reforestation and reclaiming eroded and polluted land more effectively than natives (Daehler & Gordon, 1997), providing habitat and food for other species, replacing the ecosystem functions of extinct flora and potentially more likely to persist following environmental change (Schlaepfer et al., 2011). However, even these positive effects are controversial, Vitule et al. (2012) claiming they are infrequent, transient and often overstated. Therefore, assessing net effects of invasion on ecosystem services is an important and increasingly studied area (Charles & Dukes, 2007; Dickie et al., 2014; Pejchar & Mooney, 2009).

MANAGEMENT AND REMOTE SENSING

Early detection and rapid response (EDRR) are key to managing invasive species with minimum ecosystem damage and economic cost (Kaiser & Burnett, 2010; Mehta et al., 2007). Rapid removal also prevents the potential for unexpected 'surprises', such as another, previously suppressed, non-native becoming invasive, or longer-term effects such as extinction debt (Caut et al., 2009). Localised populations can be eradicated before they spread, techniques for which have become increasingly successful (Genovesi, 2011). Management of more established invaders is more difficult – irreversible changes may have occurred, making control the only feasible option; success necessitates careful restoration planning and ongoing monitoring for reinvasion (Simberloff et al., 2013).

EDRR is built into new frameworks for invasive species management, such as those implemented by the US Department of Agriculture – these recommend standardised strategies and the development of cost-effective detection tools (USDA, 2013). Much detection is still ground-based, but with the rapid spread of IAS, these data rapidly become obsolete (Jarnevich et al., 2013). Extensive, non-targeted detection is not cost-effective (Kaiser & Burnett, 2010). Remote sensing

(RS) offers a solution: large areas can be monitored in a short time period, particularly important in wilderness areas where field detection would be impractical (Hestir et al., 2008; Hunt et al., n.d.; Nagendra et al., 2013).

The applicability of RS to map IAS will depend on its 'detectability', for example whether distinct differences in phenological leaf or flower colouration, 3D structure, or biochemical composition exist (Gavier-Pizarro et al., 2012; Houborg et al., 2015; Mehta et al., 2007). One way of detecting plants is through their functional traits – the measurable biochemical, physical and structural characteristics of plants which impact their growth, survival and reproduction (Violle et al., 2007); characteristics which can be linked to leaf and canopy spectral reflectivity (Figure 1; Ustin & Gamon, 2010). Therefore RS can also go beyond merely mapping applications to provide quantitative estimates of species and community traits, ecosystem processes, and the effects invasion thereon (Lavorel et al., 2011). The relationships between plant traits and their spectral profile can then be used for wide-scale automated and systematic monitoring of invasions and their ecosystem impacts (Ustin & Santos, 2010). Hyperspectral imagery, utilising many narrow contiguous bands of the electromagnetic spectrum, maximises the detectability of a species and allows the distinction of many different traits – structural, phenological and physiological, which can then be associated with plant function and condition (Ustin & Santos, 2010; Vane & Goetz, 1993).

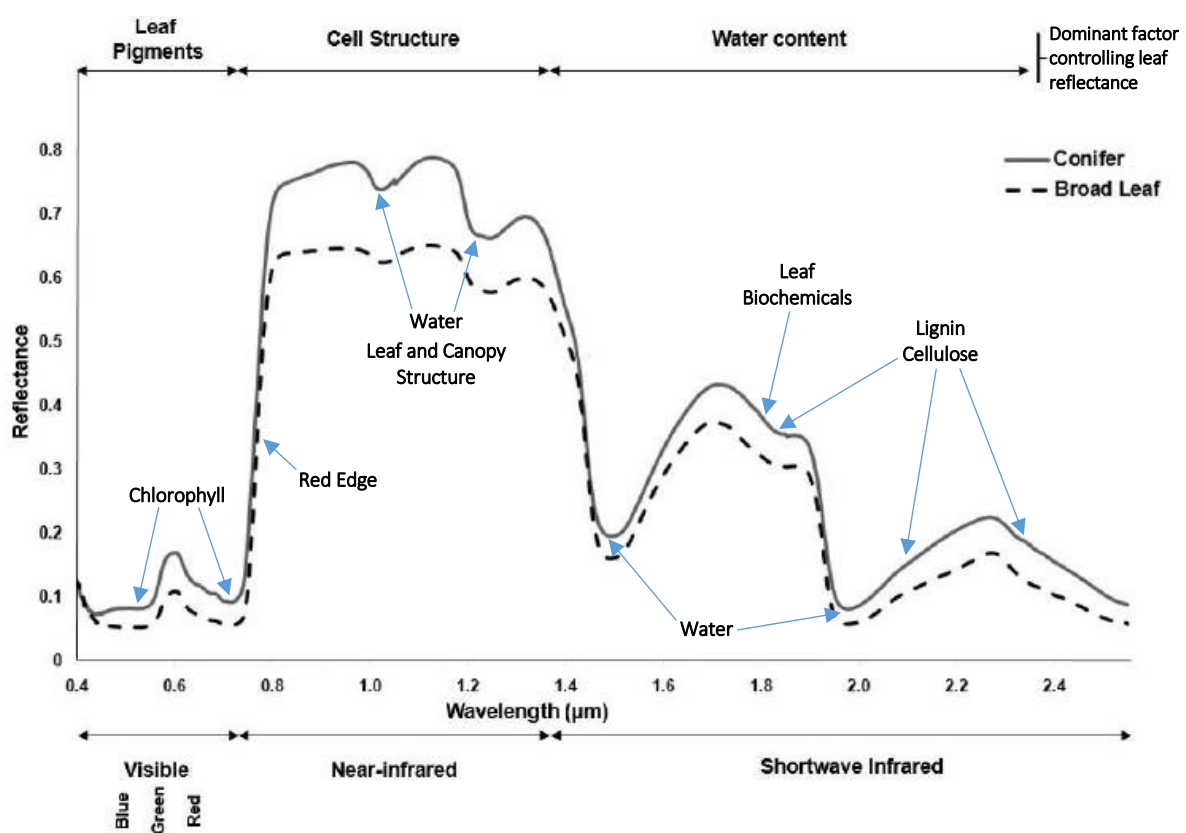


Figure 1. Conifer and broad leaf spectral signatures highlighting reflectance peaks and troughs characteristic of plant constituents, namely chlorophyll, water, lignin, leaf and canopy structure (modified from Cárdenas et al., 2015). The spectral signature has three main regions: visible (400–700 nm, VIS), related to foliar photosynthetic pigment absorption, dominated by chlorophylls; near infrared (700–1300 nm, NIR), related to leaf structure; and shortwave infrared (1300–2500 nm, SWIR), related to water, protein and other biochemical absorptions (Homolová et al., 2013).

TRAITS RELATED TO INVASION

Invasive success is also based upon traits: those of the introduced species which allow them to outcompete native species – *invasiveness*; and those of the invaded ecosystems which provide space or resources for the IAS to establish – *invasibility* (Richardson & Pyšek, 2006). Such traits are critical in explaining and predicting invasions (Rejmánek, 1996).

INVASIVENESS

Many traits potentially make IAS more successful. These are often related to:

- *Reproduction* – traits include short time before becoming reproductive, producing high numbers of viable seeds, and dispersing them over wide areas (Colautti et al., 2006; Kolar & Lodge, 2001; Pyšek & Hulme, 2005; Rejmánek & Richardson, 1996).
- *Environmental tolerance* – as well as broad physiological tolerances, this also includes resilience to and recovery from disturbance, such as fire, and phenotypic plasticity, the ability to alter growth form to suit local conditions (Daehler, 2003; Higgins & Richardson, 2014; Rejmánek, 1996; Turner et al., 2015).
- *Competition* – these traits allow for established IAS to outcompete natives. This ranges from faster growth and height, to being less affected by enemies, to the ability to utilise unused local resources, for example through a deeper root system (Colautti et al., 2006).

While traits can predispose a species to become invasive (Richardson & Pyšek, 2006), few are consistently associated with invasiveness (Alpert et al., 2000; Colautti et al., 2006; Williamson & Fitter, 1996). Theoharides & Dukes (2007) suggest that common key processes and filters which control invasion success can be identified by looking at specific invasion stages (transport, colonization, establishment and spread) – different traits will be important at each stage. For example, vegetative and asexual reproduction may enhance survival at low population densities, but wide seed dispersal would aid further spread when established (Kolar & Lodge, 2001). Which traits aid invasion will also depend on the invaded environment – while generalists typically perform best (Richardson & Pyšek, 2006), stress, disturbance, and competition, for example, can conversely allow species with more extreme features to take advantage (Pyšek & Richardson, 2010).¹

INVASIBILITY

Many factors affect ecosystem vulnerability to invasion. Climatic and environmental conditions relative to the tolerances of the introduced species will be critical – e.g. temperature and precipitation (maximum, minimum and seasonal distribution), light, and soil conditions (pH, waterlogging, porosity, salinity etc.). Resource availability is also important: increased invasibility is linked to both unused resources (Davis, et al., 2000; Davis & Pelsor, 2001), and intermittent resource enrichment (Seabloom et al., 2003). Disturbance, such as tree harvesting, treefalls, fire and flooding can also increase invasion success by opening up empty sites and increasing access to light and soil; along with resource availability, Colautti et al. (2006) found this the only significant predictor of invasibility.

Biodiversity has a controversial role in resilience to invasions – some argue higher diversity makes areas more susceptible due to instability or resource availability (Lonsdale, 1999; Stohlgren et al., 1999), others less, as niches are likely to be already filled (Fridley & Sax, 2014). Byers & Noonburg (2003) indicate biodiversity effects are scale dependent: at smaller-scales competition due to higher biodiversity decreases invasion success, while at larger-scales the resource availability which supports more biodiversity also increases invasibility. Habitat and pathway connectivity is also important: Vicente et al. (2014) found that while environmental conditions limit the number of species invading a particular site, pathways are the most important determinant in invasive species richness and composition.

Invasions can be extremely unpredictable, depending on the complexity of the ecosystem, non-linear feedbacks, time lags, and species specific traits (Williamson, 1999). Once a minimum viable population is established some species may be predisposed to immediate expansion, others may take decades or centuries to adapt to local conditions or hybridise

¹ Many other, often contrary indicators of invasive success exist – perhaps the most consistent is the historical success of an IAS (Kolar & Lodge, 2001). Successful invaders are more likely to come from areas of high genetic potential, with strong competition; being mainland rather than island species (Fridley & Sax, 2014). The region of origin was the only variable found by Kolar & Lodge (2001) to be consistently significantly related to invasion success. However, while some found closer related introduced species, or those from similar habitats more likely to be invasive (Colautti et al., 2006; Daehler, 2001; Duncan & Williams, 2002), others showed the more distinct the invader the higher impacts and the greater invasiveness (Rejmánek & Richardson, 1996; Ricciardi & Atkinson, 2004).

before rapid expansion (Simberloff et al., 2013). Furthermore, interaction drives some non-natives to become invasive, therefore relations with other species should be considered (Grosholz, 2005). Interaction can also take place with invasive pathogens and pests, which can stress ecosystems and open niches for plant invasion. Propagule pressure was found by Colautti et al. (2006) to be a significant indicator of both invasibility and invasiveness (in 55 of 64 studies); such is the relationship that 'propagule biases' may confound these other traits and patterns. It provides a better chance at being introduced into a suitable habitat, while introduction from a number of sources increases genetic variability and survivability (Lockwood et al., 2005).

TRAIT DETECTION

Therefore, numerous traits are related to the success of IAS. Many of these, optical traits, can be detected and measured by hyperspectral RS – traits which directly or indirectly affect the reflectance of the plant at specific wavelengths of the electromagnetic spectrum, producing an individual spectral signature (Figure 1; Ustin & Gamon, 2010). For example, chlorophyll in leaves can be directly detected by absorption in the red wavelength (around 630 nm), allowing estimation of photosynthetic processes (Gitelson & Merzlyak, 1997).

Commonly used optical traits and their functions are summarised in Table 1. Even traits which are not directly observable, such as pollination, can be differentiated based on their influence on the spectral signature of a species (Feilhauer et al., 2016). Therefore traits ranging from growth form, to flammability, to photosynthetic pathway can be assessed (Homolová et al., 2013). While the strength of optical traits will vary with environmental factors, such as elevation (Asner et al., 2016), generally interspecific is larger than intraspecific variation (Asner et al., 2014), and in the right circumstances—such as sufficient vegetation density, and adequate canopy illumination IAS signatures can be differentiated from native ones (Asner et al., 2008).

Table 1. Key functional plant traits remotely observable from space (modified from Jetz et al., 2016)

Trait	Trait definition	Trait functions and associations	Spectral region
<i>Chlorophyll</i>	Green pigments	Converts light into stored chemical energy, therefore relate directly to the primary productivity of a plant. Associated with other traits, such as nutrient status, as it incorporates much of leaf nitrogen (Filella et al., 1995), and vegetation stress and senescence (Merzlyak & Gitelson, 1995).	400–700 nm
<i>Carotenoids</i>	Orange and yellow pigments	Involved in xanthophyll cycle for dissipating excess energy and avoiding oxygen radical damage in stress conditions (drought, chilling, low nutrients).	400–700 nm
<i>Leaf Area Index</i>	Leaf area per unit ground area	Important structural parameter to quantify energy and mass exchanges e.g. photosynthesis, transpiration, respiration, rainfall interception, and carbon and nutrient cycling. Related to primary productivity and evapotranspiration. (Gong et al., 2003)	400–1300 nm
<i>Leaf water content</i>	Water volume per unit leaf area	Critical for photosynthesis, and therefore relates to primary productivity. Linked to flammability (Yebra et al., 2013).	1300–2500 nm
<i>Lignin-cellulose</i>	Complex organic phenol and glucose polymers	Provides structural stability – lignin is used in secondary cell wall formation in woody plants, cellulose forms cell walls (Jung et al., 2015). Lignin provides rigidity, acts as a barrier to pests and pathogens, cold and other stresses, and is used within xylem for water transport (Boudet, 2000). Negatively correlated with litter decomposition (Godoy et al., 2010).	1300–2500 nm
<i>Nitrogen</i>	Concentration of elemental nitrogen in leaf or canopy	Important for photosynthesis and other metabolic processes as a constituent of plant enzymes.	1300–2500 nm
<i>Non-structural carbohydrates</i>	Assimilable products of photosynthesis (sugars and starches)	Indicator of tolerance to environmental stress.	1300–2500 nm

RESEARCH NEEDS

The intersection of plant traits, hyperspectral RS and invasion ecology provides an exciting avenue for research. Assessment of impacts often is on a small number of species, in temperate environments – not necessarily the research priority; measurement neglects effects on ecosystem services or environmental degradation (Hulme et al., 2013). RS, in particular the use of hyperspectral data, is currently underused in invasion ecology (He et al., 2011), despite its clear value for spatial and temporal coverage. The identification of effective spectral regions and the algorithms based upon these for robust vegetation classification remains open (Houborg et al., 2015).

The use of functional traits to differentiate IAS from native species has been found to increase mapping accuracy, and can be increasingly successfully assessed from space (Niphadkar & Nagendra, 2016). While phenological and structural traits have been studied, physiological traits have had limited utilisation (Niphadkar & Nagendra, 2016). Using hyperspectral imaging to map plant traits can help to fill the knowledge gap between field studies and regional climate modelling, to predict invasion likelihood on a landscape-scale more suitable for management purposes (Asner et al., 2015). Establishing the relationship between current species (both native and non-native), their traits, and environmental conditions is critical; as the matching between functional traits and the target environment is the most consistent predictor of invasion success (Hayes & Barry, 2008).

Here, *Tamarix* spp.² (commonly tamarisk, or salt cedar), a known invasive in the US, but one for which low resolution RS has had limited effectiveness in previously mapping (Evangelista et al., 2009; Jarnevich et al., 2013), is used to explore the value of optical traits in differentiating an IAS and assessing the changes it makes to plant traits, which will in turn impact ecosystem services. Existing research focuses almost exclusively on *Tamarix* spp. in downstream riparian environments (Akasheh et al., 2008; Fletcher et al., 2011; Richardson et al., 2007). By comparing it with native co-occurring *Parkinsonia microphylla* (syn. *Cercidium microphyllum*, commonly yellow paloverde), we can explore its invasiveness in upland areas under drier conditions, an even more fragile environment. Current monitoring and recent distribution models have focussed on the regional or continental scale, often at low spectral resolutions (Cord et al., 2010; Jarnevich et al., 2013; Maruthi Sridhar et al., 2010; Morissette et al., 2006). Mapping and predicting the location of *Tamarix* spp. on the smaller landscape scale will have the most benefit for prioritising effective site-specific management.

CASE STUDY – TAMARIX SPP.

Several species of the genus *Tamarix* (Figure 2) are invasive across the western United States. With numerous traits linked to invasiveness, which give it the potential for severe ecosystem impacts, it provides an ideal case study. *Tamarix* spp. is by consensus one of the worst invasives in the United States (Zavaleta, 2000), the Nature Conservancy featuring it in their top twelve 'least wanted' (Stein & Flack, 1996), and the California Invasive Plant Inventory rating it as severe in terms of impacts, invasiveness and distribution (Cal-IPC, 2006).

Spreading shrubs or small trees, with pink to white flowers, and scale-like 1.5 to 3.5 mm long leaves, invasive *Tamarix* spp. usually grow around 6 m tall, and are found in salty, dry and riparian habitats (Lovich, n.d.). Native to Africa and Eurasia, *Tamarix* spp. was introduced to the US in the early 1800s, initially as ornamentals, then as a wind-break, for erosion control, and shade (Horton, 1964; Neill, 1985 in DiTomaso, 1998). It was recognised as invasive by the 1920s as it spread across the waterways of the southwest, growing explosively from the 1930s to now occur in every watershed in the southwest (Brotherson & Field, 1987; Everitt, 1998; Zouhar, 2003). Invasion has been linked to reduced flood

² For the purposes of this study, *Tamarix* spp. refers to all introduced *Tamarix* species, excluding *T. aphylla*. Classification of *Tamarix* species is complex, as the invasives become distinct from their native populations, and widespread hybridisation occurs (Gaskin & Schaal, 2003). The only easily visually identifiable species in the southwest US is *T. aphylla*, a much larger evergreen tree, which is not seriously invasive there, as it does not reproduce sexually in the climate (Allred, 2002), and is therefore not included in this study. The study area contains the highly invasive *T. chinensis*, seen as synonymous to *T. ramosissima* and *T. pentandra*, by Baum (1978 in Zouhar, 2003) – structural and DNA comparisons appear to confirm this (Allred, 2002; Gaskin & Schaal, 2003). Apart from *T. aphylla*, the other invasive *Tamarix* spp. generally share traits and can only be distinguished by close inspection of floral organs (Allred, 2002).

disturbance³, allowing *Tamarix* spp. to displace native flood-dependent trees such as cottonwood (*Populus* spp.) and willows (*Salix* spp.) (Perkins et al., 2016; Stromberg et al., 2007). Cattle raising can also have an impact: cattle graze natives cottonwood and willow preferentially, giving *Tamarix* spp. a competitive advantage (Stein & Flack, 1996).



Figure 2. *Tamarix chinensis* (source: Invasive Species Council of British Columbia, <http://bcinvasives.ca/invasive-species/identify/invasive-plants/tamarisk>, 11/12/2016)

TRAITS

Tamarix spp. has many traits which aid its invasiveness, summarised on Table 2. Its huge reproductive potential allows it to survive in the dispersed populations typical of introductions, and then rapidly spread. It can self-pollinate and propagate from woody fragments, as well as outcrossing through insect and potentially wind pollination (Brotherson & Field, 1987; Shmida, 1991). A mature plant can produce up to 500,000 seeds per year, with high viability, and long hairs which allow for long-distance wind as well as water distribution (Tomanek and Ziegler, 1960 in Brotherson & Field, 1987).

With its fast growth, shoots growing up to 4 m in one growing season (Davy et al., 2008), height, and extensive roots, *Tamarix* spp. can outcompete native woody species for light and water (Busch & Smith, 1995). Concurrently the allelopathic effects of salt deposition from its salt-glands can limit under-canopy species to halophytes (Brotherson & Field, 1987; Ladenburger et al., 2006) – although Lesica & DeLuca (2004) found no support for this around Fort Peck Reservoir, Montana, suggesting instead a fertilising effect.

It can thrive in numerous environments, from riparian uplands to intertidal salt marsh, an area previously not considered vulnerable to invasion (Whitcraft et al., 2007). It is tolerant of a wide range of environmental conditions: salt, alkali, wet and dry soils, and wide variations in soil and mineral gradients (Brotherson & Winkel, 1986; Glenn & Nagler, 2005). The primary root, measured to a depth of 30 m, allows it to survive with little to no surface water (Gatewood et al., 1950)⁴. It also resists disturbance, and can vegetatively resprout after fire, flood or herbicide treatment, while its flammable litter actively promotes the spread of wildfire (Busch, 1995; Warren & Turner, 1975). High levels of hybridisation were found at the edges of its distribution, potentially further increasing its ecological range and facilitating further invasion (Gaskin & Kazmer, 2009; Whitcraft et al., 2007).

³ Although Graf (1982) asserts sedimentation caused by flooding can also provide a suitable habitat for other species.

⁴ However, *Tamarix* spp. began to disappear when the water table dropped below a 10 m threshold (Horton & Campbell, 1974; in Graf, 1982); water table depth shown be a major predictor of its distribution (Graf, 1982). Despite this, it was still found to be better adapted to drought conditions than the natives of the floodplains of the Mojave Desert, Nevada (Cleverly et al., 1997).

Table 2. Invasiveness traits of *Tamarix* spp. (based on Brotherson & Field, 1987)

Reproductive	Source
Continuous seed production through growing season	Brotherson & Field, 1987
High seed output (>500,000 per individual per year)	Tomanek and Ziegler, 1960, in Brotherson & Field, 1987
High seed viability	Merkel & Hopkins, 1957
Long range seed dispersal adaptations for wind and water transport	Brotherson & Field, 1987
Cross-pollination by wind	Shmida, 1991
Self-compatible	Brotherson & Field, 1987
Vigorous vegetative reproduction capability	Brotherson & Field, 1987; Merkel & Hopkins, 1957

Competitive	
Allelopathic – salt dispersal	Brotherson & Field, 1987; Lesica & DeLuca, 2004
Tall (2 m+, up to 10 m) – shades competitors	DiTomaso, 1998
Deep and extensive root system	Merkel & Hopkins, 1957

Tolerant	
Tolerates wide range of environmental conditions	Brotherson & Field, 1987; Carman & Brotherson, 1982
Salt tolerant (>15000 ppm soluble salt)	Carman & Brotherson, 1982; Carter & Nippert, 2011, 2012
Alkali and other soil conditions tolerant	Carman & Brotherson, 1982
Vigorous root sprouter following fire, flood, cutting or herbicide treatment	Brotherson & Field, 1987
Ability to live in inundated (for 70 - 90 days) or dry soils (can survive almost indefinitely in absence of surface saturation)	Brotherson & Field, 1987; Everitt, 1980
Brittle stem, not easily drawn from ground	Brotherson & Field, 1987

IMPACTS

The impacts of *Tamarix* spp. invasion can be significant, particularly in fragile arid ecosystems. They will likely increase as climate change expands climatically suitable areas for *Tamarix* spp. across the US (Bradley et al., 2009). Riparian woodlands, which support the greatest biodiversity in arid ecosystems, are most threatened – bird, mammal and invertebrate diversity is significantly reduced when natives are replaced (Stein & Flack, 1996). Native cottonwoods and willows have been displaced from large sections of riparian ecosystems; the rapidity of colonisation has suggested riparian woodlands, such as on the Rio Grande, will become dominated by exotic shrubs in 50 to 100 years (Howe & Knopf, 1991). Displacement can occur from competition, changes to fire regime, and increasing local salinity.

Tamarix spp. can also dramatically alter the physical and chemical conditions of its environment. In the case of salt marsh invasion, naturally succulent-dominated areas around the Tijuana River estuary, California, have shifted to stands of woody trees (Whitcraft et al., 2007). Natural hydrology can be affected: local water tables lowered, and flood risk increased as dense stands block channels (Graf, 1982; Stein & Flack, 1996)⁵. Economic costs are also high – Zavaleta (2000) estimates eradication would have a net benefit of \$3.8 to \$11.2 billion over 55 years, given its impact on flood control, water availability, and wildlife. *Tamarix* spp. invasion was found to increase evapotranspiration by 300 - 460 mm per year, attributed to high leaf area (Zavaleta, 2000), and use substantial amounts of agricultural water (Brotherson & Field, 1987), although Glenn & Nagler (2005) found transpiration losses to be similar to natives along river corridors.

⁵ Findings are mixed however: active displacement and changes to river hydrology along the central Rio Grande are disputed by Everitt (1998), while Johnson, Kolb, & Medina (2010) found a greater abundance of all vegetation, including native understory species, at sites on the Verde River, Arizona, where *Tamarix* spp. has a minor presence.

However, there are major sources of uncertainty concerning invasion impacts – if and how long *Tamarix* spp. will remain invasive, how long negative effects will persist, and indeed the very nature of these negative effects (Schlaepfer et al., 2011). Several recent studies have contradicted the prevailing negative perceptions of *Tamarix* spp. Stromberg et al. (2009) argue *Tamarix* spp. has been ‘monstered’ in academia – a self-perpetuating vilification founded on an uncritical repetition of extreme impacts which are based upon outmoded and inflated sources; Chew (2009) suggesting *Tamarix* spp. has become a scapegoat for government water management problems. As Schlaepfer et al. (2011) highlight, this perception can impede the reporting of beneficial and neutral effects of *Tamarix* spp. Indeed, *Tamarix* spp. provides an important habitat for the federally endangered southwest willow flycatcher (*Empidonax traillii extimus*), 75.7% of riverine nesting sites in Arizona are in *Tamarix* spp., with fledgling success equivalent to native species (Ellis et al., 2008). It has also established habitats for tree nesting birds along the Grand Canyon where none have previously existed (Brown & Trosset, 1989). These uncertainties, however, provide the opportunity to investigate if the relative trait values concur with the prevailing negative perspective.

Early detection of *Tamarix* spp. is important to allow rapid management actions and the counteracting of negative effects of invasion. It can be managed by mechanical and chemical means, but multiple, labour-intensive treatments are required, and wider-scale spraying can have toxicity problems; while promising attempts at biological control have their own negative impacts (Dudley & Kazmer, 2005; Shafroth et al., 2005). Long-term recovery is possible, in particular with changes towards a more natural flooding regime, where native *Populus* spp. and *Salix* spp. can outcompete *Tamarix* spp. at the seedling stage (Sher et al., 2002). However, the benefits and costs of control are as unpredictable as invasion impacts (Sogge et al., 2008). If *Tamarix* spp. is indeed a passenger rather than a driver of change (Stromberg et al., 2009), then removal could simply leave depauperate habitats of little value, rather than stimulating recovery (Sogge et al., 2008).

PARKINSONIA MICROPHYLLA

Invasive optical traits of *Tamarix* spp. will be contrasted with an important co-occurring native species: *Parkinsonia microphylla* (syn. *Cercidium microphyllum*, commonly yellow paloverde, foothill paloverde or small-leaf paloverde; Figure 3; Warren & Turner, 1975). This is a woody upland species dominant on the uplands and alluvial plains of the Sonoran Desert, southwest US, but also present in nearby riparian areas (Niering & Lowe, 1984; Turner et al., 1995). They grow in arid to semi-arid climates with mild winters, hot summers, and biseasonal rain, requiring regular summer moisture (Turner et al., 1995).



Figure 3. *P. microphylla* (source: Leslie Landrum, Southwest Environmental Information Network <http://swbiodiversity.org/seinet/taxa/index.php?taxon=8100>, 12/12/2016).

It is slow-growing, living up to several hundred years (Bowers & Turner, 2002), and typically grows to 5 m, although it can reach 7 m (Turner et al., 1995). It is extremely drought tolerant: with extensive roots, tiny 1 mm wide leaflets minimising transpiration loss, and drought deciduous leaves and branches – the green photosynthesising bark allowing survival when leafless (Shreve, 1917; Turner et al., 1995). However, this reduces CO₂ uptake and productivity (Gibson, 1963 in Turner et al., 1995). Diebacks generally only occur in aging populations after severe summer droughts (Bowers & Turner, 2001).

Small pale yellow flowers occur in April and May, and are pollinated by insects, although flowering and seed crop will depend on rainfall, and it can reproduce asexually (Turner, 1963). With sufficient water soft pods of one to five large seeds are produced, spread by mammals, uneaten seeds forming a seed bank that can last several years (Bowers, 1994; McAuliffe, 1990). Only around 1.7% of seeds survive after germination given their sensitivity to drought and predation (Bowers & Turner, 2002).

The thin-barked stems are not resistant to fire – after the King Valley Fire, Arizona, all individuals charred over 10% of their surfaces were completely top-killed, only 0.4% resprouting (Esque et al., 2013). Resprouting after top removal is fair to poor, indicating a poor response to disturbance (Carr et al., 1986); 20 years may be required to recover to previous densities post fire (Rogers & Steele, 1980). These long recovery times make effective protection critical.

ECOSYSTEM IMPORTANCE

P. microphylla is critical to the structure of Sonoran desert scrub community, and is endemic to the region (Turner et al., 2005). This community is ranked as one of the highest priorities in rare plants inventories in California (Holland, 1986). The ecosystem is extremely shallow – *P. microphylla* represents both the climax, and the first to reappear from disturbance (Reynolds, 1962). *P. microphylla* acts as browse for mammals such as larger bighorn sheep and mule deer (Krausman et al., 1990; Seegmiller et al., 1990), and smaller jackrabbits and rodents, while also being a habitat for desert shrews and mice (Szaro & Belfit, 1987). It is also an important bird habitat (Kennedy, 1983), used for foraging significantly more than other species (Parker, 1986).

EFFECT OF INVASION ON OPTICAL TRAITS

The effect of *Tamarix* spp. invasion on native *P. microphylla* is therefore uncertain, depending on the contested properties of *Tamarix* spp. to, for example increase salinity and fire frequency, as well as invasion extent and the local ecological and environmental context. Everitt (1998) finds no evidence of the displacement of natives in the central Rio Grande, rather *Tamarix* spp. establishing in areas newly available. In contrast, Birken & Cooper (2006) show that *Tamarix* spp. was prevalent before river regulation on the Green River in Utah, suggesting active invasion. RS optical traits offer a way of estimating the effects of invasion by showing the changes in trait values with invasion.

Combining optical traits (Table 1) and traits related to *Tamarix* spp. invasiveness (Table 2) leaves several traits associated with established spectral features, which we can expect to show significant differences between the IAS and the native species. As invasive traits, they are all hypothesised to show higher values for *Tamarix* spp.:

- *Chlorophyll* – *Tamarix* spp. has higher reported rates of photosynthesis reported than other natives (Sher & Quigley, 2015), larger and more dense leaves, and also, given the links between chlorophyll and productivity, a faster growth rate
- *Leaf Area Index* – *Tamarix* spp. has larger leaves, which form a denser canopy
- *Leaf Water Content* – larger *Tamarix* spp. leaves have a high water content (Busch, 1995), and higher evapotranspiration rates, maintained through droughts by longer roots
- *Lignin-cellulose* – this relationship is more complex⁶ as concentrations and ratios vary significantly with age, growth stage and environmental conditions (Bajpai, 2016). *Tamarix* spp. as a taller, woodier tree could be expected to have higher values, although it is the more productive species, which lignin is typically inversely related to (Novaes et al., 2010). Given under-canopy litter will contribute to the reflectance shown, the increased

⁶ Reported values for the relevant *Tamarix* species were not found, although *P. microphylla* leaves ranged from 6.53 to 11.66% for lignin dry weight, and 22.94 to 41.28 % for cellulose in Arizona (Krausman et al., 1990) – illustrating the large intra-species differences. As a taller woodier tree, *Tamarix* spp. could be expected to have higher values of lignin – the taller *Tamarix aphylla* (7.85%) and *Tamarix articulata* (13.6%) both have higher mean percentages than *Parkinsonia aculeata* (7.48%), another native which shares many traits with *P. microphylla* (Al-Masri, 2013).

litter of *Tamarix* spp. will however mean that the slow to decompose lignin and cellulose are expected to show higher values.

- *Salinity* – *Tamarix* spp. both produces salt through its glands and is highly tolerant of saline conditions, more so than other riparian natives (Sher & Quigley, 2015).

These traits can then be linked to ecosystem services, de Bello et al. (2010) highlighting the connection between terrestrial plant traits and multiple ecosystem services from hazard prevention to water regulation and soil fertility. Combining the worst reported traits, replacement could worsen food and habitat value for local flora and fauna, increase fire frequency and salinity, decrease water levels. Mapping these traits, as Lavorel et al. (2011), can highlight hotspots where ecosystem services are particularly threatened by IAS, but can also identify areas in which they might be enhanced.

RESEARCH QUESTIONS

This research therefore aims to assess the changes in plant optical trait values on the landscape scale.

Firstly, in order to examine differences in optical traits, we must establish whether the selected invasive and native species can be spectrally separated, that is:

Do the reflectance properties of invasive Tamarix spp. and native Parkinsonia spp. differ significantly across the electromagnetic spectrum?

If they can, as is hypothesised given previously reported differences in their spectral signatures (see Figure 5), we then ask:

Which of the optical traits of invasive Tamarix spp. differ significantly from those of native Parkinsonia spp.?

We will explore the selected optical traits (above) to assess which show significant differences between the plants. We can next ask:

Does Tamarix spp. show higher measurements for these optical traits?

The methodology outlines the specific definitions of these traits, while Table 1 shows trait descriptions and related spectral regions. Utilising the most important spectral regions for each trait, those found to both separate the species and denote invasiveness, we can then construct mappable trait indicators. This will allow us to answer our final question:

What are the effects of Tamarix spp. invasion on plant optical traits on the landscape scale?

Assessing the effect on plant optical traits, will finally allow us to examine the potential effects of invasion on ecosystem functioning and services.

METHODS

STUDY AREA

Field and airborne environmental hyperspectral data for the study species were collected from southwest of Yuma Proving Ground (YPG), a U.S. army facility in southwest Arizona, United States. This area is located in the Sonoran Desert, a warm desert with an arid Mexican monsoon climate – typically clear skies, light surface winds, low precipitation and relative humidity. Average maximum temperatures reach 41.4 °C in July, while minimums fall to 5.94 °C in December (National Oceanic and Atmospheric Administration, 2017). Annual rainfall is 95 mm, with temporally and spatially variable convective storms in the dry season from April to June, and low intensity rainfall from Pacific frontal storms in the November to March wet season (National Oceanic and Atmospheric Administration, 2017; Sutfin et al., 2014). Such storms are critical to the recharge of local groundwater, and are followed by short growth periods of annuals and cryptophytes (CSTARS, 2004; Efroymsen et al., 2008).

Located several kilometres east of the Colorado River, it contains a wide range of landforms associated with the river plain, including alluvial plains and fans, as well as badlands and dunes with similarly heterogeneous soil characteristics (Bacon et al., 2008) and surface types ranging from bedrock and desert pavement to alluvial sediment (McDonald et al., 2009). Most perennial vegetation is concentrated around the intermittent channels in the desert washes (CTARS, 2004; Figure 4).

Local habitats are mainly xeroriparian – dry washes with very sparse vegetation. Xeroriparian vegetation is dominated by *Parkinsonia* spp., *Tamarix* spp. and creosote (*Larrea tridentata*), while white bursage (*Ambrosia dumosa*), Asian mustard (*Brassica tournefortii*) and saguaro cactus (*Carnegiea gigantea*) are also found across the site (CSTARS, 2004). As well as the rare *P. microphylla* community, local vegetation provides an important source of forage and habitat to much wildlife, including larger mammals, such as the desert mule deer (*Odocoileus hemionus crooki*) and endangered Sonoran pronghorn (*Antilocapra americana sonoriensis*) (Efroymsen et al., 2008; Morgart et al., 2005). Local riparian areas are an important stopover habitat for migratory birds (Fischer et al., 2012). As well as its importance as a habitat, remote sensing of IAS is of particular value here given the access restrictions due to military activity. The YPG has identified *Tamarix* spp. as a target weed, which has been expanding from the riverine and irrigated areas in the southwest of the site, into the desert washes to the east and north traditionally dominated by *Parkinsonia* spp., to the surprise of local ecologists (CSTARS, 2004).



Figure 4. *P. microphylla* dominated alluvial fan deposit east of Yuma, smaller plants are *A. dumosa* and *L. tridentata* (source: McAuliffe & McDonald, 2006)

DATA COLLECTION

Data collection and processing was performed by the Center for Spatial Technologies and Remote Sensing at the University of California Davis in 2002 and 2004 (detailed in CSTARS, 2004). The data consists of handheld field spectrometry and aerial imagery, referred to respectively as ASD when collected using the commercially available Analytical Spectrum Devices handheld spectrometer, and AVIRIS, corresponding to the NASA Jet Propulsion Lab Airborne Visible/Infrared Imaging Spectrometer. The ASD spectrometer provides the most precise data, at the greatest spectral resolution, so is expected to provide the greatest spectral separability between the species, and the most accurate detection of traits; but sample size is limited by the need to collect data from the field. Conversely, AVIRIS data overcomes the sampling limitation by providing wall-to-wall sampling, allowing for the collection and analysis of spectral data on the landscape scale, if at a coarser spatial and spectral resolution. Spectra are generally of a similar shape (examples from this dataset shown in Figure 5), but, amongst others, atmospheric and mixed-pixel effects will cause differences – for example the water absorption features at 970 nm and 1200 nm are usually stronger in the airborne data (Ustin & Santos, 2010).

Field data were collected on 21-23 April 2002 using an ASD spectrometer with a spectral range of 350 to 2500 nm and an average bandwidth of 1 nm. This comprised of 10 samples each, taken from 1 m above the canopy, from seven *Tamarix* spp. plants, three *P. microphylla*, and three similar *P. florida* plants. Bands from 1364 to 1377 nm, and 1815 to 1937 nm (inclusive) were removed, due to the spikiness of data which was uncharacteristic with reference spectra (from Ustin & Santos, 2010).

AVIRIS imagery consisted of two flightlines over YPG (Figure 6), collected on 14 April 2002, from an altitude of 4572 m, with a width of around 2.9 km and a nominal spatial resolution of 4 m. This was sufficient to distinguish near homogenous patches of the target IAS (Ustin & Santos, 2010). The AVIRIS is an aircraft mounted sensor which collects data in 224 contiguous spectral bands from 400 to 2500 nm and an average bandwidth of around 10 nm (Vane & Goetz, 1993). The usable portions were around 18 and 15.75 km in length. Further details on collection and calibration methods are detailed in Ustin & Santos (2010).

The raw AVIRIS flightlines were preprocessed using ENVI version 5.2 (Environment for Visualization of Images; Exelis Visual Information Solutions, Boulder, Colorado), detailed in Appendix 1. The irrigated agricultural area to the southwest of the flightlines was excluded from analysis, given its unrepresentativeness of the rest of the area (CSTARS, 2004). This excluded many *Tamarix* spp. data points, but focuses the study on differentiating *Tamarix* spp. traits under more typical conditions, and within wash areas where the effects of its invasion on ecosystem function are less known. The reflectance information from the pixels containing *Tamarix* spp. and *Parkinsonia* spp. was then extracted. The regions of interest (ROIs) shapes of the ground-truthed pixels represent the most accurate classifications, with 70 samples of *Tamarix* spp., 59 of *P. microphylla* and 100 of the similar *P. florida* taken from across the site (Figure 7). These were mapped in April 2004 using a GPS, after initial field data from unusable areas of the flightlines or the irrigated southern section was deemed inadequate at representing the full spectral variability of the species (CSTARS, 2004).

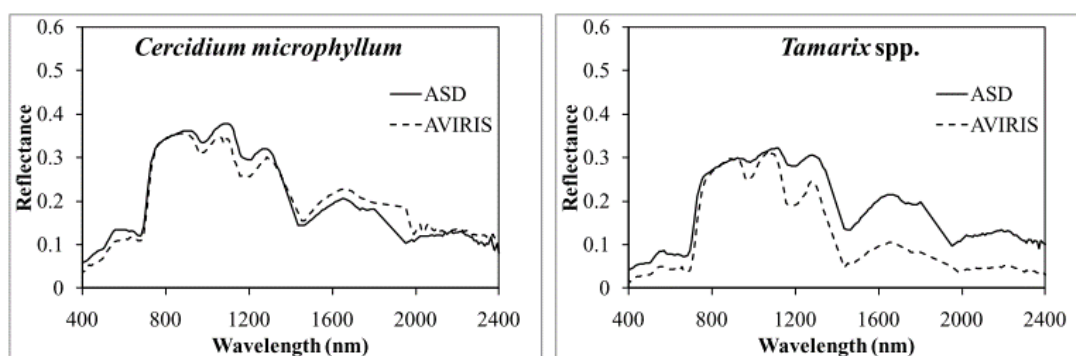


Figure 5. Reflectance of *P. microphylla* (labelled as *C. microphyllum*) and *Tamarix* spp. for handheld (ASD) and airborne (AVIRIS) spectrometers (source: Ustin & Santos, 2010)

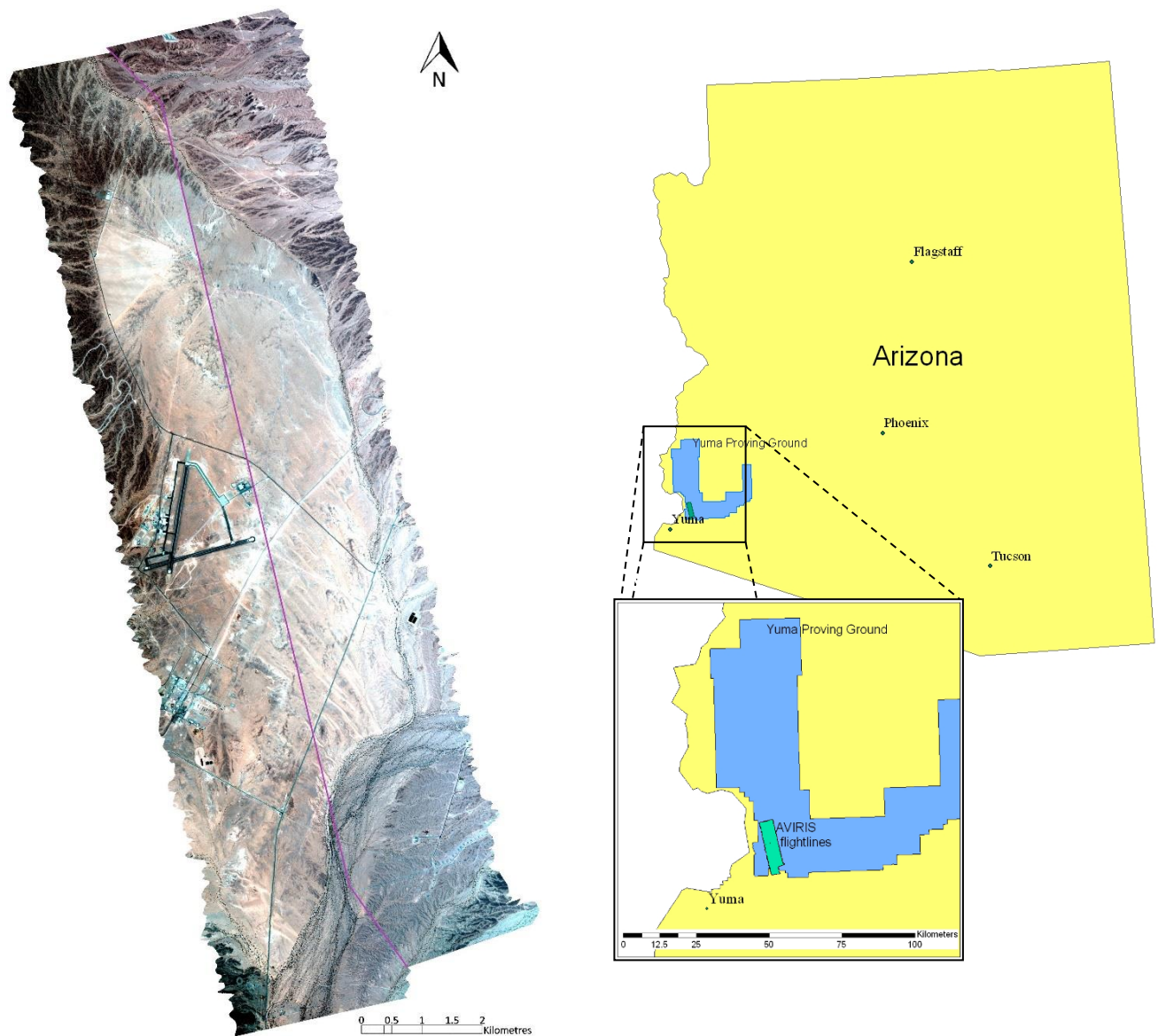


Figure 6. Final mosaicked image of AVIRIS flightlines taken within Yuma Proving Ground (left, line delineates east and west flightlines). The map, right, indicates the location of the study area within Arizona (source: CSTARS, 2004).

VEGETATION CLASSIFICATIONS

To increase the sample size, and allow the estimation of traits on the landscape scale, vegetation maps attempted in the original CSTARS (2004) study were included in my analysis. These maps predict the location of *Tamarix* spp. and native species using various input variables (reflectance, library and image spectra, minimum noise fraction (MNF), and physiological indices), and classification algorithms (maximum likelihood classification (MLC), spectral angle mapping (SAM) and mixed tuned matched filtering (MTMF)). They combine *P. microphylla* with *P. aculeata* (Mexican palo verde) and *P. florida* (Blue palo verde) under the name *Parkinsonia*⁷ spp. Comparison between the mapped species and the ground truth pixels showed overall accuracy, and producer's and user's accuracy per species (errors of omission and inclusion respectively).

⁷ *Parkinsonia* spp. will also be used here to refer to all three species. The effect of this combination will be addressed in the discussion. As Figure 7 shows, *P. aculeata* was recorded in relatively few areas compared to the other species.

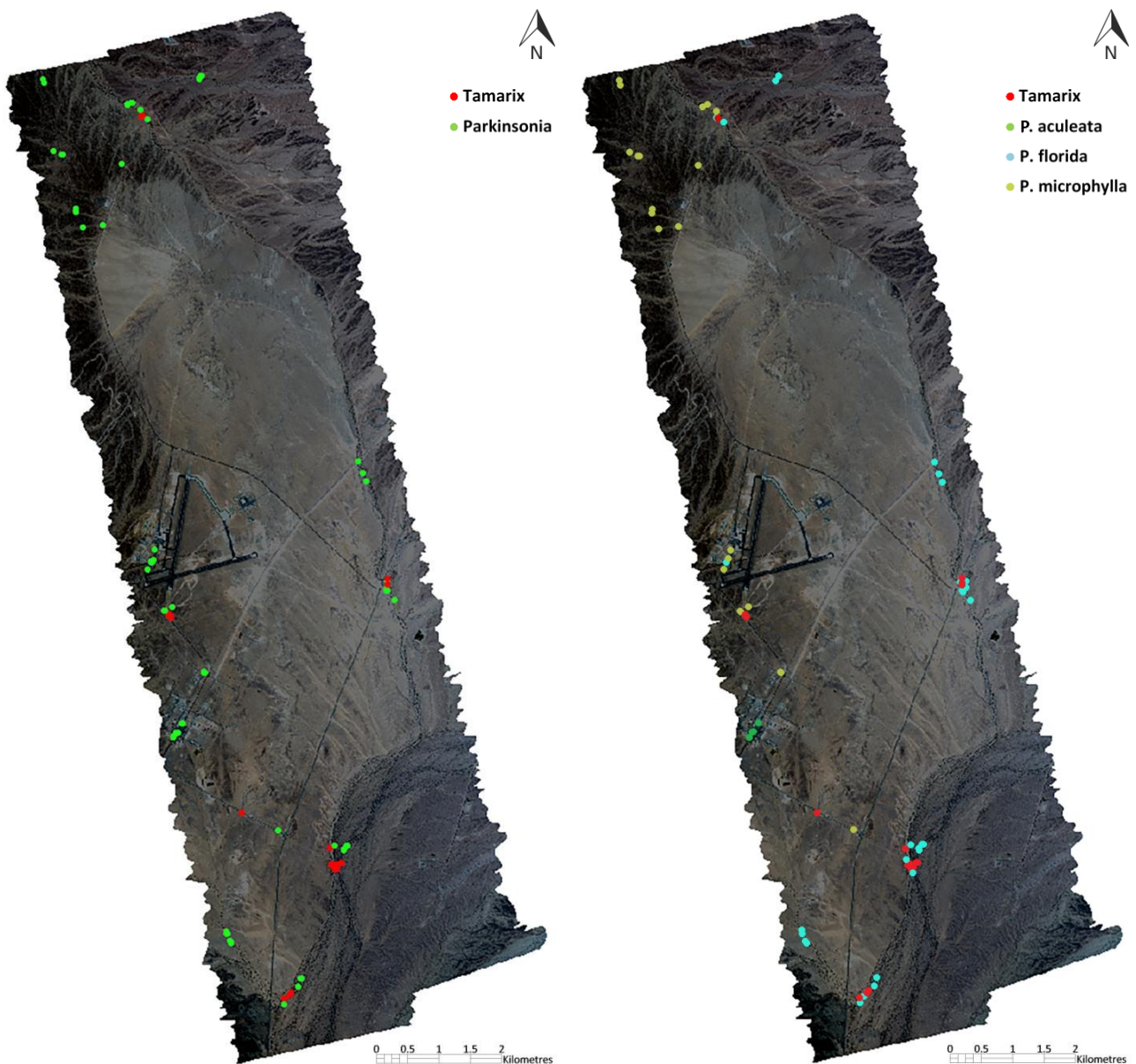


Figure 7. Location of *Tamarix* spp. and *Parkinsonia* spp. ground-truthed samples, left, and with *Parkinsonia* identified by species, right (images darkened and ROI pixels enlarged for clarity)

The two most accurate maps were chosen (Table 3, Figure 8), produced by the MLC and the MTMF. The MLC assigns each pixel into the class it has the greatest probability of being a member of, depending on variance and covariance with the class. These classes were built using selected physiological vegetation indices (of the same type discussed in the next section) to distinguish between the recorded species. Unlike most classifications, this MLC differentiated *Tamarix* spp. from agriculture, and reduced confusion between *Tamarix* spp. and *Parkinsonia* spp. (CSTARS, 2004), although only identifying 65 *Tamarix* spp. pixels (barely visible in the very southwest of Figure 8) in comparison to 89055 *Parkinsonia* spp. in the selected area.

In contrast, MTMF uses a partial unmixing technique to find the proportion of endmembers of each vegetation class within each pixel. It does so by comparing the image spectra with different combinations of spectra that represent pure pixels of a surface type, from a spectral library. Several endmembers were selected for each vegetation class from across the study area. Highest classification accuracy was obtained assigning pixels to the class with the highest score above a threshold value of 0.3. This threshold meant little of the overall image was mapped, but 9960 *Tamarix* spp. and 10162 *Parkinsonia* spp. pixels were still identified (CSTARS, 2004). This produced a higher overall accuracy than the MLC classification, and a much higher user's accuracy for *Tamarix* spp., meaning far fewer *Tamarix* spp. pixels were omitted.

Overall accuracy was relatively low, but the high producer accuracy indicates that MTMF is correctly classifying the input data, i.e., the algorithms are picking the spectral features that allow mapping the species. The class maps of these classifications were converted into ROIs, and the corresponding AVIRIS spectral data extracted.

Table 3. Total and user/producer accuracies for each classification methodology.

Algorithm	Input	Accuracy	<i>Tamarix</i> spp.		<i>Parkinsonia</i> spp.	
			User	Producer	User	Producer
MLC	Physiological Indices	39.3% (247/629)	37.0% (113/305)	95.8% (113/118)	57.3% (133/232)	57.6% (133/231)
MTMF	Endmembers	51.6% (394/764)	81.5% (268/329)	91.2% (268/294)	34.5% (82/238)	93.2% (82/88)

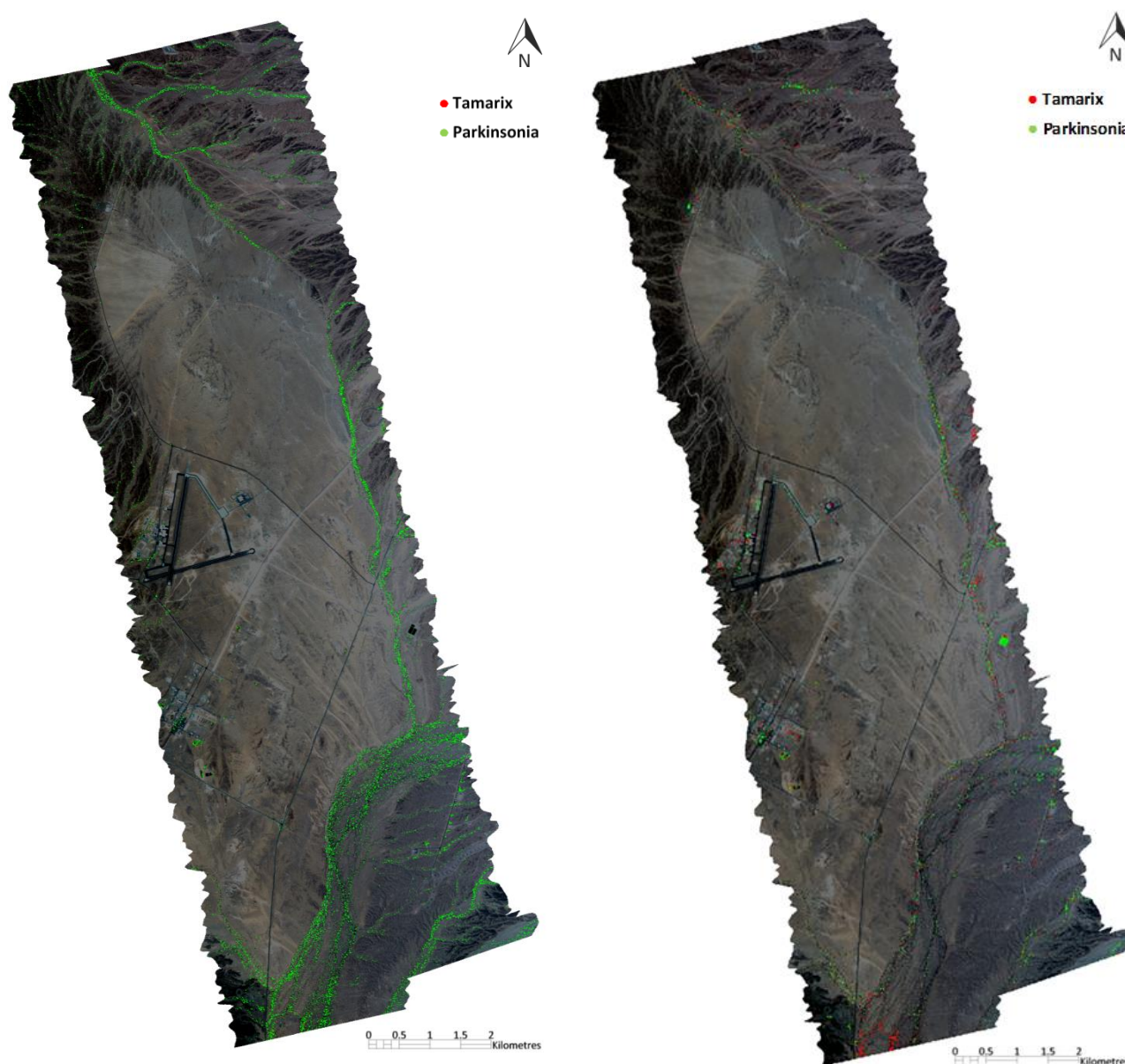


Figure 8. *Tamarix* spp. and *Parkinsonia* spp. pixels classified by MLC, left, and MTMF, right (images darkened for clarity)

OPTICAL VEGETATION TRAITS

The extracted data was assessed for spectral separability based on all wavelengths, and the vegetation indices most relevant to the optical traits selected. Vegetation indices are a relatively simple, computationally efficient approach which have been determined experimentally to relate plant traits to the ratio or formula of reflectances at specific wavelengths (Kaufmann et al., 2010). They have many advantages over raw reflectances because they integrate information across different spectral regions, but can still outperform full spectrum comparisons (Lehmann et al., 2015). Even simple ratios can eliminate the differences in overall reflectance, potentially caused by time of day, dampness of ground etc., which could cause systematic errors where target species are sparse and/or unevenly spread (Kaufmann et al., 2010). The use of hyperspectral data with these indices allows the use of specific smaller absorption features related to the traits, and thus a larger range of traits to be observed as a more precise scale (Roberts et al., 2012).

Indices relevant to the traits selected were collated from various sources:

- The *EnMAP Hyperspectral Algorithms* report (Kaufmann et al., 2010), which includes a comprehensive review of indices used in agriculture and forestry. Their criteria for the inclusion of algorithms matches the needs of this study, amongst others being as far as possible geographically and temporally transferable.
- The *hsdar* package for R (see below, Lehnert et al., 2016)
- The *Index Database* website of remote sensing indices (<http://www.indexdatabase.de/>; Henrich et al., 2017)
- The “Hyperspectral Vegetation Indices” chapter from the book *Hyperspectral Remote Sensing of Vegetation* (Roberts et al., 2012)
- Google scholar searches for indices of each trait post 2010⁸.

As Lehmann et al. (2015) highlight, identification of suitable spectral regions and indices for trait measurement remains open. Therefore all suitable indices, those designed and found to effectively measure the relevant trait, were selected, to investigate which highlight the expected difference in optical traits between the two species. These are collated on the tables in the next section. Many of the indices have been used to investigate multiple traits. MCARI (Modified Chlorophyll Absorption in Reflectance Index), developed to measure chlorophyll, has been used to examine LAI, while conversely LAI-developed indices such as TVI (Triangular Vegetation Index), SAVI (Soil Adjusted Vegetation Index) and NDVI (Normalised Difference Vegetation Index) have been used to measure chlorophyll (Kaufmann et al., 2010). Similarly, the red edge inflective position (REIP) has been found to correlate with both LAI and chlorophyll (Heiskanen et al., 2013). They are selected here, as far as possible, for the trait they were developed for to provide the optimal indicator for that trait and to maximise separability between species.

Indices were calculated using R version 3.41 (R Development Core Team, 2016). The *hsdar* hyperspectral data package version 0.51 (Lehnert, Meyer, & Bendix, 2016) was used to calculate the vegetation indices it includes, and expanded with code for the others. Several indices were calculated manually to check the accuracy of the package (NDVI, MSAVI, MCARI, mSR2); the same results were obtained. However, when inspecting the code, incorrect wavelengths had been used for the CARI, CRI2, Datt7, Datt8 and SRWI indices; these were corrected. The weighted option in the package, which interpolates the reflectance to fit the wavelength specified by each index (rather than the nearest neighbour) was used to obtain wavelengths closest to those specified for each index.

The following section outlines the optical traits, the spectral regions relevant to them, and the indices selected to estimate them.

⁸ These looked at all relevant results from the top five pages of results. The Google search algorithm prioritises both number of citations and recency (Beel & Gipp, 2009), so this was considered a reasonable number to cover any important indices that had been developed more recently. The terms used were: “remote sensing (index OR indices)”, with separate searches for “chlorophyll”, “cellulose”, “lignin”, “leaf area index OR LAI” “leaf water content OR LWC” and “salt OR salinity”, repeated with and without “vegetation”.

CHLOROPHYLL

Chlorophyll is interpreted as total concentration of chlorophyll (a and b) per unit area. The wavelengths most sensitive to normal-range chlorophyll concentrations are the lower and upper flanks (530 to 630 nm and 700 to 750 nm) of the chlorophyll absorption feature, although the centre of the feature (660 to 680 nm) can be used to estimate low chlorophyll concentrations (Kaufmann et al., 2010; Sims & Gamon, 2002). The 440, 480, 650 and 680 nm wavelengths were used to differentiate chlorophyll content in aquatic species (Santos, et al., 2012). The red edge inflective position (REIP), the wavelength with the most rapid increase in reflectance within the red edge (the sharp increase in reflection vegetation displays between the visible and NIR regions), is also sensitive to chlorophyll content, shifting to longer wavelengths at higher concentrations (Heiskanen et al., 2013). The 43 indices selected are shown in Table 4, exclusively using visible and lower NIR wavelengths from 445 nm (violet/blue) to 925 nm, the vast majority (37) from 550 nm (green) to 925 nm.

Table 4. Vegetation indices for chlorophyll. R indicates reflectance at that wavelength. D indicates the derivative at that wavelength. L is an adjustment factor in the SAVI₆₆₄ index, relating to vegetation density, set at 0.25, 0.5 or 1 for high, intermediate and very low vegetation densities respectively. Both intermediate and very low vegetation densities were tested. Abbreviations within brackets after the index name indicate a different name given within the hsdar package. Some indices share names – these have been differentiated here by adding a changed reflectance value after the name. The older reference given indicates the source of the index. Other references indicate the efficacy of the index in measuring the trait indicated.

Chlorophyll		
Index	Formula	Source
CAInt (Chlorophyll Absorption Integral, CIAInt)	$\int_{600nm}^{735nm} R$	Oppelt & Mauser, 2004
CARI (Chlorophyll Absorption in Reflectance Index)	$R_{700} \cdot (abs(a \cdot R_{550} + R_{670} + b) / R_{670}) \cdot (a^2 + 1)^{0.5}$ $a = (R_{700} - R_{550}) / 150$ $b = R_{550} - (a \cdot R_{550})$	Kim et al., 1994; Broge & Leblanc, 2001
CI2 (Chlorophyll Index)	$R_{760} / R_{700} - 1$	Gitelson et al., 2003
Datt (New chlorophyll reflective index)	$(R_{850} - R_{710}) / (R_{850} - R_{680})$	Datt, 1999b
Datt4	$R_{672} / (R_{550} \cdot R_{708})$	Datt, 1998
Datt6	$R_{860} / (R_{550} \cdot R_{708})$	Datt, 1998
DD (Double Difference)	$(R_{749} - R_{720}) / (R_{701} - R_{672})$	le Maire et al., 2004
DDn (new Double Difference)	$2 \cdot (R_{710} - R_{660} - R_{760})$	le Maire et al., 2008
EGFN (Normalised ratio of first derivatives at red edge and green regions)	$(\max(D_{650:750}) - \max(D_{500:550})) / (\max(D_{650:750}) + \max(D_{500:550}))$	Peñuelas et al., 1994
First derivative of reflectance (Datt3)	D_{754} / D_{704}	Datt, 1999b
Gitelson	$1 / R_{700}$	Gitelson et al., 1999
Green NDVI (Green Normalised Difference Vegetation Index)	$(R_{800} - R_{550}) / (R_{800} + R_{550})$	Gitelson et al., 1996
MCARI (Modified Chlorophyll Absorption in Reflectance Index)	$((R_{700} - R_{670}) - 0.2(R_{700} - R_{550})) \cdot (R_{700} / R_{670})$	Daughtry et al., 2000
MCARI/OSAVI	$MCARI / OSAVI$	Daughtry et al., 2000
MCARI2/OSAVI2	$MCARI2 / OSAVI2$	Wu et al., 2008
MCARI ₇₅₀ (MCARI ⁹)	$((R_{750} - R_{705}) - 0.2 \cdot (R_{750} - R_{550})) \cdot (R_{750} / R_{705})$	Wu et al., 2008
mND ₆₉₉ (modified Normalised Difference)	$(R_{722} - R_{699}) / (R_{722} + R_{699} - 2R_{502})$	le Maire et al., 2004

⁹ MCARI2 labelled by hsdar is a modified MCARI, not the MCARI2 designated by Haboudane et al. (2004).

mND ₇₀₅	$(R_{750} - R_{705}) / (R_{750} + R_{705} - 2R_{445})$	Sims & Gamon, 2002
mNDVI (modified Normalised Difference Vegetation Index)	$(R_{800} - R_{680}) / (R_{800} + R_{680} - 2R_{445})$	Sims & Gamon, 2002
mSR (modified Simple Ratio)	$(R_{800} - R_{445}) / (R_{680} - R_{445})$	Sims & Gamon, 2002
mSR ₇₀₁	$(R_{722} - R_{502}) / (R_{701} - R_{502})$	le Maire et al., 2004
mSR ₇₀₅	$(R_{750} - R_{445}) / (R_{705} - R_{445})$	Sims & Gamon, 2002
MTCI (MERIS Terrestrial Chlorophyll Index)	$(R_{754} - R_{709}) / (R_{709} - R_{681})$	Dash & Curran, 2004
ND _{chl} (Normalised Difference)	$(R_{925} - R_{710}) / (R_{925} + R_{710})$	le Maire et al., 2008
NDVI2 (Normalised Difference Vegetation Index)	$(R_{750} - R_{705}) / (R_{750} + R_{705})$	Gitelson & Merzlyak, 1994
NDVI3	$(R_{682} - R_{553}) / (R_{682} + R_{553})$	Gandia et al., 2004
OSAVI (Optimised Soil Adjusted Vegetation Index)	$(1 + 0.16) \cdot ((R_{800} - R_{670}) / (R_{800} + R_{670} + 0.16))$	Rondeaux et al., 1996
OSAVI2	$(1 + 0.16) \cdot ((R_{750} - R_{705}) / (R_{750} + R_{705} + 0.16))$	Wu et al., 2008
RE3/RE2 (Red Edge, Volgelmann)	R_{740} / R_{720}	Vogelmann et al., 1993
Red Edge Derivatives (Volgelmann3)	D_{715} / D_{705}	Vogelmann et al., 1993
REIP (Red Edge Inflective Position, REP_Li)	$R_{re} = (R_{670} + R_{790}) / 2$ $700 + 40((R_{re} - R_{700}) / (R_{740} - R_{700}))$	Dash & Curran, 2004; Guyot & Baret, 1988
REP_LE	<i>Red-edge position through linear extrapolation</i>	Cho & Skidmore, 2006
SAVI ₁₆₆₄ (Soil-Adjusted Vegetation Index)	$(1 + L) \cdot ((R_{778} - R_{664}) / (R_{778} + R_{664} + L))$	Gat et al., 2000
SR ₅₅₀ (Simple Ratio, SR3)	R_{750} / R_{550}	Gitelson & Merzlyak, 1997
SR ₆₈₀	R_{800} / R_{680}	Sims & Gamon, 2002
SR ₆₉₀ (SR2)	R_{752} / R_{690}	Gitelson & Merzlyak, 1997
SR ₇₀₀ (SR1)	R_{750} / R_{700}	Gitelson & Merzlyak, 1997
SR ₇₀₅	R_{750} / R_{705}	Sims & Gamon, 2002
TCARI (Transformed Chlorophyll Absorption in Reflectance Index)	$3 \cdot ((R_{700} - R_{670}) - 0.2 \cdot (R_{700} - R_{550}) \cdot (R_{700} / R_{670}))$	Haboudane et al., 2002
TCARI/OSAVI	$TCARI / OSAVI$	Haboudane et al., 2002
TCARI2	$3 \cdot ((R_{750} - R_{705}) - 0.2 \cdot (R_{750} - R_{550}) \cdot (R_{750} / R_{705}))$	Wu et al., 2008
TCARI2/OSAVI2	$TCARI2 / OSAVI2$	Wu et al., 2008
TGI (Triangular Greenness Index)	$-0.5 \cdot (190(R_{670} - R_{550}) - 120(R_{670} - R_{480}))$	Hunt et al., 2012

LEAF AREA INDEX

LAI is the one-sided green leaf area per unit ground surface area (Watson, 1947). Leaf development affects reflectance throughout the spectral range given its association with other traits, such as chlorophyll or water content; therefore LAI indices likewise use wavelengths across the visible, NIR and SWIR regions; high reflectance in NIR linked to scattering by leaves (Kaufmann et al., 2010). The red edge and SWIR regions were found to be the best predictors of LAI across different vegetation types by Lee et al. (2004), whereas Gong et al. (2003) found bands centred in the NIR and SWIR regions, at 820, 1040, 1200, 1250, 1650, 2100, and 2260 nm among the most important in measuring forest LAI. A total of 23 indices

were selected, shown in Table 5, which while including wavelengths from visible, NIR and SWIR regions, focusses mainly on the chlorophyll absorption feature, only two of the indices not using this area.

Table 5. Vegetation indices for LAI. R indicates reflectance at that wavelength. D indicates the derivative at that wavelength. L is an adjustment factor in the SAVI index, relating to vegetation density, set at 0.25, 0.5 or 1 for high, intermediate and very low vegetation densities respectively. Both intermediate and very low vegetation densities were tested. Abbreviations within brackets after the index name indicate a different name given within the hsdar package. Some indices share names – these have been differentiated here by adding a changed reflectance value after the name.

Leaf Area Index		
Index	Formula	Source
1DZ_DGVI (First-order derivative green vegetation index derived using zero baseline, Sum_Dr1)	$\sum_{i=626}^{795} D1i$	Elvidge & Chen, 1995
Area of red edge peak (Sum_Dr2)	$\sum_{i=680}^{780} D1i$	Filella & Peñuelas, 1994
ARVI2 (Atmospherically Resistant Vegetation Index)	$\frac{(R_{781:1399} - (R_{640:760} - y(R_{640:760} - R_{420:480}))) / (R_{781:1399} + (R_{640:760} - y(R_{640:760} - R_{420:480})))}{y = 1 \text{ (quotient derived from atmospheric reflectance)}}$	Kaufman & Tanré, 1992
CSI (Canopy Structure Index)	$CSI = 2sSR - sSR^2 + sWI^2$ $sSR = (R_{800}/R_{680} - 1) / (R_{800}/R_{680} - 1)_{max}$ $sWI = (R_{900}/R_{1180} - 1) / (R_{900}/R_{1180} - 1)_{max}$	Sims & Gamon, 2003
D _{LAI} (Difference)	$R_{1725} - R_{970}$	le Maire et al., 2008
GDVI (Generalised Difference Vegetation Index)	$\frac{(R_{800}^n - R_{680}^n) / (R_{800}^n + R_{680}^n)}{n = 2, \text{ adjustment for best correlation with LAI}}$	Wu, 2014
MCARI2	$\frac{1.5 \cdot ((2.5 \cdot (R_{800} - R_{670}) - 1.3 \cdot (R_{800} - R_{550})) / ((2 \cdot R_{800} + 1)^2 - (6 \cdot R_{800} - 5 \cdot (R_{670})^{0.5}) - 0.5))^{0.5}}$	Haboudane et al., 2004
MSAVI (Modified Soil Adjusted Vegetation Index)	$0.5 \cdot (2 \cdot R_{800} + 1 - ((2 \cdot R_{800} + 1)^2 - 8 \cdot (R_{800} - R_{670}))^{0.5})$	Qi et al., 1994
mSR2 (modified Simple Ratio)	$((R_{750}/R_{705}) - 1) / (R_{750}/R_{705} + 1)^{0.5}$	Chen, 1996
MTVI (Modified Triangular Vegetation Index)	$1.2 \cdot (1.2 \cdot (R_{800} - R_{550}) - 2.5 \cdot (R_{670} - R_{550}))$	Haboudane et al., 2004
MTVI2	$\frac{1.5 \cdot ((1.2 \cdot (R_{800} - R_{550}) - 2.5 \cdot (R_{670} - R_{550})) / ((2 \cdot R_{800} + 1)^2 - (6 \cdot R_{800} - 5 \cdot (R_{670})^{0.5}) - 0.5))^{0.5}}$	Haboudane et al., 2004
NDVI	$(R_{800} - R_{680}) / (R_{800} + R_{680})$	Tucker, 1979
NDVI ₇₈₀	$(R_{780} - R_{680}) / (R_{780} + R_{680})$	Ray et al., 2006
NDVI ₈₄₆	$(R_{846} - R_{655}) / (R_{846} + R_{655})$	Lee et al., 2004
RDVI (Renormalised Difference Vegetation Index)	$(R_{800} - R_{670}) / (R_{800} + R_{670})^{0.5}$	Roujean & Breon, 1995
RSR (Reduced Simple Ratio)	$\frac{R_{760:860} / R_{630:690} \cdot (1 - (R_{1600:1700} - R_{1600:1700min})) / (R_{1600:1700max} - R_{1600:1700min})}{}$	Brown et al., 2000; Heiskanen et al., 2013
SARVI2 (Soil and Atmosphere Resistant Vegetation Index, EVI)	$2.5 \cdot ((R_{800} - R_{670}) / (R_{800} - (6 \cdot R_{670}) - (7.5 \cdot R_{475}) + 1))$	Huete et al., 1997
SAVI (Soil-Adjusted Vegetation Index)	$(1 + L) \cdot (R_{800} - R_{670}) / (R_{800} + R_{670} + L)$	Huete, 1988
sLAIDI (standardised LAIDI)	$\frac{S \cdot (R_{1050} - R_{1250} / R_{1050} + R_{1250})}{S = 5 \text{ (scaling factor to rescale value between 0 and 1)}}$	Delalieux et al., 2008
SR (Simple Ratio)	R_{800} / R_{680}	Jordan, 1969
TVI (Triangular Vegetation Index)	$0.5 \cdot (120 \cdot (R_{750} - R_{550}) - 200 \cdot (R_{670} - R_{550}))$	Broge & Leblanc, 2001
VAR ₁₇₀₀ (Visible Atmospherically Resistant Index)	$\frac{(R_{700} - 1.7 \cdot R_{660:680} + 0.7 \cdot R_{470:490}) / (R_{700} + 2.3 \cdot R_{660:680} - 1.3 \cdot R_{470:490})}{}$	Gitelson et al., 2002

VARI _{green}	$(R_{545:565} - R_{660:680}) / (R_{545:565} - R_{660:680} - R_{470:490})$	Gitelson et al., 2002
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LEAF WATER CONTENT

This is interpreted as leaf equivalent water thickness (EWT), the depth of liquid vegetation water per unit area (Cheng et al., 2006). Many other measures exist, such as canopy water content (CWC), relative water content (RWC) and leaf gravimetric water content, and spectrally these may display very similar relations, particularly on the canopy scale (Kaufmann et al., 2010). However, EWT has been found to have a stronger relationship with reflectance than other measures (Colombo et al., 2008), and a good relationship with indices such as the moisture stress index (MSI; Ceccato et al., 2001). While related to LAI, it maintains more independence than CWC, which multiplies EWT by LAI (Yebara et al., 2013).

Water has many absorption features throughout the near-infrared (NIR) and shortwave-infrared (SWIR) regions. These include 850-860, 970, 1200, 1240, 1450, 1530, 1600, 1720, 1940 and 2500 nm (Kaufmann et al., 2010; Sims & Gamon, 2003; Ustin et al., 2004). At the canopy level, bands at shorter wavelengths (below 1600 nm) appear to be better predictors of water content, these weaker absorption features less likely to be saturated (Sims & Gamon, 2003). However, given the dryness of desert environments in general, and during the study period in particular, it can be expected that the more sensitive longer wavelengths may show the greatest distinction between the species. A total of 12 leaf water content indices were chosen, see Table 6, which in seven cases combine NIR and SWIR wavelengths, and in the rest use only the NIR region.

Table 6. Vegetation indices for leaf water content. R indicates reflectance at that wavelength. Abbreviations within brackets after the index name indicate a different name given within the hsdar package. Some indices share names – these have been differentiated here by adding a changed reflectance value after the name.

Leaf Water Content		
Index	Formula	Source
EWT ₁₇₈₈ (Equivalent Water Thickness Index Datt8)	$(R_{850} - R_{1788}) / (R_{850} - R_{1928})$	Datt, 1999a
EWT ₁₂₂₁₈ (Datt7)	$(R_{850} - R_{2218}) / (R_{850} - R_{1928})$	Datt, 1999a
GVMi (Global Vegetation Moisture Index)	$((R_{860} + 0.1) - (R_{1640} + 0.02)) / ((R_{860} + 0.1) + (R_{1640} + 0.02))$	Guerschman et al., 2009; Ceccato et al., 2002
LWCI (Leaf Water Content Index) ¹⁰	$(-\log(1 - R_{780} - R_{1400})) / (-\log(1 - R_{780max} - R_{1400min}))$	Hunt et al., 1987
LWVI (Leaf Water Vegetation Index, LWVI1)	$(R_{1094} - R_{983}) / (R_{1094} + R_{983})$	Galvão et al., 2005
LWVI2	$(R_{1094} - R_{1205}) / (R_{1094} + R_{1205})$	Galvão et al., 2005
MSI (Moisture Stress Index)	R_{1600} / R_{817}	Hunt & Rock, 1989
NDII2 (Normalised Difference Infrared Index)	$(R_{819} - R_{1649}) / (R_{819} + R_{1649})$	Hardisky & Klemas, 1983
NDWI (Normalised Difference Water Index)	$(R_{860} - R_{1240}) / (R_{860} + R_{1240})$	Gao, 1996
SIWSI (Shortwave Infrared Water Stress Index)	$(R_{860} - R_{1240}) / (R_{860} + R_{1240})$	Cheng et al., 2006; Fensholt &

¹⁰ While suggested for its applicability to canopies (Kaufmann et al., 2010), the original index is based on a ratio with reflectivity at maximum leaf turgor, limiting the use of this index to lab conditions (Hunt & Rock, 1989). However, given its successful applications (Kaufmann et al., 2010), it was adopted here – maximum turgor was found in several species to increase whole-plant reflectance at 780 nm and decrease it at 1400 nm (Hunt et al., 1987), so the maximum and minimum values for these from the study area were used. Given the dry spell when data was collected, this is unlikely to match experimental maximum turgor, but its inclusion allows the exploration of an area of the spectrum (1400 nm) not covered by the other water indices.

		Sandholt, 2003
SR ₈₂₀	R_{1600} / R_{820}	Ceccato et al., 2001
SRWI (Simple Ratio Water Index)	R_{858} / R_{1240}	Zarco-Tejada & Ustin, 2001
WI (Water Index, PWI)	R_{900} / R_{970}	Peñuelas et al., 1997

LIGNIN-CELLULOSE

One index is available for lignin, and one for cellulose (Table 7). Absorption bands are found higher in the spectrum, at 1120 and 1420 nm for lignin, and 1820 and 2340 nm for cellulose, while a ligno-cellulose absorption band was found at 2100 nm (Curran, 1989).

Table 7. Vegetation indices for lignin-cellulose content. R indicates reflectance at that wavelength.

<i>Lignin-cellulose</i>		
Index	Formula	Source
CAI (Cellulose Absorption Index)	$0.5 \cdot (R_{2000} + R_{2200}) - R_{2100}$	Daughtry, 2001; Nagler et al., 2003
NDLI (Normalised Difference Lignin Index)	$(\log(1/R_{1754}) - \log(1/R_{1680})) / (\log(1/R_{1754}) + \log(1/R_{1680}))$	Serrano et al., 2002

SALINITY

Salinity has been related to *Tamarix* spp., both as a tolerator of saline conditions, and a producer of salt from its glands (mainly sodium, but also chlorine, potassium, calcium, magnesium, lithium and manganese salts; Imada et al., 2012). This relationship can potentially be detected directly, by the effect on the plant itself, and indirectly, through saline soils. While salt is spectrally neutral, reflectance in the visible spectrum increases with its presence (Metternicht & Zinck, 1997), this would indicate that the smoother surface created by salt evaporites on leaves, and the surrounding soil should increase reflectivity. The presence of salt glands should therefore be distinguishable by increasing reflectivity, which should be seen particularly in the blue band (Metternicht & Zinck, 1997).

Vegetation salinity indices are predominantly based on stress (e.g. Hernández et al., 2014) and its effect on plant function – often using spectral regions or vegetation indices related to chlorophyll (and thereby productivity) and water content (Hamzeh et al., 2012). Salt stress has been linked to decreases in net photosynthetic rates, cell damage, reduced root and stomatal conductance, and decreased potassium ion concentration (Huang et al., 1994; Sohan et al., 1999). Salinity can also be measured by the response of water absorption bands, salt affecting hydrogen bonding (Begley et al., 1984), their area and slopes decreasing with salt concentration (Lugassi et al., 2017). However, these responses are species dependent: halophytes such as *Tamarix* spp. are adapted to resist such stress, leading to a poor correlation with salinity (Zhang et al., 2011). The SASI (Soil Adjusted Salinity Index) developed by Zhang et al. (2011) aims to reduce sensitivity to species differences, leading to indices that allow more robust estimation of salinity in areas where halophytes dominate.

Soil salinity will be reflected through the canopy in mixed pixels from the AVIRIS data, although this will likely be less pronounced in the ASD data, where purer vegetation readings would be expected given the proximity to the canopy. Vegetation response is often used as a proxy for soil salinity, however, small amounts of salt in surface soil has been found to modify spectra (Hick & Russell, 1990). Halite (sodium chloride) is spectrally featureless in the VIS-SWIR region, but has been correlated with moisture and organic matter, as well as gypsum and other evaporites (Ben-Dor et al., 2002; Hunt et al., 1972). Through these effects saline soils have been shown to display features related to iron oxides from 500 to 700 nm (Clark, 1999), reflectance plateau from 800 to 1100 nm, hydrate-related absorption features at 1010, 1180,

1780, 1950 and 2210 nm, and widened water absorption features at 1950 and 1400 nm (Dehaan & Taylor, 2003). Whereas saline crusts display absorption features at 1442, 1851, 1958 and 2226 nm, (Howari et al., 2002). Salinity has also been associated with increased reflectance in visible wavelengths, although this is linked to moisture content (Mougenot et al., 1993) – particularly in red wavelengths 600 to 700 nm for surface crusts (Allbed et al., 2014).

The 12 indices selected for both vegetation and soil salinity are shown in Table 8. The vegetation indices focus mainly on the visible and NIR areas of the spectrum, whereas soil salinity indices generally use the SWIR region.

Table 8. Vegetation indices for salinity. R indicates reflectance at that wavelength. L is an adjustment factor in the SASI indices, relating to vegetation density, set at 0.25, 0.5 or 1 for high, intermediate and very low vegetation densities respectively. Both intermediate and very low vegetation densities were tested.

Salinity		
Index	Formula	Source
BI (Brightness Index)	$(R_{620:680}^2 + R_{770:860}^2)^{0.5}$	Khan et al., 2005
Blue Band	$R_{450:520}$	Metternicht & Zinck, 1997
COSRI (Combined Spectral Response Index)	$((R_{430:525} + R_{510:600}) / (R_{600:700} + R_{780:1100})) \cdot NDVI$	Fernández-Buces et al., 2006
GIR (Green Indigo Ratio)	R_{554} / R_{436}	Rud et al., 2013
NDSI (Normalised Difference Salinity Index)	$(R_{1600:1700} - R_{2145:2185}) / (R_{1600:1700} + R_{2145:2185})$	Al-Khaier, 2003
SASI (Soil Adjusted Salinity Index)	$(1 + L) \cdot \frac{\lambda_2 - \lambda_1}{\lambda_2 + \lambda_1 + L}$ <i>SASI1</i> $\lambda_1 = R_{546:575}, \lambda_2 = R_{560:590}$ <i>SASI4</i> $\lambda_1 = R_{655:764}, \lambda_2 = R_{889:903}$	Zhang et al., 2011
SI (Salinity Index)	$(R_{450:520} \cdot R_{620:680})^{0.5}$	Khan et al., 2005
SSI (Soil Salinity Index)	$(R_{2203} - R_{2052}) / (R_{2203} + R_{2052})$	Weng et al., 2008
SSSI-1 (Soil Salinity and Sodcity Index)	$R_{1550:1750} - R_{2080:2350}$	Bannari et al., 2013
SSSI-2	$(R_{1550:1750} \cdot R_{2080:2350} - R_{2080:2350}^2) / R_{1550:1750}$	Bannari et al., 2013
SVSI (Sentinel-2 Vegetation Salinity Index)	$(R_{665} - R_{490}) / (R_{705} + R_{1610})$	Lugassi et al., 2017
WI/NDVI ₇₅₀₋₇₀₅	$WI / NDVI2$	Hernández et al., 2014

ANALYSIS

Raw reflectance and index values were calculated for ASD, the ground-truthed AVIRIS and the MLC and MTMF classification outputs (see Table 9). The raw reflectance and vegetation index values were analysed to assess whether they would allow the species to be separated based on their spectral characteristics, and which traits differed between them. To do this, a similar methodology was adopted to that Santos et al. (2012) used to examine native and non-native aquatic plants, and Punalekar et al. (2016) used to compare the spectra of wetland species communities. Statistical tests were performed with SPSS version 23.0 (IBM Corp, Armonk, NY). Raw reflectance values were retrieved from both the ASD and the AVIRIS data, at 5 nm intervals for the ASD and using a weighted average to calculate the equivalent intervals for the AVIRIS data. Both reflectances and index values were non-normal, confirmed by Shapiro-Wilk tests, and displayed heteroscedasticity in Levine tests. Attempted transformations did not normalise the data. Therefore non-parametric Mann-Whitney U tests were used to differentiate the species, significant at $\alpha = 0.05$.

To assess the difference in the optical traits between the species, indicators were created, combining the most robust indices into an overall measure of each trait. Using multiple indices for each trait ensures a greater diversity of spectral features is included, which can aid discrimination at different densities and different environmental conditions, increasing

the applicability of the final indicator (Roberts et al., 2012). Robustness of indices was based on their ability to differentiate between the species across the methods used (field, ground-truthed and the classification maps). A simple count was made, scoring one for each method in which the index values could separate the species at $\alpha = 0.05$. Given that ASD and ROI data was based on confirmed rather than predicted species locations, these were given extra weight by counting significant differences between *Tamarix* spp. and both *P. microphylla*, and *Parkinsonia* spp. This gives each index a potential score of six (from the methods on Table 9).

Table 9. List of methods used to compare the native and invasive species, and score index robustness. Label later applied in graphs and tables.

Sensor	Data collection	Species compared	Label
ASD	Field	<i>Tamarix</i> spp. against <i>Parkinsonia</i> spp.	ASD
ASD	Field	<i>Tamarix</i> spp. against <i>P. microphylla</i>	ASD Pm
AVIRIS	Ground-truthed ROI	<i>Tamarix</i> spp. against <i>Parkinsonia</i> spp.	ROI
AVIRIS	Ground-truthed ROI	<i>Tamarix</i> spp. against <i>P. microphylla</i>	ROI Pm
AVIRIS	MLC vegetation map	<i>Tamarix</i> spp. against <i>Parkinsonia</i> spp.	MLC
AVIRIS	MTMF vegetation map	<i>Tamarix</i> spp. against <i>Parkinsonia</i> spp.	MTMF

This also weighs the selection towards the AVIRIS results (four to two), which is preferable given that indicator performance with aerial imagery will be necessary to measure IAS impacts on the landscape scale. Depending on count scores, further selection of robust indices would be based upon the transferability and effectiveness of the indices reported in the literature, and on total effect size:

$$r = \frac{z}{\sqrt{N}}$$

r = effect size z = z-value
 N = total number of observations

This provides a standardised measure of the importance of the effect – on a generic level, 0.1 indicates a small effect (difference in the groups accounting for 1% of total variance), 0.3 a medium effect (9%) and 0.5 a large effect (25%) (Rosenthal, 1991). Significance alone indicates the groups are different (with a 95% probability), but does not show the importance of an effect, and is also more likely to show significant results in large samples, such as the MLC and MTMF classifications (Field, 2013).

Principal component analysis (PCA) was performed to weigh the contribution of the indices to the trait measured, as used by Almeida & Filho (2004) to effectively discriminate between vegetation types, similarly with vegetation indices. Unlike other feature selection techniques, PCA can combine non-parametric and very highly correlated variables (Field, 2013); such collinearity is expected from indices based on similar wavebands. It separates the trait variable into several independent principal components made up of weighted indices, ordered by the proportion of variance they explain; therefore assuming larger variances show the most interesting dynamics (Field, 2013). In order to make their variances comparable (as Lehmann et al., 2015), the results from the robust indicators were firstly standardised:

$$Y = \frac{X - \mu}{\sigma}$$

Y = standardised value X = sample
 μ = mean σ = standard deviation

Then indices with a negative relationship to the trait were reversed, meaning all increased values of all indices should indicate a higher measurement of the trait. Next, several PCAs were performed to select an acceptable minimum number of principal components to explain a large proportion of the variance in the dataset, also using eigenvalues, and the point of inflexion on the produced scree plots. Due to the expected correlation between components, oblique rotation (direct oblimin) was used. Reliability analyses (Cronbach’s α) and correlation matrices were used to further reject uncorrelated variables, those with several correlations of under 0.3 with the other variables inspected for elimination.

The final indicator for each trait was made up of the summed loadings of the extracted components, for example:

$$\text{Indicator 1} = \text{PC1} + \text{PC2}$$

$$\text{PC1} = (\text{Index A * loading}) + (\text{Index B * loading}) + (\text{Index C * loading})$$

$$\text{PC2} = (\text{Index A * loading}) + (\text{Index B * loading}) + (\text{Index C * loading})$$

MAPPING TRAITS

To assess the effect of the invasion on optical traits on the landscape scale, trait indicators were mapped by applying the loaded indices to the AVIRIS mosaic using ENVI band math¹¹. Indices were then applied individually and the mean and standard deviation across the image calculated to standardise each. The relevant PCA loadings were then applied to these standardised indices, to produce an indicator map for each trait. This was then normalised using the image maximum and minimum values to produce a score from zero to one:

$$Y = \frac{X - \text{min}}{\text{max} - \text{min}}$$

Y = normalised value X = sample
max = maximum value min = minimum value

Due to the influence of extreme values and high values in non-vegetated pixels on some of the indicators, the pixel values returned by the indicators required different amounts of winsorising before normalisation in order that each trait used as much of the scale (zero to one) as possible¹². This ensured greater comparability between the indicators, and gave the final total invasiveness score a more meaningful range. Masks were then applied to set the values below zero or above one as zero and one respectively. The scores from the individual indicators were summed to create a combined score map for invasive optical traits.

To assess the difference in the traits between the invasive and native species, the indicator values for the classified *Tamarix* spp. and *Parkinsonia* spp. positions were mapped. These positions were based on a combination of the MLC and MTMF classifications, which were used to mask the rest of the indicator maps, different colour scales chosen to highlight the relative strength of optical traits, and the overall invasive trait score in each population. Finally, the indicator values for these cells were extracted and U-tests performed to evaluate overall trait differences between the predicted populations of the species.

¹¹ ENVI was used due to difficulties in dealing with large hyperspectral rasters within the experimental hsdar R package. However, indices within ENVI use the nearest band to the required wavelength, usually within 5 nm, rather than the weighted average that hsdar uses. Given the number of indicators combined however, this is likely to have minimal effect on the outputted maps.

¹² Different percentages of pixels were used as maximum and minimum values for normalisation to emphasise variation within the clearly vegetated areas in the southwest, while making sure scores remained significantly different from non-vegetated areas nearby. This was done through trial and error. For LAI 0.005% of the highest and lowest pixel values were winsorised, for chlorophyll and LWC 0.05%, and for lignin-cellulose and salinity 2.5% (having a larger proportion of high values in non-vegetated areas).

RESULTS

SPECTRAL SEPARABILITY OF SPECIES

The reflectance properties of *Tamarix* spp. and *Parkinsonia* spp. differed significantly across almost all wavelengths in the visible and NIR regions for the ASD data, the MLC and the MTMF, but not for the AVIRIS data extracted from the ground-truthed ROI (Figure 9). The mean reflectances of the species for each method are shown on Figure 10.

The robustness of the wavelengths, their ability to show a significant difference between the species over the various methods, is shown on Figure 9. The most robust wavelengths are concentrated in the visible and SWIR regions, with five of six methods showing significant differences for most wavelengths (68%) until 1320nm, with a notable reduction around the red edge and absorption features. Spectral separability is weak until 1940 nm, with zero to two methods significantly different, except between 1400 and 1560 nm. While this region is important for indices in LAI, lignin, soil salinity and particularly LWC, other indices for these traits relied on the better performing regions, so their use as trait indicators is still valid. At 1940 nm it again increases to four or five methods being significantly different for the rest of the spectra, except between 2210 and 2240 nm.

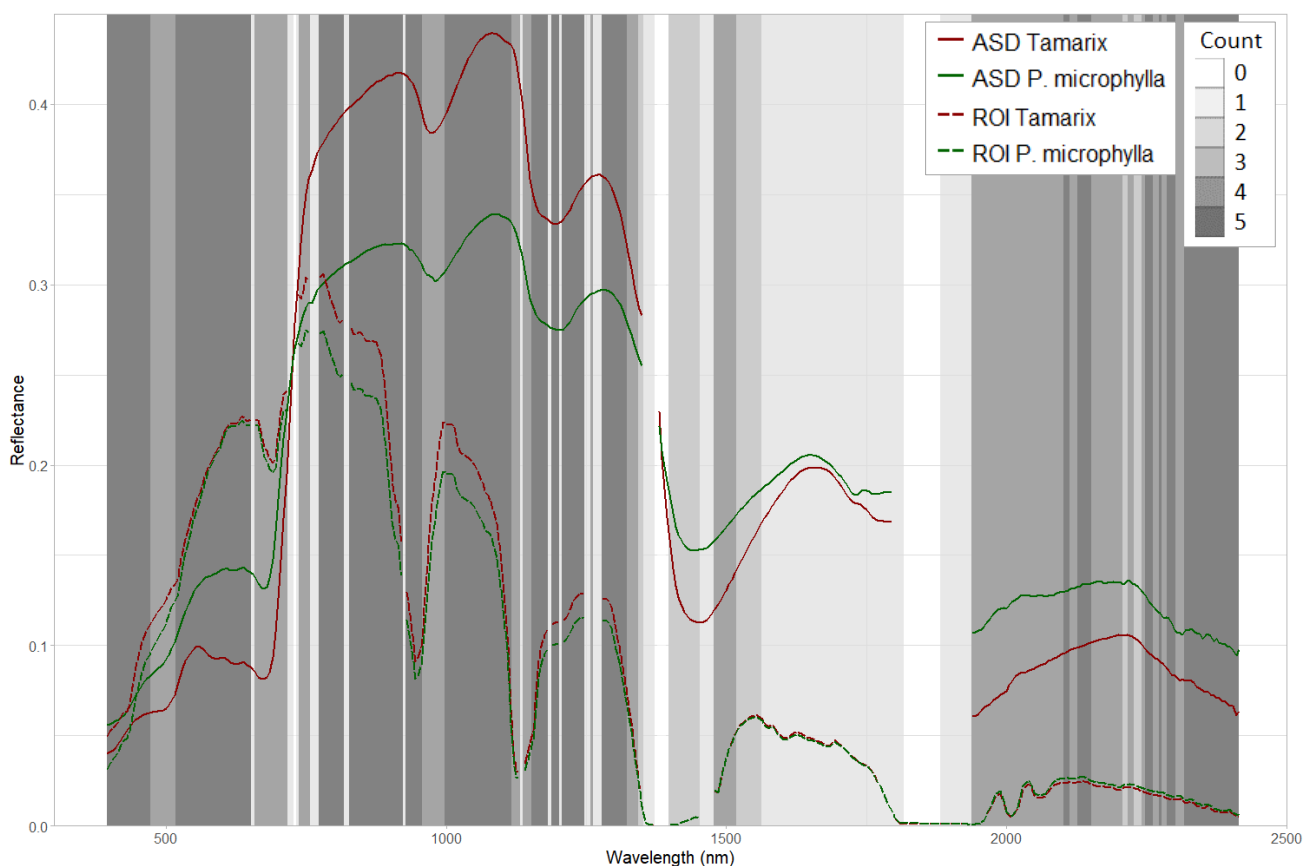


Figure 9. Mean spectral signatures of ASD and AVIRIS ROI for *Tamarix* spp. and *P. microphylla* overlaid upon count of number of methods each waveband (5 nm width) was able to successfully differentiate between the species ($\alpha = 0.05$). The six methods used were ASD and AVIRIS ROI for *Tamarix* spp. against both *Parkinsonia* spp. and *P. microphylla*, and MLC and MTMF, although the largest count of methods significantly differentiated by a wavelength was five.

The ASD data allowed for the strongest differentiation between the species, over 75% of the 406 wavelengths were significantly different (U-tests, summarised in Figure 9) between *Tamarix* spp. and both *Parkinsonia* spp. and *P. microphylla*. Percentage differences between the species across the methods are shown in Appendix 2. *Tamarix* spp. showed lower reflectance in the visible spectra between 395 and 735 nm (by 20 to 40% difference), a stronger red edge and greater NIR reflectance (consistently around 40% higher) before dropping below the reflectance of *Parkinsonia* spp. from the water absorption feature at 1450 nm (differences ranging from 20 to 60%). Differences of *Parkinsonia* spp. and

P. microphylla were less, around 5 to 10% throughout, *P. microphylla* being more similar to *Tamarix* spp. than *Parkinsonia* spp. in the visible and SWIR regions, but lower in the NIR plateau.

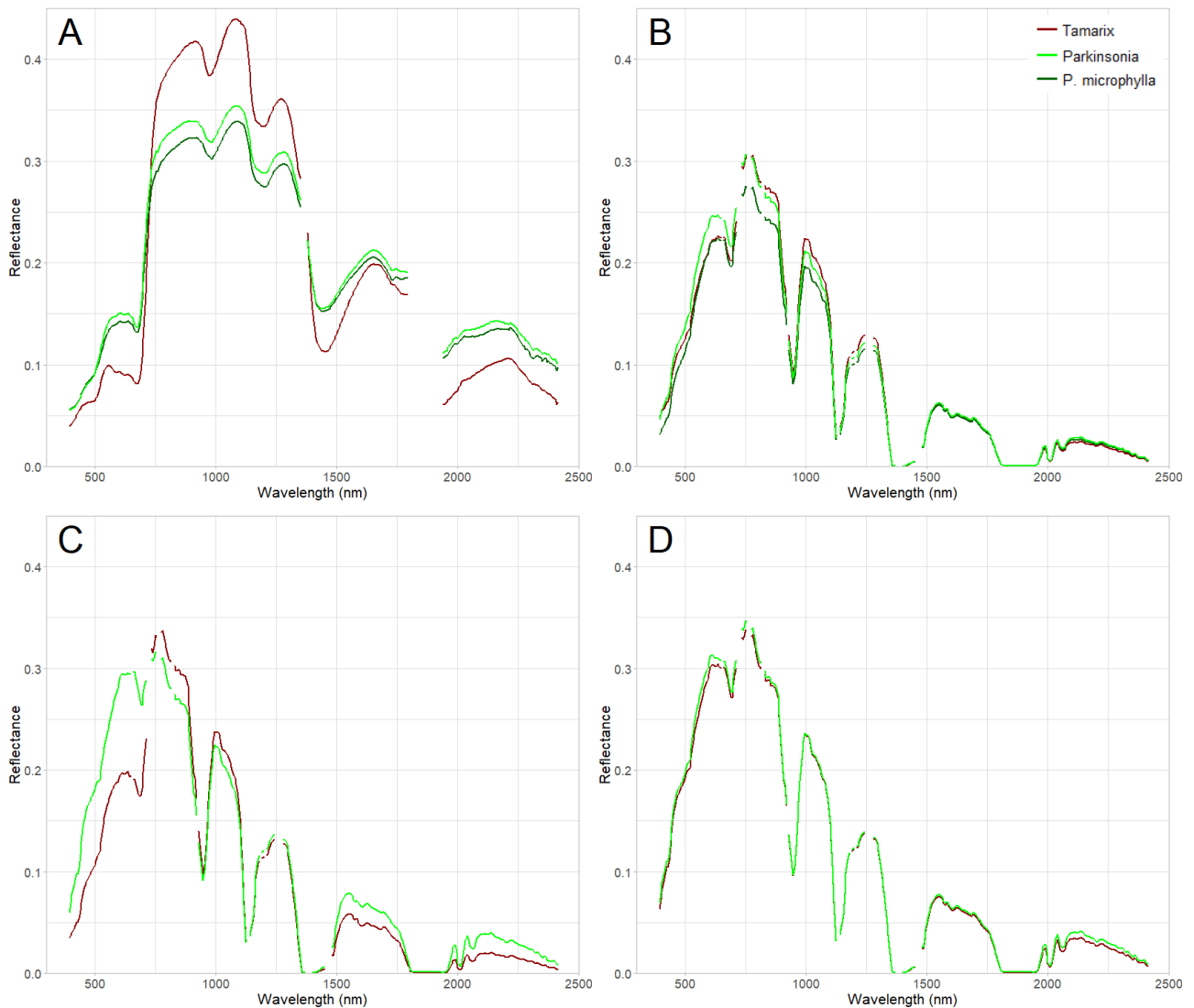


Figure 10. Mean spectral signatures for *Tamarix* spp. and *Parkinsonia* spp. from the ASD data (A), the ground-truthed ROIs (B), the MLC (C) and the MTMF classification (D).

The AVIRIS ground-truthed ROI results show similar trends, albeit a far lower difference in reflectances between the species – generally around 10%. However, in contrast, *P. microphylla* showed lower reflectance than *Tamarix* spp. in the visible region, at 400 nm barely half the reflectance, moving to around 10% less. There was no significant difference between *Tamarix* spp. and *Parkinsonia* spp. for regions outside 520 to 650 nm or over 2100 nm. This is due to the spectra of the other *Parkinsonia* species, as significant differences between *Tamarix* spp. and *P. microphylla* were more frequent – found at almost double the amount of wavelengths (5 nm intervals), although these are all under 1340 nm, where 75% of the region was significantly different. The red edge at around 670 nm is far weaker than the ASD results (absolute reflectance increasing by 10% as opposed to 30%), and reflectances in the visible region increase sharply until red wavelengths at 635 nm where *Tamarix* spp. reflectance is more than double that of the ASD data. This is most likely due to the influence of the surrounding soil and sand within the mixed pixels (Appendix 3). Similarly, absorption features centred around 970 and 1200 nm, related to water and canopy structure, are much stronger (absolute reflectance dropping by around 20% each time, compared to 5 to 1% for the ASD data), probably influenced by the channels much of the wash vegetation borders.

The MLC and MTMF classifications are visually similar to the AVIRIS ground-truthed ROI pixels, and share the strong absorption features, but have some important differences. The more overall accurate MTMF classification is most similar

to the ROI, but with an even narrower difference in reflectance between the species (generally less than 5%, increasing to 15% over 1890 nm). *Tamarix* spp. is less reflective at all wavelengths, which combined with the large overall sample size probably contributed to the significant differences found between the species for every wavelength in this classification, despite the smaller differences compared to the other methods. In contrast the MLC shows the same relationship between the species as the ASD data – *Parkinsonia* spp. with higher reflectance in the visible and SWIR regions, although showing much greater differences than the other AVIRIS results – absolute reflectance in the red region almost 10% higher, while almost double that of *Tamarix* spp. over 1890 nm. This larger inter-species difference is probably influenced by the small sample and narrow vegetation and environmental conditions of the *Tamarix* spp. pixels in the classification, all from the southwest portion of the map.

OPTICAL TRAIT DIFFERENCES BETWEEN SPECIES

Given the spectral differences in regions relevant to optical traits, it is reasonable to assume indices and the optical traits built upon them will also differ. Combined effect size of these indices was compared to the number of methods each index significantly ($\alpha = 0.05$) separated the species for. Median effect size showed a significant decrease as the count dropped (Figure 11). This showed individual methods generally did not have unduly large or small effects, and count could, to an extent, proxy for combined effect size. Average effect sizes per method were generally medium (from 0.24 to 0.33, species difference accounting for around 9% of the variance), but small for LWC (0.09, accounting for around 1% of the variance), drought conditions perhaps minimising variance (Figure 11). However, every trait included indices which successfully separated the species for at least four of six methods (ASD and ROI using both *Parkinsonia* spp. and *P. microphylla*, MLC and MTMF). Therefore all traits were used as indicators of invasiveness.

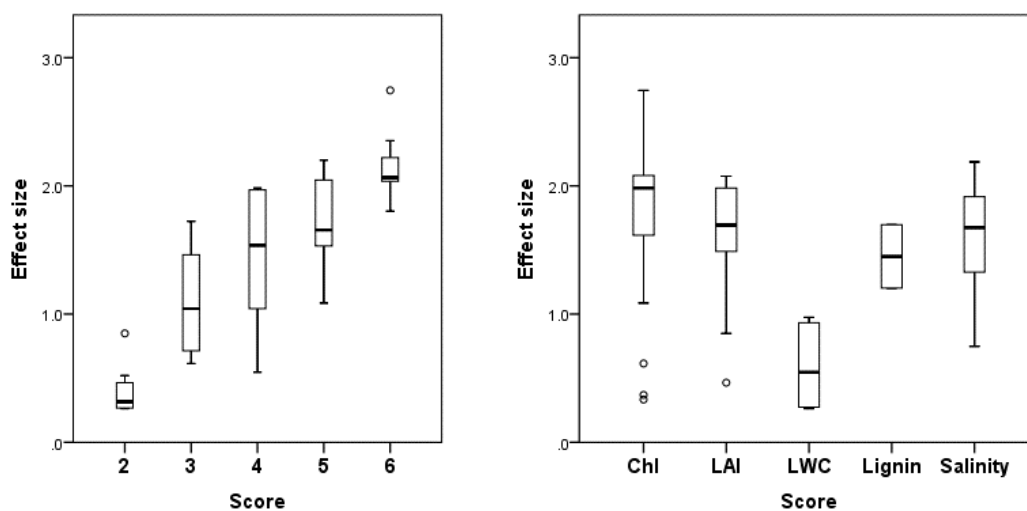


Figure 11. Total effect size in relation to method score (left), and indices for each trait (right). Outliers (circles) over 1.5 times the inter-quartile range.

Tamarix spp. had higher index values for each trait across the large majority of indices and methods, detailed below as we examine the traits individually. Table 10 summarises the robust trait indices, their U-test results, and whether they showed the hypothesised relationship with *Tamarix* spp. (having higher index scores for all traits). See Appendix 4 for expanded U-test results for the different methods.

Table 10. Robust indices selected for each trait, their mean values across the methods, and U-test significance ($\alpha = 0.05$) for each method. T indicates *Tamarix* spp., *P Parkinsonia* spp., and Pm *P. microphylla*. Highlighted red cells not significant to show outlying results where the robust index did not differentiate the method. +/- indicates the relationship of the index to the trait, + shows the trait increases with the index value. Totals section indicates the summed effect value (Effect), the count of significant methods (Sig.), and the number of methods for which the trait increases with *Tamarix* spp., as hypothesised (Trait). Low expected trait direction values are highlighted in red. The SAVI based indices (SAVI, SAVI664, SASI1 and SASI4) use an L constant based upon vegetation density – values of 1 (for very low density) and 0.5 (for intermediate density) were used. In all cases, the L value for intermediate vegetation density better differentiated between the species, so was used in preference.

Trait	Index	+/-	Mean across methods			U-test asymptotic sig.						Totals		
			T	P	Pm	ASD	ASD Pm	ROI	ROI Pm	MLC	MTMF	Effect	Sig.	Trait
Chl	DD	+	0.222	0.077	0.008	0.000	0.000	0.002	0.000	0.000	0.001	-2.353	6	6
	EGFN	+	1.480	0.786	0.687	0.000	0.000	0.000	0.001	0.000	0.000	-2.055	6	6
	Datt3	+	1.503	0.877	0.362	0.000	0.000	0.000	0.000	0.000	0.000	-2.745	6	6
	MCARI2	+	0.638	0.184	0.111	0.000	0.000	0.031	0.004	0.000	0.004	-2.026	6	5
	mND705	+	1.063	0.555	0.331	0.000	0.000	0.004	0.001	0.000	0.036	-2.159	6	6
	mNDVI	+	1.562	0.837	0.679	0.000	0.000	0.009	0.022	0.000	0.000	-2.065	6	6
	mSR	+	6.771	7.374	5.174	0.000	0.000	0.009	0.022	0.000	0.000	-2.051	6	5
	MTCI	+	5.954	7.912	5.900	0.000	0.000	0.000	0.005	0.000	0.000	-2.252	6	2
	NDchl	+	-0.079	-0.509	0.058	0.000	0.000	0.000	0.003	0.000	0.000	-2.299	6	6
	NDVI2	+	0.796	0.384	0.239	0.000	0.000	0.008	0.016	0.000	0.042	-2.076	6	6
	OSAVI	+	0.940	0.457	0.385	0.000	0.000	0.015	0.026	0.000	0.002	-2.011	6	6
	Vogelmann3	+	4.399	2.515	1.270	0.000	0.000	0.000	0.001	0.000	0.000	-2.278	6	6
	REP_LE	+	2327.193	2287.725	1053.567	0.000	0.000	0.000	0.000	0.000	0.000	-2.293	6	6
	SAVI664	+	0.810	0.408	0.308	0.000	0.000	0.044	0.028	0.000	0.015	-1.831	6	6
SR705	+	5.726	4.184	2.096	0.000	0.000	0.008	0.016	0.000	0.042	-2.076	6	6	
LAI	MSAVI	+	0.759	0.348	0.291	0.000	0.000	0.016	0.016	0.000	0.003	-1.803	6	6
	mSR2	+	3.739	2.028	1.125	0.000	0.000	0.008	0.016	0.000	0.042	-2.076	6	6
	NDVI846	+	1.020	0.445	0.440	0.000	0.000	0.014	0.030	0.000	0.000	-2.046	6	6
	RDVI	+	0.745	0.358	0.299	0.000	0.000	0.015	0.018	0.000	0.003	-1.914	6	6
	RSR	+	2.128	1.070	1.067	0.000	0.000	0.012	0.037	0.000	0.000	-2.048	6	2
	SAVI	+	0.785	0.377	0.315	0.000	0.000	0.016	0.018	0.000	0.003	-1.864	6	6
Water	GVMi	+	1.944	1.773	0.643	0.000	0.002	0.296	0.065	0.000	0.000	-0.940	4	6
	LWV11	+	206.929	197.041	37.627	0.040	0.946	0.824	0.003	0.004	0.000	-0.547	4	5
	MSI	-	0.903	0.953	0.712	0.000	0.001	0.793	0.301	0.000	0.000	-0.854	4	3
	LWCI	+	31.436	-5.142	-13.520	0.000	0.000	0.405	0.088	0.000	0.028	-0.975	4	2
	NDII2	+	1.930	1.721	0.559	0.000	0.001	0.408	0.071	0.000	0.003	-0.932	4	6
	SR820	-	0.884	1.081	0.724	0.000	0.001	0.407	0.089	0.000	0.028	-0.932	4	6
Lignin	CAI	+	-0.028	-0.039	-0.007	0.001	0.000	0.026	0.265	0.000	0.000	-1.203	5	4
Salinity	GIR	+	10.134	8.229	3.853	0.000	0.000	0.082	0.000	0.000	0.000	-1.589	5	3
	SASI1	-	0.037	0.058	0.020	0.000	0.000	0.238	0.029	0.000	0.000	-1.889	5	5
	SASI4	+	0.199	-0.067	0.127	0.000	0.000	0.000	0.030	0.000	0.000	-2.187	6	6
	WINDVI	-	12.186	55.498	10.767	0.000	0.000	0.014	0.020	0.000	0.007	-2.059	6	6

CHLOROPHYLL

This trait was assessed with the greatest number of indices, 43, and 15 showed significant differences in their results between the species across every method (Figure 16). Therefore these 15 were selected as robust. They all use the visible spectrum and the red edge, with a variety of methods from simple ratios to derivatives and position of the red edge. 12 of 15 methods showed the expected direction of results, higher values for *Tamarix* spp.. In initial analyses a correlation matrix showed very weak correlations (< 0.3) between the majority and the MTCI, which for which only two of the methods were in the expected direction, as well as the mSR, Datt3 (first derivative of reflectance) and Vogelmann3 (red edge derivatives) indices. A reliability analysis confirmed Cronbach's α would increase with the removal of these variables. The rotated PCA contains two components which explain 81.44% of the variation in the dataset.

LEAF AREA INDEX

LAI had six indices which showed significant differences between the species across all methods (Figure 15), which were used as the robust indices. Five covered the red edge region and wavelengths from 655 to 846 nm, all showing the expected trait direction for every method. The exception, RSR, also used SWIR wavelengths (1600 and 1700 nm) found above to display a weak relationship between the species. RSR showed higher trait values for *Parkinsonia* spp. in four cases – the correlation matrix also showed weak correlations here, so this index was excluded. Only the first principal component was extracted, which explained 95.57% of the variation in the dataset.

LEAF WATER CONTENT

Water indices were the least effective in differentiating the species, six (of 13) statistically significant in four of the methods – these were selected as robust (Figure 12). These all used reflectances in the NIR region, comparing them in four cases to the water absorption band at 1600 nm, in the others at 980 and 1400 nm. Half the robust indices confirmed the expected trait relationship for all methods, LWVI2 for all expect MTMF, MTCI only for the ROI and ASD data, while LWCI showed higher values for *Parkinsonia* spp. in all the AVIRIS data. The correlation matrix showed weak correlations with LWCI and LWVI1 so these were excluded. Only the first principal component was extracted, which explained 96.75% of the variation in the dataset.

LIGNIN-CELLULOSE

The CAI index was the superior indicator of lignin-cellulose, significant differences in species shown in five of six methods (Figure 14), using the longer SWIR region over 2000 nm. The other index, NDLI had a count of only three, performing poorly for the AVIRIS data, despite its large effect size for the ASD. This can be expected given the lack of spectral separability in the shorter SWIR bands it employs. Therefore CAI alone was used as an indicator of this trait, measuring the cellulose content of the plant.

SALINITY

While two indices were successful for all methods, to expand the spectral information used by the indicator, indices with a count of five and six were considered robust (Figure 13). These were all vegetation indices, using vegetation as a proxy for soil salinity, and based around visible and SWIR reflectance. The correlation matrix showed weak correlations with GIR and WNDVI and the other indices, furthermore, their inclusion reduced the KMO measure of sampling adequacy below 0.5, deemed unacceptable (H. F. Kaiser, 1974). Given this, and that the SASI indices were developed especially and found to be effective for halophytic species, they were removed. Only the first principal component was extracted, which explained 74.37% of the variation in the dataset.

The robust indices were weighted using a PCA to create the trait indicators – the final loadings for each are shown on Table 11¹³. The indicators were applied to the AVIRIS image over the study area.

¹³ The EGFN index was not included in the scaled indicator (based on another PCA without it) due to difficulty in calculating derivatives of spectra within the ENVI interface. Given its correlation with the other indices, and the number of other indices, it is unlikely to have made any visible difference to the chlorophyll mapping.

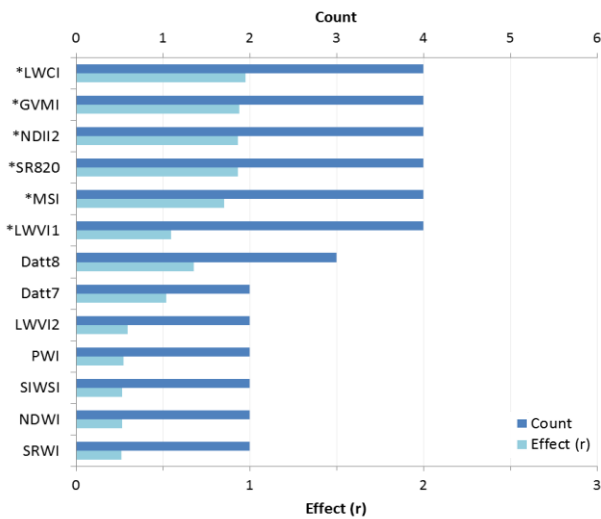


Figure 12. LWC indices ordered by count (number of methodologies in which the index differentiated the species, $\alpha = 0.05$) and combined effect size. Robust indices starred.

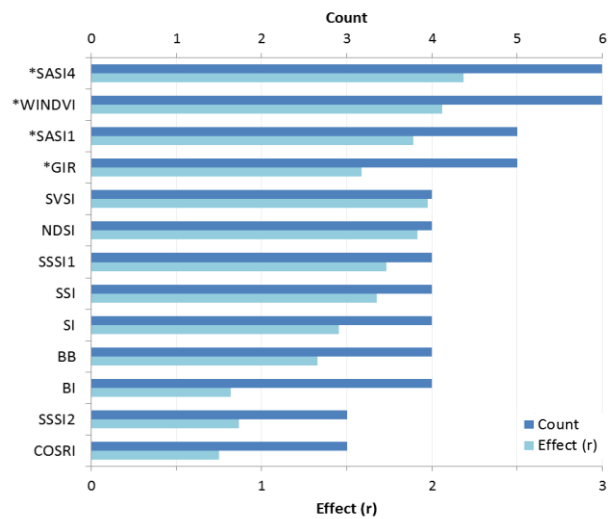


Figure 13. Salinity indices ordered by count (number of methodologies in which the index differentiated the species, $\alpha = 0.05$) and combined effect size. Robust indices starred.

Table 11. PCA loadings for each trait. Chlorophyll shows rotated factor loadings. KMO indicates Kaiser-Meyer-Olkin measure of sampling adequacy.

Chlorophyll		
Index	PC 1	PC 2
NDVI2	0.98538	-0.00412
SR705	0.97894	-0.04647
OSAVI	0.95735	0.08392
MCARI2	0.95407	-0.16168
REP_LE	0.91828	-0.01401
SAVI664	0.89282	0.05702
NDchl	0.87849	0.12969
EGFN	0.87456	0.14536
DD	0.71309	-0.54807
mND705	0.67353	0.11499
mNDVI	0.40268	0.69641

Eigenvalues 8.09874 0.859549
 % of variance 73.62491 7.814079
 KMO 0.800687

LAI	
Index	PC 1
SAVI	0.99763
RDVI	0.99727
MSAVI	0.99617
NDVI846	0.95189
mSR2	0.94348

Eigenvalue 4.778425
 % of variance 95.5685
 KMO 0.860549

LWC	
Index	PC 1
NDI12	0.99426
GVM1	0.99254
SR820	0.99150
MSI	0.95565

Eigenvalue 3.870007
 % of variance 96.75018
 KMO 0.859679

Salinity	
Index	PC 1
SASI4	0.86243
SASI1	0.86243

Eigenvalue 1.488
 % of variance 74.37899
 KMO 0.5

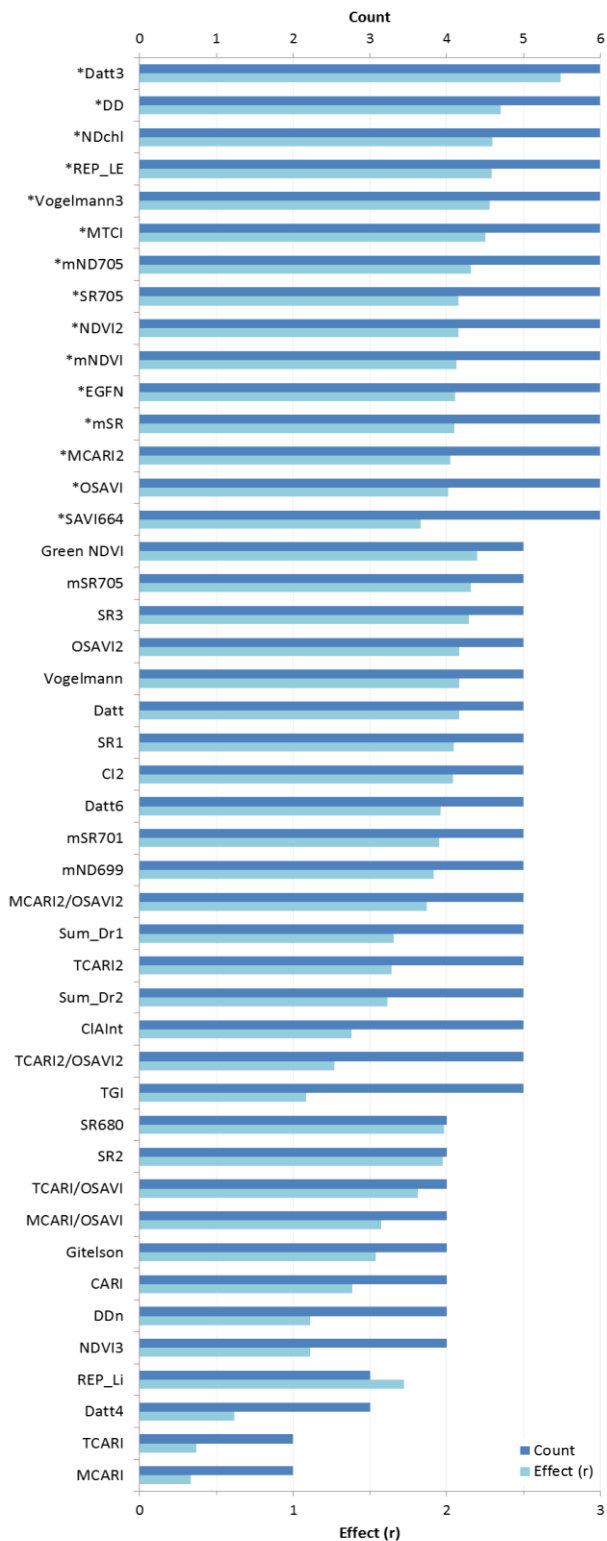


Figure 16. Chlorophyll indices ordered by count (number of methodologies in which the index differentiated the species, $\alpha = 0.05$) and combined effect size. Robust indices starred.

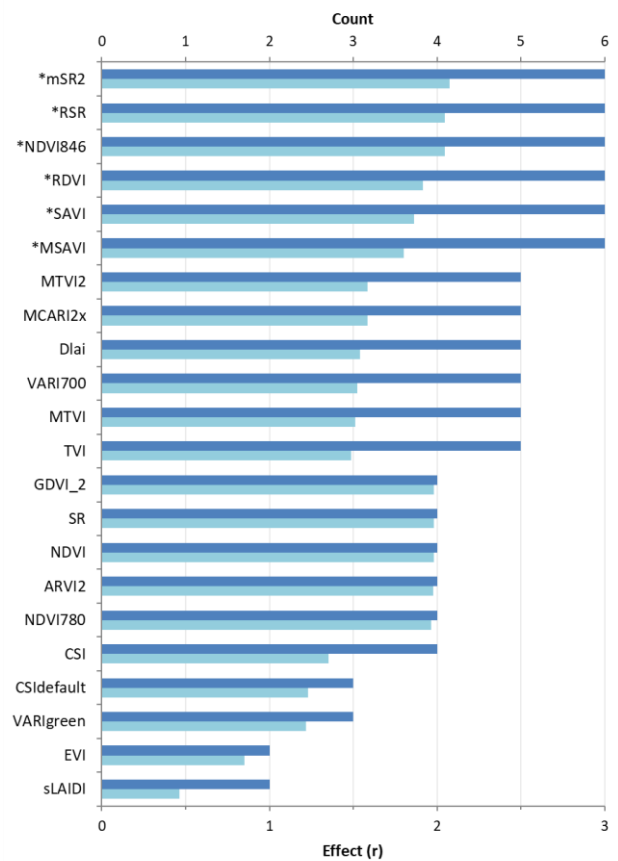


Figure 15. LAI indices ordered by count (number of methodologies in which the index differentiated the species, $\alpha = 0.05$) and combined effect size. Robust indices starred. CSidefault uses the values from Sims and Gamon (2003), rather the maximums and minimums from the study area.

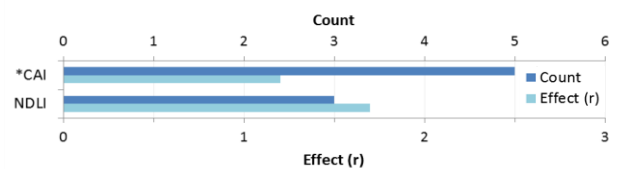


Figure 14. Lignin-cellulose indices ordered by count (number of methodologies in which the index differentiated the species, $\alpha = 0.05$) and combined effect size. Robust indices starred.

OPTICAL TRAIT SEPARABILITY OF CLASSIFICATIONS

The optical trait indicators showed different effectiveness at differentiating the invasive and native plant depending on the classification used (U-test results on Table 12). The combined vegetation map, using all the predicted vegetation positions, found significant differences between the species for all of the traits, with small to moderate effect sizes, the largest in LWC (0.219) and lignin-cellulose (0.184). *Tamarix* spp. scored higher for all invasive traits (Figure 17). However, visual inspection of the mapping showed lower values were often found on smaller vegetation further from the channels. This was perhaps wrongly classified as *Parkinsonia* spp. – the MLC with almost five times the samples as MTMF dominates the combined classification, yet with a 57.6% error of commission for *Parkinsonia* spp., would identify many pixels as this species incorrectly. Therefore we also examined this trait to species relationship on the more accurate but less extensive MTMF vegetation map (Figure 18).

Table 12. U-test results assessing differences between *Tamarix* spp. and *Parkinsonia* spp. in the combined (MLC and MTMF), MTMF and ground-truthed ROI classifications. Significant results marked with asterisk, non-significant highlighted red, $\alpha = 0.05$

<i>Combined</i>	Total	Chl	LAI	LWC	Lignin	Salinity
U	292911550	346175468.5	343519454	266239071.5	285805376	367294289
Z	-52.201	-33.494	-32.937	-65.322	-55.121	-26.047
r (effect)	-0.175	-0.112	-0.110	-0.219	-0.184	-0.087
Sig.	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*

<i>MTMF</i>	Total	Chl	LAI	LWC	Lignin	Salinity
U	59514744	56413778.5	55370837	58030957.5	50915224.5	58559168.5
Z	-0.229	-14.081	-9.736	-11.029	-19.956	-10.326
r (effect)	-0.002	-0.094	-0.066	-0.074	-0.133	-0.069
Sig.	.819	0.000*	0.000*	0.000*	0.000*	0.000*

<i>ROI</i>	Total	Chl	LAI	LWC	Lignin	Salinity
U	6425.0	7132.0	6807.0	6969.0	7112.5	6365.0
Z	-3.307	-2.194	-2.706	-2.451	-2.226	-3.408
r (effect)	-0.197	-0.130	-0.161	-0.146	-0.132	-0.203
Sig.	0.001*	0.028*	0.007*	0.014*	0.026*	0.001*

The MTMF results were surprising – it was expected that removing the sparser, less easy to classify vegetation would strengthen the signal of the *Parkinsonia* spp. and increase the difference in the trait indicators. However, while each individual indicator remained significantly different, effect size was universally smaller. Further, the total invasiveness score displayed no significant difference between the species, and *Parkinsonia* spp. showed significantly higher values for all indicators barring LWC (Figure 18). This therefore raises some uncertainty about the linkage of traits to the invasive and native species. A possible explanation is that while less likely to include erroneous *Parkinsonia* spp., the MTMF classification is more likely to omit correct plants, and the smaller plants omitted may have been more representative of *Parkinsonia* spp. as a whole.

Given this, I tested species differences for each indicator in the AVIRIS ROI data. This is a much smaller sample size (283 points in total), self-selected, and unlikely to be representative of the species traits across the area, but provides ground-truthed data. It followed the same pattern as the combined MTMF and MLC map – *Tamarix* spp. with significantly higher scores for every trait (Figure 19), with a comparable effect size (0.197 for ROI, 0.175 for the combined classification). This also enabled us to examine the differences between the *Parkinsonia* species. Largest differences were seen between *Tamarix* spp. and *P. microphylla*, *P. florida* being more similar to *Tamarix* spp., while *P. aculeata* has a higher median score for every indicator except lignin-cellulose. This is likely due to the numerically and spatially limited sample of *P. aculeata* (Figure 7), which may have been in more favourable conditions, and a more vigorous state given the high water

content shown. The influence of these other species on the classifications, given they are less spectrally distinct from this small sample, should therefore also be considered.

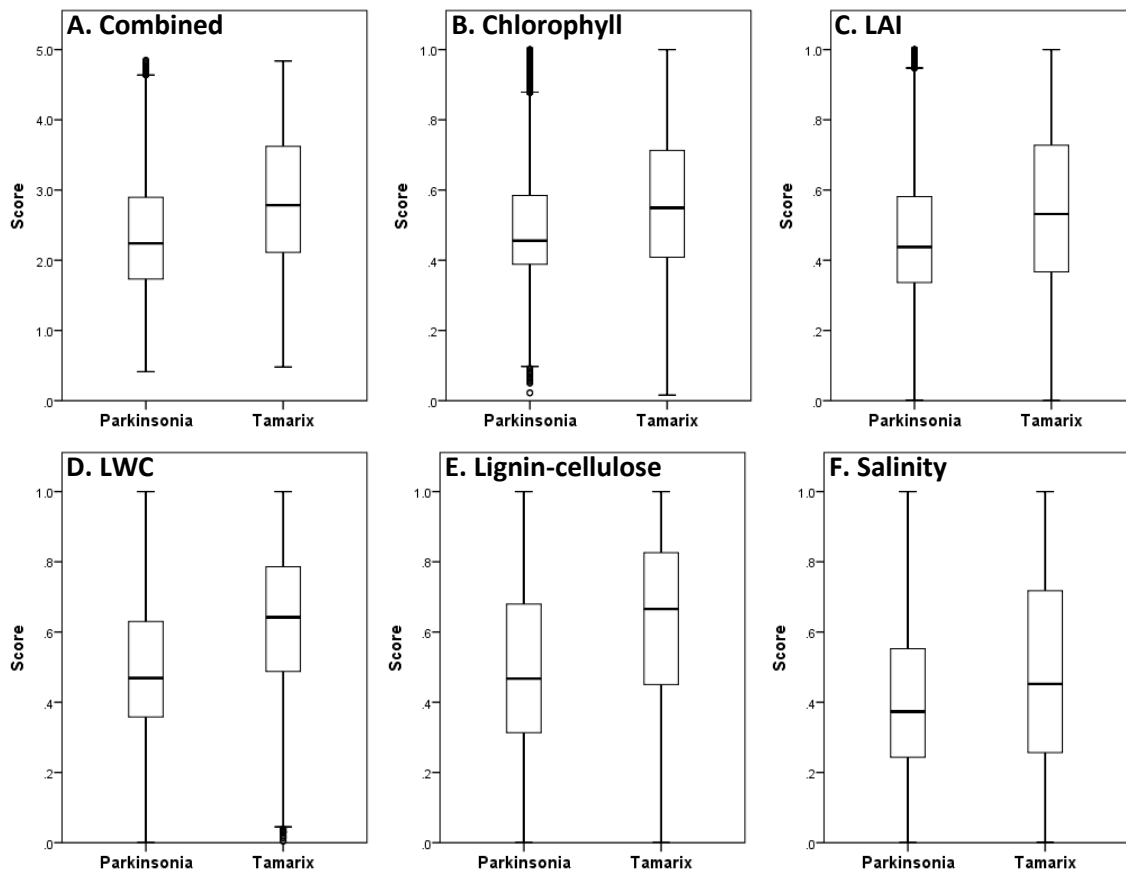


Figure 17. Combined classification (MLC and MTMF) trait indicator scores. Outliers (circles) over 1.5 times the inter-quartile range.

In summary, for most measures all the selected optical traits are significantly higher for invasive *Tamarix* spp. than the native *Parkinsonia* spp. Large numbers of indices with established links to the traits showed significant differences between the species for the majority of methods. Weighted indicators based on these indices also showed significantly higher trait scores for the most extensive, and the ground-truthed classification – although other classifications showed opposite results. It should be noted that effect size was never moderate (0.3, accounting for 9% of the variance) for any of the traits, so these differences are limited.

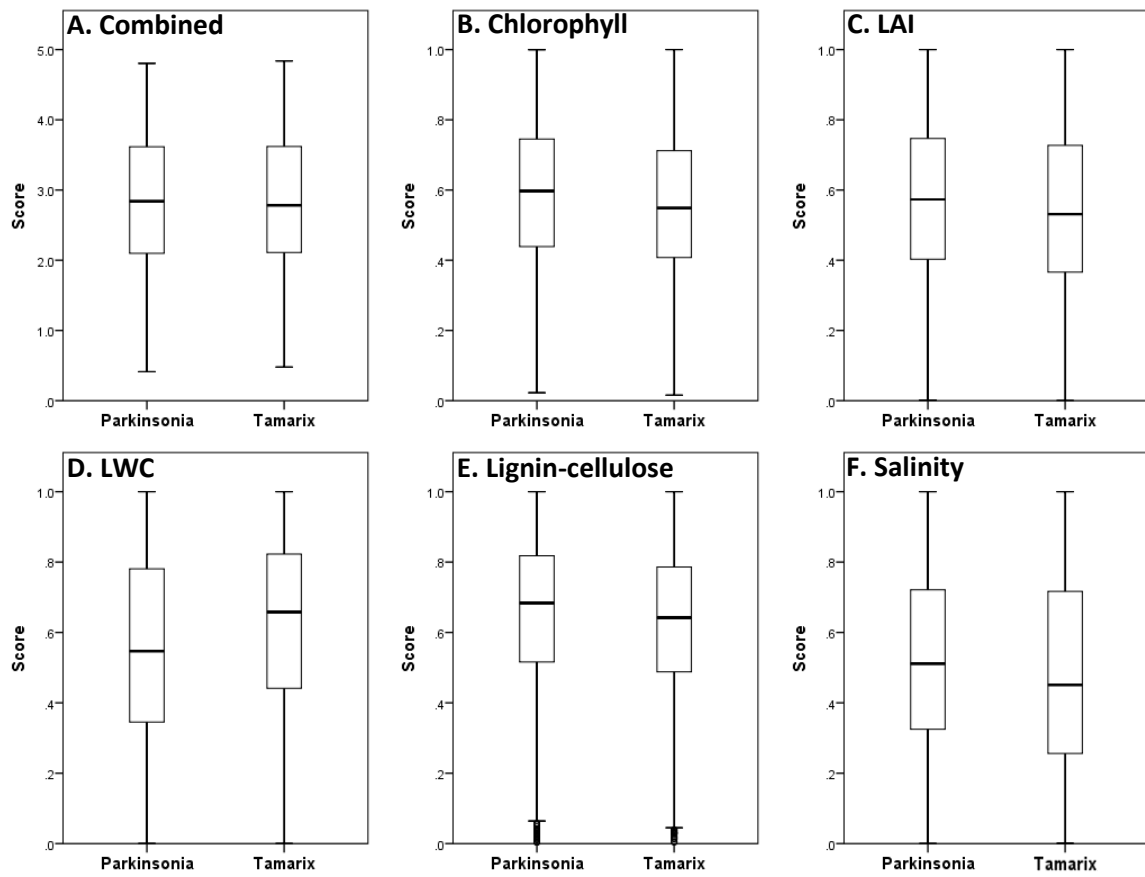


Figure 18. MTMF classification trait indicator scores. Outliers (circles) over 1.5 times the inter-quartile range.

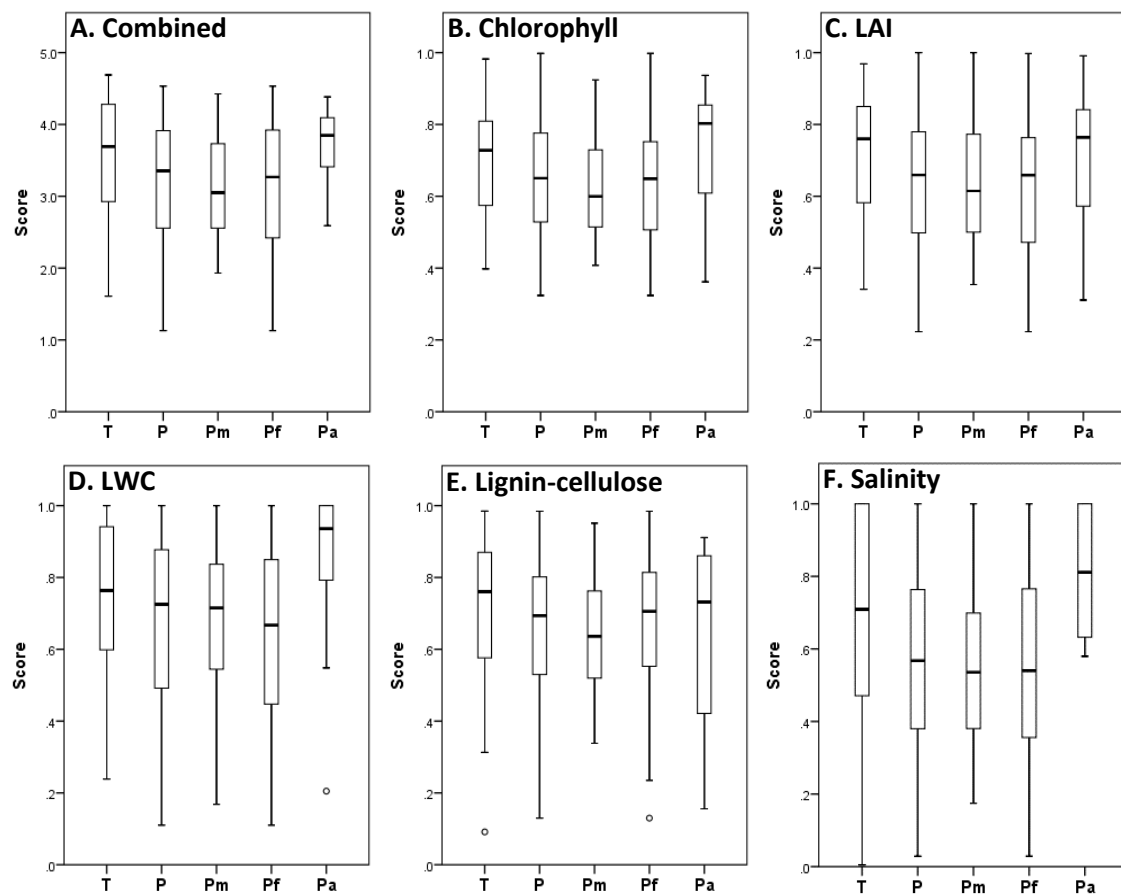


Figure 19. Ground-truth ROI trait indicator scores for species. T denotes *Tamarix* spp., P *Parkinsonia* spp., Pm *P. microphylla*, Pf *P. florida*, and Pa *P. aculeata*. Outliers (circles) over 1.5 times the inter-quartile range.

LANDSCAPE OPTICAL TRAIT EFFECTS

To assess the effects of these traits on the landscape scale, each trait was mapped individually and the maps combined (Figure 20). Areas with invasiveness scores of over 2.5 out of five are highlighted on Figure 21, which uses the ROIs to highlight the exact pixels rather than the ENVI colour scale, which appears to exaggerate the size of higher values. The use of the NDVI to eliminate non-vegetated pixels from images was attempted, but even selecting pixels with a value of over 0.1 (typically representing bare ground; Purevdorj et al., 1998) resulted in very few pixels in the centre of vegetated patches being extracted. It should be noted however, that some extreme values were also found in vegetation towards the very southwest, and the agricultural areas to the east.

Generally similar patterns were found with each indicator mapping the vegetation along the washes. Indicators varied in their ability to eliminate non-vegetated features – leaf water content, lignin-cellulose and salinity all showed extremely high values for buildings and tarmacked runways and roads. Chlorophyll and LAI show broadly the same pattern, highest values along water courses and the washes to the south east, the eastern edge and the north of the image. LWC showed many more of the features of the terrain. Along with lignin-cellulose and salinity it also shows highest values along the channels, but in contrast to chlorophyll and LAI a lower value immediately bordering the channels, then higher values in the washes even further outside. This appears to be detecting soil or surface vegetation distinct from the sparse shrubs with higher trait values.

The combined map better highlights these larger shrubs – generally appearing to have a trait score of over 2.5. However, it also fails to eliminate spurious pixels found in tarmac and buildings until a score of 3.5, while presumably irrigated agricultural patches to the west also have high values. The highest invasiveness trait scores are again concentrated bordering the channels across the map, although there is little differentiation between areas – consistently the larger the vegetation patch, the larger the trait score for its central pixels. These border effects were also noted by the original CSTARS (2004) report – vegetation would be classified differently from the outside of a patch to the inside based purely on density.

The indicators were also plotted as bands within RGB maps to assess their differing importance over the landscape (Figure 22). Given the visual correlation between the chlorophyll and LAI maps, chlorophyll was selected to represent them both, and compared with lignin, water and salinity. These maps both highlight vegetation well as the white combination of bands, the darker central areas indicating its absence. The Chl-Lignin-Salinity map shows chlorophyll (green) as dominant around the washes and channels to the north, east and south, surprising given the drought conditions. Salinity appears dominant in the southern area of the map, bordering on the agricultural area, while also highlighting the buildings and roads. Interestingly, the white trees are surrounded by red lignin-cellulose, implying the detection of leaf litter, which in some areas, such as the south east becomes purple, showing the influence of salinity also. The Chl-Lignin-LWC map conversely shows with purple the combination of lignin-cellulose and water content across the washes, while the yellow areas around for example the central channel in the south show the combination of chlorophyll and lignin-cellulose which differentiates it from the other channels.

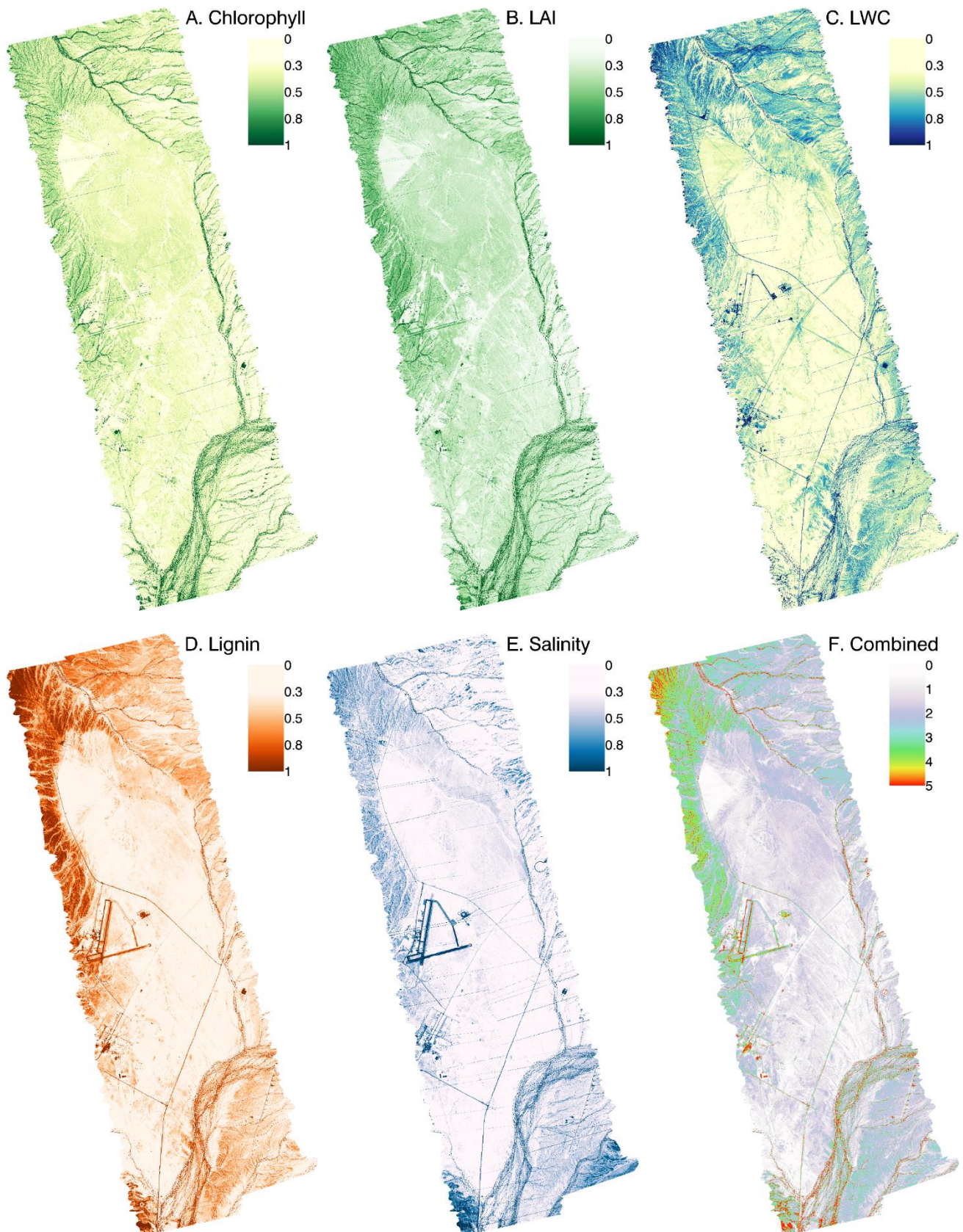


Figure 20. Trait maps showing normalised indicator (from minimum to maximum value found in image) for A) chlorophyll, B) leaf area index, C) leaf water content, D) lignin-cellulose and E) salinity. Map F) shows the combined invasive traits maps. The effect of higher values is exaggerated by the ENVI software, compare to Figure 21.

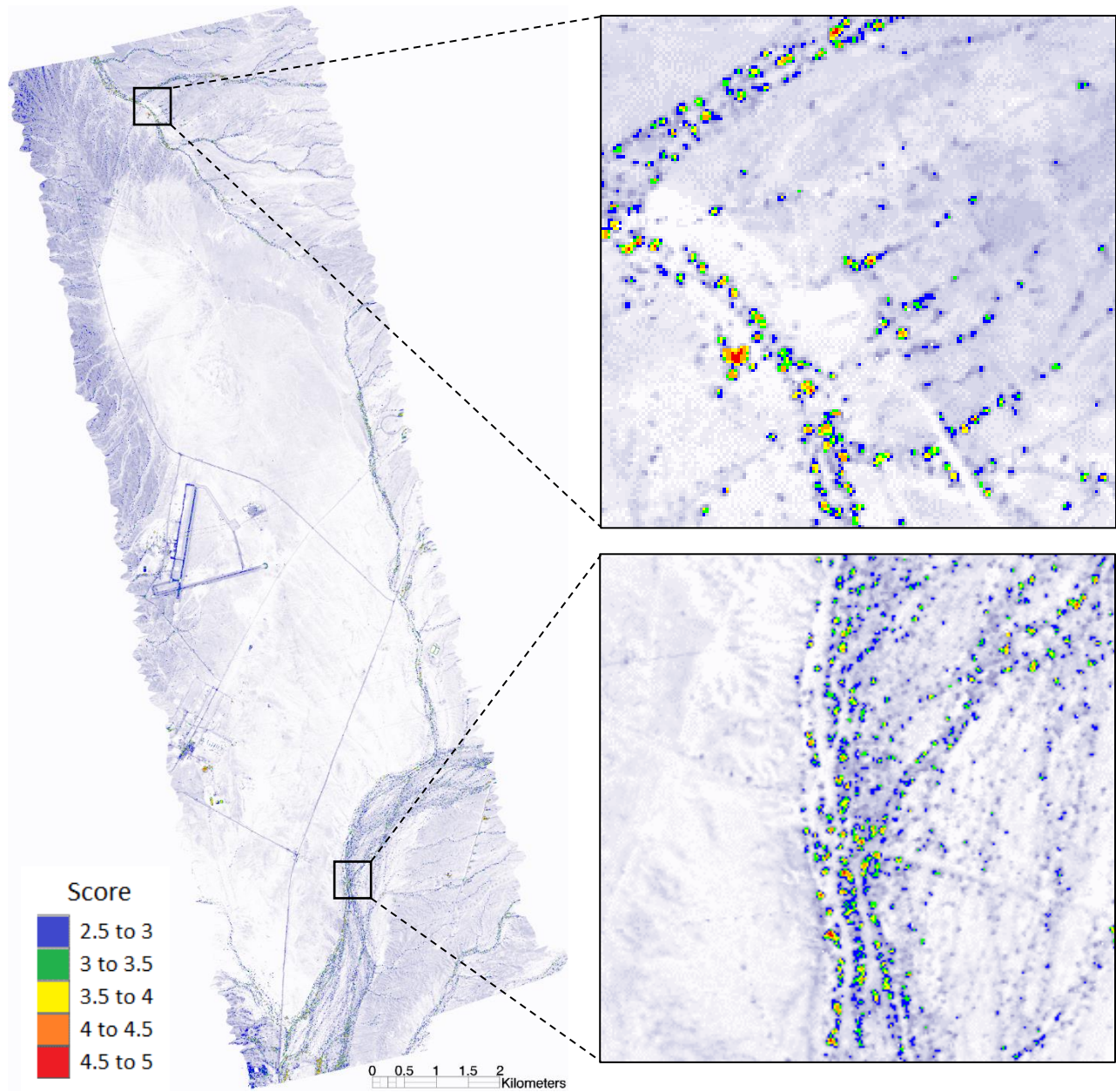


Figure 21. Combined invasive traits, based on summed score of trait maps. Scores of below 2.5 shown in graduated purple. Areas containing ground-truthed *Tamarix* spp. and *Parkinsonia* spp. shown to right.

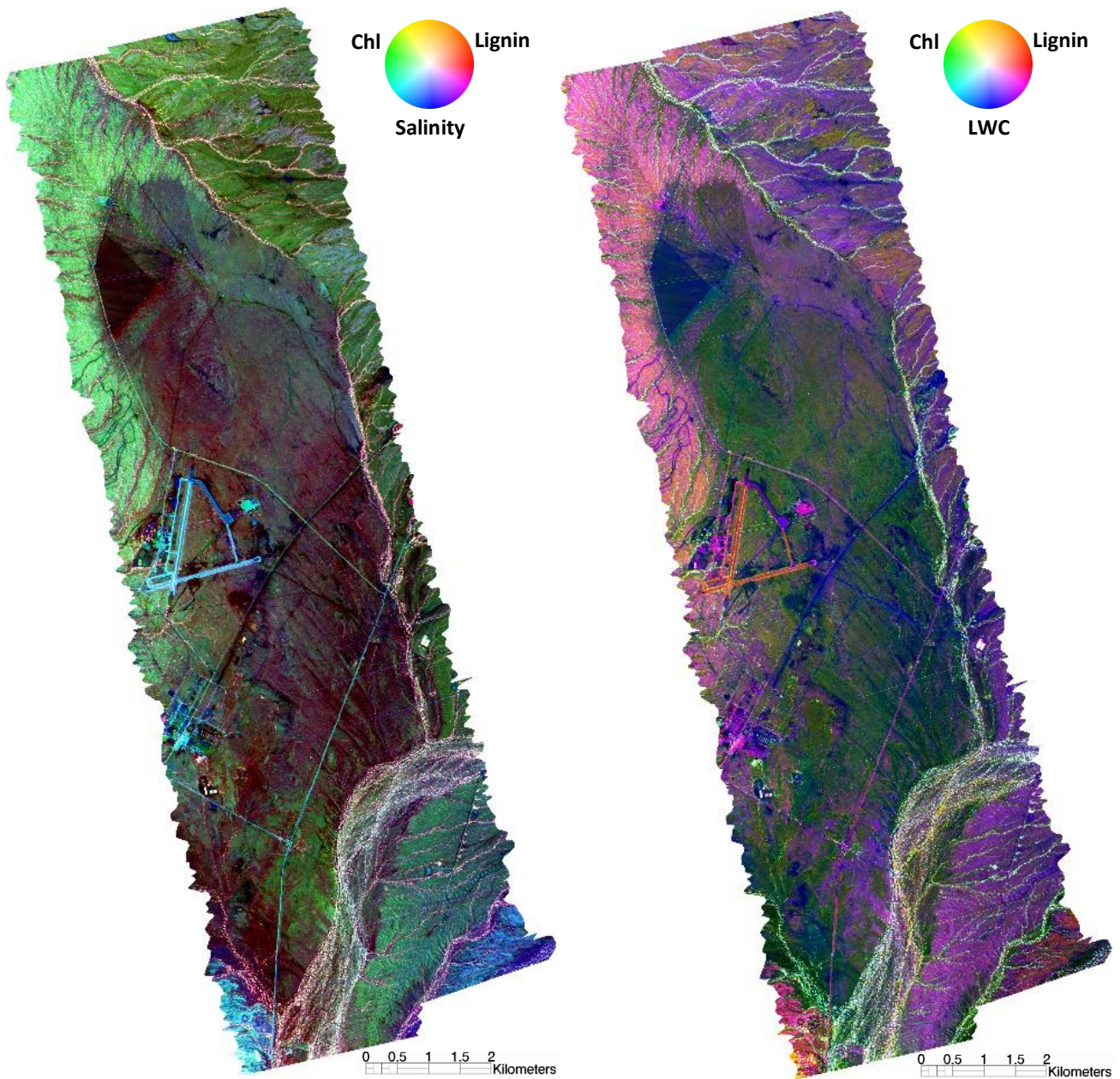


Figure 22. Combined indicator with bands representing chlorophyll (green), lignin-cellulose (red), leaf water content (blue) and salinity (blue)

Finally, the indicators were plotted on the combined classifications of the invasive and native species to assess if a trait or overall invasiveness hotspot was linked with either species. However, a similar effect is seen – traits appear stronger at the centre of the patches of each species, with little visual difference in strength between the plants. *Tamarix* spp. appears in larger patches, and so can appear stronger, particularly compared to the sparse vegetation outside the channels which is mostly identified as *Parkinsonia* spp. Some *Tamarix* spp. patches appear to have higher values, but there is little clear difference in scores, even in the southwest area bordering the agricultural land where the increased plant vigour associated with water access may have been expected to create a greater distinction. Individual trait maps show some differences but a broadly similar pattern (Appendix 5). This was also attempted with the MTMF classification. Less extensive, this maps vegetation in close proximity to the channels. Despite the contrary overall results (see above), mapping was overall very similar, the density effect still being dominant for every trait.

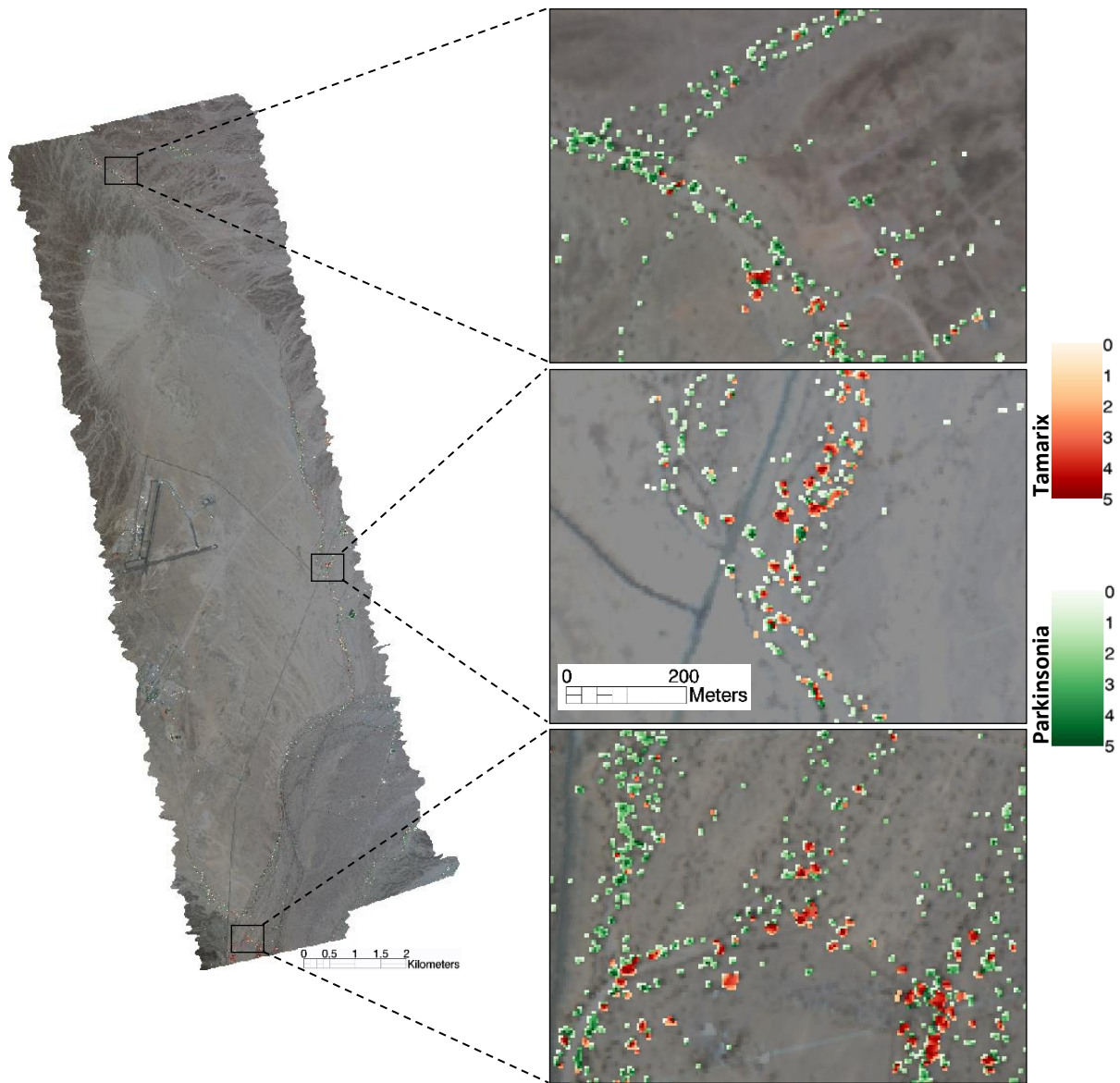


Figure 23. Total invasiveness indicator (on scale to right) for the combined *Tamarix* spp. and *Parkinsonia* spp. classifications. Zoomed in sections referred to in text as north, east and south.

We have illustrated several methods by which traits can be mapped. Due to both the potential lack of clear spectral diversity between plants in the same localities, and the definite problems with scaling and visualising the indicators, invasive trait hotspots can be identified along the channel areas, but these are distinct to neither species.

DISCUSSION

We will firstly examine how our results answer our research questions – the issues and implications brought up then examined in the following sections.

Do the reflectance properties of invasive Tamarix spp. and native Parkinsonia spp. differ significantly across the electromagnetic spectrum?

Reflectance properties of *Tamarix* spp. and *Parkinsonia* spp. differ significantly in many areas of the electromagnetic spectrum, particularly in the visible and near-infrared, as well as over 1940 nm. This suggests that native and IAS have very different constituents, their concentration, physiology and structure. As would be expected, these differences are stronger in the ASD field data, but are also present in the AVIRIS data across both vegetation classifications. However, the weakest responses in terms of significance were from the AVIRIS ground-truthed data – this is perhaps cautionary as these should represent the purest pixels of vegetation cover, with the strongest signal, yet were unable to separate the majority of the data. This could have been caused by a number of factors: canopy structural traits, data collection and processing and the classification algorithms used.

Which of the optical traits of invasive Tamarix spp. differ significantly from those of native Parkinsonia spp.?

Every optical trait showed significant differences between *Tamarix* spp. and *Parkinsonia* spp. Indices related to each trait were able to robustly separate the species for the majority of methods chosen, with generally a moderate effect size. Leaf water content was the least divisive trait, both in terms of effect size and number of methods in which it could be separated – perhaps expectedly given the drought conditions. It could be argued, particularly given that some canopy traits cannot be effectively measured with low LAI (Asner et al., 2000), that this was due to the differences in spectral profiles rather than detection of actual structural and biochemical traits. However, every trait: chlorophyll, LAI, leaf water, lignin-cellulose and salinity showed the hypothesised higher values for *Tamarix* spp. across the large majority of the robust indices, particularly notably for every single ASD result except one (for LWVI1).

These results were mirrored by the trait indicators constructed, although here the choice of vegetation map had a clear effect – the relationship was reversed, *Parkinsonia* spp. with higher trait values, when the more accurate but less extensive MTMF map was used to classify the species. This shows the importance of the classifiers to the results – it could have been justified to exclude the MLC map given it identified very little of *Tamarix* spp. in the study area. The combined MLC and MTMF classification map supported the hypothesised increased invasive trait values in *Tamarix* spp., as did the ASD and ground-truthed results, so we can broadly accept this association between *Tamarix* spp. and higher values in all the traits. On the other hand, sample sizes and extent for the field data were necessarily limited, so is unlikely to represent the full range of species conditions on the image.

Does Tamarix spp. show higher measurements for these invasive traits?

Tamarix spp. invasion, its assumed replacement of *Parkinsonia* spp., therefore will likely increase the value of the optical invasive traits selected – higher chlorophyll and leaf water concentrations, higher LAI and lignin-cellulose, and greater salinity. When mapped, while larger patches of *Tamarix* spp. appeared to high slightly higher values, there was little distinct visible difference between the species for any of the trait indicators or the summed invasiveness score. This could have been due to issues of map scaling and visualisation. The clearest association, present in patches of both species, was the increase in every individual trait towards the centre of the vegetated areas, presumably where the canopy is densest. This shows either the overlap in traits, which would be expected, or traits were also affected by vegetation density – showing a “border effect” where spectral reflectance of the vegetation is mixed with the undercanopy (Almeida et al., 2004).

INVASION AND ECOSYSTEM EFFECTS

The trend towards higher invasive optical trait values under *Tamarix* spp. invasion allows us to make tentative and general assessments as to the changes in ecosystem functions and services as it replaces *P. microphylla*. Our findings, on a population level concur with the hypothesised trends of invasive traits being significantly linked to *Tamarix* spp. replacement, and in turn support some of the more traditional negative impacts associated with *Tamarix* spp. The CSTARS (2004) report was surprised to find *Tamarix* spp. in the dry washes. This contradicts some of the literature which espouses that invasion in the area is based on artificial changes to flood regimes rather than displacement of native species (Stromberg et al., 2009); either indicating that environmental change such as fire or flooding has created gaps for *Tamarix* spp. to exploit, or that *Tamarix* spp. is able to spread amongst, if not definitively displace, native *Parkinsonia* spp.

Increasing chlorophyll and LAI values are linked to competitiveness, productivity, denser canopies and more shade. While denser canopies are preferred by some birds, such as the endangered southwestern willow flycatcher (Ellis et al., 2008), they can have negative effects on understory species (Brotherson & Field, 1987). Tall IAS capable of forming cover were found by Hejda et al. (2009) to have the most severe effects on local ecosystems and species richness, with lower undercanopy light and moisture availability (te Beest et al., 2014). This general increase in primary productivity, and decline in species richness and abundance was also found in the global analysis of invasive impacts by Vilà et al. (2011). The allelopathic effects of increasing salinity will decrease habitat value around *Tamarix* spp. stands. Leaf water content can be linked to water use and evapotranspiration, reducing water availability to local biota, channel flow, and agriculture. Water catchments within the YPG provide drinking water, forage and bathing for 34 species of mammals, birds, reptiles and amphibians (O'Brien et al., 2006), which may be threatened.

Litter deposition will also increase with productivity, shown by the higher cellulose values for *Tamarix* spp. Higher lignin content within the litter will slow its decomposition, potentially slowing nutrient cycling at the ecosystem scale (Godoy et al., 2010), while also reducing forage nutritive value and digestibility (Allinson & Osbourn, 1970). This can impact on the decomposer community – changes to the decomposer fauna and reduced litter decomposition was found after it was unable to adapt to a *T. ramosissima* invasion in the short-term (Bedano et al., 2014).

While a higher leaf water content reduces *Tamarix* spp. flammability, accumulation of litter means stands can be extremely flammable, increasing fire frequency and severity (Busch, 1995). This creates one of its greatest ecosystem impacts, given the severity of impacts on *Parkinsonia* spp., and the extremely long recovery times for vegetation and soil biota (Kade & Warren, 2002). Another IAS, *Pennisetum ciliare* (African buffelgrass), has been identified as an even more serious local threat due to its association with an increased fire regime (Van Devender & Dimmitt, 2006). As a more effective pioneer, *Tamarix* spp. could exploit the gaps created to establish a more homogenous community of far less habitat value.

However, these are continuous, rather than discrete traits (Dukes & Mooney, 2004), and overall effects will clearly be density dependent. Even small amounts of heterogeneity greatly boosted habitat use and stopover value for migrants, even if greatest abundances and species richness was found in native stands (Fischer et al., 2015). Negative impacts may slowly increase, or they may have thresholds, for example certain salinity values, which will have serious effects on the local ecosystem when crossed (Ladenburger et al., 2006). While more discriminating indicators are required to clearly show invasive hotspots, trait values could be usefully be linked to these threshold values, perhaps associated with pure *Tamarix* spp. stands, to warn that management intervention is required. While associated with higher values of these traits, which in net terms probably have negative ecosystem impacts, the moderate increase in traits, comparable to other species of *Parkinsonia*, does not support the dramatic monsterring perspective of *Tamarix* spp., at least in drought conditions.

Management will depend, amongst other things, on the amount of invasion and the surrounding landscape. In irrigated areas such as the southwest of YPG, recovery may be linked to the return of natural water conditions (Stromberg et al., 2007). In other areas, the potential for traits such as salinity to increasingly worsen habitat quality may suggest removal before it can gain a foothold, or management to maintain heterogeneity, depending on local conditions. Given that even the more effective biocontrol is unlikely to eliminate *Tamarix* spp. but help reduce it to coexist with native species, the

latter may likely be the best that can be achieved (Catling, 2005). In a fragile ecosystem, the habitat value of *Tamarix* spp. cannot be overlooked, and in the long-term it is likely to be better adapted to the land use, hydrological, fire regime and climate changes seen (Schlaepfer et al., 2011).

RESULT ROBUSTNESS

Several issues regarding the robustness of this study must be considered when assessing its results.

DATA

The AVIRIS data was high resolution, with good bands available in all spectral regions relevant to the optical traits selected. However, unavoidable data collection and processing issues likely reduced the spectral separability of the species, and in turn the identification of optical trait hotspots. The ground-truthed AVIRIS results extracted (Figure 10) show much smaller spectral separability, greater difference from the ASD spectroscopy, and spectra less typical of vegetation compared to those obtained from the same data by Ustin and Santos 2010 (Figure 5). An issue therefore potentially occurred in the reprocessing of the data (see Appendix 1). Atmospheric correction is a possible cause – the original FLAASH (Fast Line-of-Sight Atmospheric Analysis of Hypercubes) tool, which models and corrects for atmospheric and aerosol reflection was unavailable, so the cruder Dark Object Subtraction process was used. This subtracts manually-selected dark pixels, representing a background signature, from the rest of the image. Therefore spurious values in these pixels would affect the entire image – although likely in a systematic fashion, meaning the species comparisons are still valid even if this weakens comparability with other results.

The strong non-vegetative features in the ground-truthed pixels could also have been caused by changes in vegetation cover between the 2002 AVIRIS imagery and the 2004 ground-truthing, although unlikely as presumably established plants were sampled. However, the rapid growth of *Tamarix* spp., the drought deciduous nature of the species, and the potential for channel changes with flooding, mean locations of pure vegetation recorded in 2004 may have been sparsely covered in 2002.

The extreme drought conditions during data collection – the driest year on record for Yuma (1893 – 2004, CSTARS, 2004), would also have large effects on optical traits. High pixel coverage is required for effective measurement of biochemical and structural optical traits (Asner et al., 2000), but observable leaf area would be minimal in the drought deciduous species, meaning the signal and in turn separability of leaf-measurable traits (all those selected except lignin-cellulose) would be extremely weak. Even in more regular conditions, arid areas have many challenges to remote sensing vegetation, with mixed spectra associated with this sparse coverage, and typically high spectral variability within species, yet low variation between species (Okin et al., 2001). Other studies have been able to detect arid species (Underwood et al., 2003), but the CSTARS (2004) report concluded that reliable spectral-based identification was only possible with the less-stressed plants towards the irrigated area in the southwest.

As expected the spectral separability of the species was measured more effectively in the ASD data, at the plant scale, rather than the 4 m² canopy pixels measured by AVIRIS. Scaling up from ASD to airborne data reduces the magnitude of the reflectance differences as other factors, such as soil brightness and moisture, may add noise to the measured reflectance (Ustin and Santos, 2010). Further, the signal from canopy structural traits could have been reduced given leaf and branch deciduousness in the drought conditions, resulting in a lower differentiation in the AVIRIS data.

The MTMF and MLC classifications also separated the species more effectively than the AVIRIS ground-truthed data. Two factors contributed to this. Firstly, the algorithms on which they are based use differences in spectral information to classify the plants, so distinct differences should be expected in the output of these techniques whether or not they exist on the ground. Secondly, the very large samples (over 10,000 of each species) for each of the classification maps made the finding of significant results more likely in the U test. Effect size shows the variance in the data accounted for by this difference – this however was similar between MTMF (average of 0.099 across every wavelength) and the ROI (average of 0.096), both small effects accounting for around 1% of the variance. In contrast, MLC (average of 0.023) was far smaller

but still significant, while ASD results were moderate (average of 0.37), accounting for around 9% of the variance. The AVIRIS results are therefore to be considered with caution as several confounding factors could have altered the measured reflectance.

The final major data issue also involves the vegetation classifications. First, these included other species of *Parkinsonia* spp. – *P. aculeata* and *P. florida*, with traits more similar to *Tamarix* spp. *P. aculeata* tends to be slightly taller and faster growing than *P. microphylla*, *P. florida* more so, both with denser canopies; *P. florida* is more likely found along streamways and also hybridises with *P. microphylla* (CABI, 2017; Turner et al., 2005). The ASD results showed inter-genera variation was still lower than the differences with *Tamarix* spp., and while *P. aculeata* was found to be the most different in the ROI results, this is probably due to the limited sample. The combined *Parkinsonia* spp. classifications therefore reduce the variation between native and invasive traits, yet at least on the population level, this study still managed to show significant differences across optical traits even in poor conditions.

The greatest issue with the classifications is their use to build and map the trait indicators. All classifications failed to produce accurate and complete maps of the wash vegetation (CSTARS, 2004), and clear issues are present – MTMF classifying buildings and agricultural areas as target species, while the MLC mapped only a very small amount of *Tamarix* spp. (Figure 8). This was probably due to the drought conditions minimising separability, and the sparse vegetation, for which the assumptions of linear spectral mixing on which several classifications are based may not be valid (CSTARS, 2004; Ray & Murray, 1996). The two most successful classification maps were combined to overcome their individual problems of accuracy and coverage, but these issues still influence the extracted data. As highlighted, the choice of classification was critical to the relative strength of invasive traits recorded between the native and invasive species; they would also affect the selection of robust indices and the PCA loadings.

METHODS

VEGETATION INDICES

The relationship of vegetation indices to plant traits is critical to this study. While they have been developed through experimental links to these traits, these relationships are often moderate and non-linear, leading Glenn et al. (2008) to argue that VIs are useful simply as measurements of light absorption, rather than more complex canopy features. Often the statistical approaches used in their formulation means they are suitable only for the conditions in which they were created, and can be unsuitable for large-scale use and use in different conditions (Guisan & Thuiller, 2005; Houborg et al., 2015). Given these issues the study included as many available VIs as practical which were directly related to the traits, maximising the potential spectral information that each indicator could be built from. This wide approach necessarily ignored much of the fine detail of the indices which could have informed their selection – the conditions in which they were used, whether they had a positive or negative relationship with the trait for example; only the robust indices were studied beyond the formula used and reported effectiveness at trait measurement.

The success of the majority of the wavelengths and VIs in differentiating the species may suggest the species were simply spectrally distinct enough that significant differences could be found across the raw and manipulated reflectances without these necessarily relating to the traits mentioned. Seeming to support this are the findings of Asner et al. (2000) that optical traits were only be discernible in pixels with high vegetation cover around 70%, with an LAI of over 2. Fieldwork is required to absolutely confirm the direction of these traits. However, that the robust indices behaved in the expected direction in the majority of cases, but particularly for the more accurate ASD and ground-truthed data, shows at least an indirect relationship between the extracted spectra and the traits assessed. The relationship of the indices, and the traits to one another should also be considered, given the overlap the use of indices to measure traits such LAI and chlorophyll, the linkage between the traits themselves, and the probable relation of stronger signals, and stronger traits, to denser vegetation.

Several other methods to link traits and hyperspectral data were not used due to the difficulty of implementing them within the hsdar framework, particularly given the existence of many other robust indices. These include those based on the area, width and depth of absorption features (Pu et al., 2003), upon chi-square spectral curve fitting (Dawson et al., 1999), and wavelet analysis (Blackburn & Ferwerda, 2008) – these can minimise reflectance differences due to variation in structure and illumination, and outperform VIs in their study areas. Combining multiple indices means the addition of these would have had little impact on our indicators, but if their relationships with traits were found to be robust, they might form the basis of a more selective indicator. Methods for transforming data could also have been applied, via for example, derivatives or continuum removal, again reducing sensitivity to differing albedos (Elvidge & Chen, 1995; Pu et al., 2003). This study attempted to retain maximum spectral information using the raw data. A potential improvement would be to apply every index to each transformation (as Thulin et al., 2014), then select the most effective combinations – although this would considerably increase study complexity given the need to apply for example continuum removal to specific regions of the spectra depending on the index (Pu et al., 2003).

The next section assesses the indices used for each trait. The best performing indices in other studies, even in similar areas, did not necessarily perform better here. Different species will have different relationships between their traits and spectral profiles, particularly with different life forms and leaf morphology, so VIs will be better suited to some rather than others (Blackburn, 2002); likewise to different environmental and vegetative conditions. This uncertainty perhaps supports the process of selecting from a large collection, maximising potential spectral information, rather than relying on a few selected indices.

CHLOROPHYLL

Chlorophyll was perhaps the most discriminating trait for invasiveness, having the largest effect size, and a wide range of VIs using different wavelengths in the visible and NIR regions. As Main et al. (2011) highlight, despite the large number of chlorophyll indices, there has been little consensus on which are robust at the canopy level – they found red edge derivative based indices to be most consistent for a wide range of species, along with those based upon wavebands 690 to 730 nm, again on the red edge. This area matches the mSR, mND (both modified to overcome differences in leaf reflectivity) and DD indices found most robust across 53 tree species at the leaf level by le Maire et al. (2004). All these performed well here across the methods, along with the REP_LE and the EGFN, also based on the derivative of the red edge. The 660 to 680 nm absorption band saturates at low chlorophyll levels, so the robust VIs including this region (DD, mNDVI, OSAVI, REP_LE) may be less transferable to other areas (Kaufmann et al., 2010), although this feature was able to discriminate vegetation cover types to the level of species and age class in more homogenous forests (Kokaly et al., 1996).

A clear issue with chlorophyll measurement is its correlation with LAI. However, given that both traits are related to similar ecosystem processes, such as primary productivity and carbon assimilation, potentially it would be most effective to combine them. Red edge based chlorophyll indices have also been used to measure LAI effectively, in both coniferous and broadleaved trees – although the best VIs varied through the year with canopy development (Heiskanen et al., 2013), chlorophyll concentration also varying with leaf age and condition (Kaufmann et al., 2010). This illustrates that multi-temporal data is needed to allow comparability of indicators between areas, and that a combination of indices is required to take these varying conditions into account. Combined indices such as the MCARI/OSAVI and TCARI/OSAVI attempt to solve LAI and background reflectance effects, and were found to be more effective for measuring open canopies by Zarco-Tejada et al. (2004), but these failed to differentiate the species in the ground-truthed data.

LEAF AREA INDEX

Many LAI-developed indices, and the indicator as a whole successfully differentiated the species. This mirrors similar results from UK invasive species (Williamson & Fitter, 1996), invasive shrubs in savanna areas (te Beest et al., 2014), and woody IAS in South Africa, Australia and New Zealand (Leishman et al., 2014). Wavelengths used were similar to the chlorophyll indices, and trait mapping was very similar (Figure 20) – given the sparse cover this indicator was likely

measuring “effective” area of the pigment-containing plant components, rather than actual LAI (Gower et al., 1999), although comparisons could still be made between species.

Contrasting the findings of Gong et al. (2003) that VIs using SWIR and NIR regions produced similar correlations to forest LAI as those using red and NIR bands – all robust indices except RSR relied on the latter regions. This could be because desert or arid region vegetation has different LAI values, as well as the above suggested interaction with chlorophyll. Red and NIR bands are reported to be less effective at with higher background reflectance (Chen, 1996), and the SAVI, using a soil adjustment factor to minimise these effects was one of the best performing indices (Huete, 1988). However, the widely-used SARVI2 (EVI), which combines the SAVI soil and ARVI atmospheric corrections, performed worse than the indices on which it was based (Roberts et al., 2012), probably due to the inclusion of the 475 nm wavelength not featured in the SAVI.

This is a critical invasive trait, not least because minimum LAI is required for effective measurement of other traits (Asner et al., 2000). Larger LAI has been linked to IAS across multiple conditions (Daehler, 2003; Santos et al., 2012). It is directly related to ecosystem processes through light interception, gas exchange, biomass partitioning, productivity and water use (Nemani et al., 1993). However, its relation to leaf shape and canopy structure can make estimation difficult (Zheng & Moskal, 2009). LAI is also inextricably linked to the other traits at the canopy level – something that should be considered when weighing the indicators against one another. Indices related to water content, leaf greenness and red edge were highly and linearly correlated with LAI in clonal *Populus* stands, increasing LAI decreasing visible but increasing NIR reflectance, as well as strengthening absorption features (Roberts et al., 1998). It can also indicate water stress as a potential invisibility indicator, given the structural changes, in this case obvious leaf and branch fall that can be measured with LAI (Kaufmann et al., 2010).

LEAF WATER CONTENT

Water content was the least effective trait at separating the species. This could be expected given the drought conditions prevalent, and the adaptations of both species to water stress; although the longer root structure of *Tamarix* spp. and its greater, if contentious, rate of transpiration may have been expected to cause a greater differentiation. In these conditions, as would be expected, the stronger absorption bands at longer wavelengths, which become more easily saturated (e.g. within the MSI, NDII and NDWI indices), were more effective than those based on weaker bands (e.g. NDWI, SRWI and WI) (Kaufmann et al., 2010; Sims & Gamon, 2003). That this contrasts the findings of Serrano et al. (2000) for chaparral vegetation and Roberts et al. (2006) in scrubland perhaps emphasises the extent of the drought. With greater variation in conditions, inclusion of these NIR indices however would likely increase accuracy. Such SWIR features are influenced by leaf structure and dry matter therefore using them in combination with NIR wavelengths is recommended (Kaufmann et al., 2010), although this was the case with almost all of the indices selected.

Airborne sensing of leaf water content can be particularly difficult. Mixed pixels will have soil background reflectance, and potential moist residue over ground cover (Cheng et al., 2006). Canopy structure and viewing geometry will also effect results – canopy absorption of water bands will be linked to leaf density (Kaufmann et al., 2010) and correlation of VIs with water content decreases with lower LAI (Dawson et al., 1999). Serrano et al. (2000) found only the WI and NDWI responded to water content, rather than the structure, although our indicator based on longer wavelengths shows visible differences with LAI. Given the difficulties, it is unsurprising that the relationship between LWC and VIs is often unique to individual species (Kaufmann et al., 2010). Nevertheless, this is a potentially important invasive optical trait, which as well as invasiveness, can be linked to invisibility in terms of water stress and flammability (Roberts et al., 2006).

LIGNIN-CELLULOSE

With only two available indices, there is little opportunity for redundancy in a lignin-cellulose indicator. The NDLI was less successful and not chosen as an indicator, perhaps associated with its poor correlation with lignin at low vegetation covers, particularly for senescing leaves, despite its previous effectiveness at differentiating Mediterranean vegetation (Serrano et al., 2002). The CAI was broadly successful at differentiating the species; in contrast this VI was found to be effective even with very low vegetation cover (10%), and across different soil types (Nagler et al., 2003). With the ability

to measure woody canopies, as well as dead plants and litter – litter accumulation linked by te Beest et al. (2014) to invasive shrubs in savanna areas, this trait can be used across different seasons and environmental conditions (Roelofsen et al., 2014). Given its relationship with stress, and its effects on decomposition and nutrient cycling, lignin-cellulose is therefore an important optical trait, particularly given the laborious destructive methods involved in its traditional measurement (Giger-Reverdin, 1995).

SALINITY

The intensification of saline conditions associated with *Tamarix* spp. (Ladenburger et al., 2006) means this trait will not be as applicable to other species, although environmental tolerance has been linked to invasiveness (Daehler, 2003). However, it could also be used to show invasibility through salinity stress in natives. Several approaches were attempted to measure salinity as a trait. Most directly, indices and bands based on visible reflectance should increase with salt evaporites. While the GIR from this region differentiated the species well, in five of six methods, in only half of these was it in the expected direction, despite being a consistent indicator for halite-treated crops (Rud et al., 2011). Potentially drought conditions would reduce transpiration and salt excretion, but in any case, increased reflectance in this region would have been overwhelmed by the greater pigment-based absorption in *Tamarix* spp.

None of the indices directly measuring soil salinity performed well, despite the NDSI previously making good predictions in dry conditions (Al-Khaier, 2003; Mashimbye et al., 2012), the SSI in deltas (Weng et al., 2010), and the SVSI in irrigated semi-arid lands (Lugassi et al., 2017). Analysing soil salinity using spectrometry is problematic, even under controlled conditions – reflectance depending upon topsoil colour and roughness, mineralogy and moisture (Farifteh, 2011; Metternicht & Zinck, 1997). RS adds, amongst others, variation in illumination, mixed pixels with low signal to noise and atmospheric attenuation (Ben-Dor et al., 2002). Given vegetated pixels were selected, the soil signal would be weaker still. A multitemporal approach would also benefit salinity estimates – levels vary throughout the year, affected by rain and soil moisture, becoming easiest to measure at the end of the dry season (Metternicht & Zinck, 2003; Mougenot et al., 1993).

It might be expected that VIs such as the SASI, developed to measure the effects of salt stress as a proxy for soil salinity, would be a poor choice for halophytic species adapted to such stress. However, such indices performed best. To overcome the problem of mixed vegetation and soil cover, some indices, such as the COSRI, combine measures of soil salinity and vegetation stress, in this case using the NDVI (Fernández-Buces et al., 2006). This was unable to differentiate *Tamarix* spp. in either the ASD or the ground-truthed results, but models used to combine similar indices have shown strong relationships with salinity (Wang et al., 2013).

INDICATORS

The trait indicators provided an easily read, comparable scale which utilise a wide range of spectral information from the most effective indices. However, their accuracy and transferability, as the VIs themselves, is partly determined by the range of conditions they are based upon (Sims & Gamon, 2002) – given the limited conditions, their transferability is also limited. The formation relied on arbitrarily selected score for each number of methods an index could significantly separate the species. While all selected traits showed reasonable effect sizes, and significant differences across the majority of methods in the expected direction, expansion of the study would allow for more systematic selection criteria to be developed. Therefore the methods used may be transferable, but the indices selected and weightings are very unlikely to be.

The PCA weighted the indices for each indicator. Indices uncorrelated with the majority were discounted – potentially incorrectly given that many robust VIs used similar spectral regions. Nonetheless, these majorities supported the hypothesised trends for each trait, suggesting they were correct. A more transferable approach could use a greater variety of indices – having alternatives using different wavelengths would increase its applicability to different conditions. However, it may be more effective to follow our method to select indices relevant to specific locations, rather than

attempting to build general indicators which while more transferable, are likely to be considerably weaker at displaying differences given the variation in index values shown.

The total invasiveness indicator relies on simple addition of the individual indicators, thereby increasing the potential for trait hotspots to be indicated. As well as ignoring the overlap between traits, it also assumes they are of equal importance in displaying invasiveness. Total effect size, the amount of interspecies variance accounted for by each trait, could be used here as a weighting mechanism (although only LWC showed substantially lower effect size than the others). Weighting could also link these indicators more effectively to ecosystem services impacts – expert opinion, as Lavorel et al. (2011) could be used to scale each indicator depending on its importance.

MAPPING

The combined mapping appeared effective at identifying vegetation, but conclusions about trait and invasiveness hotspots are limited. Even given the significant spectral and trait differences on a population level, mapping failed to highlight clear local differences in traits between the species. Trait scores increased closer to the centre of vegetation patches across the image – they appear to reflect vegetation density more so than discriminating between the species, perhaps inevitably given the weak vegetation signal from the outside of the canopy. This border effect, where outlying plants interact with underlying cover, was also shown by Almeida & Filho (2004), while the CSTARS (2004) spectral angle mapper classification similarly shows how species identified changed improbably from *L. tridentata*, to *Parkinsonia* spp. to *Tamarix* spp. with vegetation density from the outside to the inside of patches.

Much of this can be explained by the above problems with the AVIRIS data, sparse vegetation and drought conditions limiting the spectral separability of the plants. Scaling of the indicators is also an issue. The normalisation of the indicators relied on trial and error to set the maximums and minimums so that the full extent of the scale was used to display differences in vegetation, a necessarily subjective process. A more systematic method could use, for example, the NDVI to restrict the area in which the scale is normalised to vegetation. Drought conditions meant this was unsuitable here, little of the vegetation discriminated even at NDVI values associated with bare soil. Nevertheless, this should be considered in future studies to more systematically and effectively normalise the indicators without influence of non-vegetated outliers, and to restrict visualisation to vegetated areas without spurious values from roads and buildings.

METHOD IMPLICATIONS AND FUTURE DIRECTIONS

The trait-based method successfully distinguished an IAS in an arid environment using differences in traits across a number of datasets. This can be used to illustrate the spatial pattern of trait distribution for both natives and IAS, highlighting areas of invasion, where the traits of the IAS have replaced the native, and of invasibility, where changes in native traits can highlight ecosystem stress which IAS could exploit. Trait selection was largely successful in separating the species, in ways linked to ecosystem processes, although there was redundancy between the LAI and chlorophyll traits. A large advantage of this approach is that trait selection can be tied to the subject of interest – from stress (Zarco-Tejada et al., 2009), to invasive mechanisms such as seed production (Joshi et al., 2006), to direct ecosystem services such as pollination (Galbraith et al., 2015) to functional diversity and ecosystem health as a whole (Díaz et al., 2007; Fontana et al., 2014). In some cases a single discrete or strongly differentiating trait may be enough to show the desired impacts.

However, given the data and classification limitations, further study is required to establish the usefulness of this approach in distinguishing definite trait and invasibility hotspots in arid areas. Fortunately the process can be adapted relatively easily to new image data. Expanding the sample over space would give a more complete picture of the spectral variability of each species in different conditions, and allow further examination of the robustness of the indices chosen. Expanding it over time would have the same effect, while also reducing the impact of phenological differences and events such as droughts. Using multiple time steps has been found to out-perform data collected from a single point in time in identifying *Tamarix* spp. and other species (Aguate et al., 2017; Evangelista et al., 2009; Lehmann et al., 2015). As Roberts

et al. (2012) highlight, there are significant seasonal changes in chlorophyll, moisture, lignin-cellulose and LAI related reflectance which a robust indicator needs to take into account. Further, time series data would allow the tracking of invasive traits, as well as the effectiveness of management employed.

Hyperspectral data was required for many of these traits, the high spectral resolution necessary to measure the specific absorption features related to traits such as lignin-cellulose. However, many broadband indices exist, particularly for chlorophyll, LAI and water content, and it would be interesting to compare their performance given the large advantages in availability, cost and spatial coverage. The need for hyperspectral data will restrict wide-scale adoption, given the cost and scarcity of airborne spectrometry (Schmidtlein et al., 2012) and storage and processing problems (Paganini et al., 2016). However, airborne spectroscopy coverage is expanding and upcoming hyperspectral satellite-borne sensors such as the EnMAP mission will enable wider-scale research in the near future (Guanter et al., 2015; Nunes et al., 2017).

Therefore its use must be justified. For individual species with known effects, simple classification through techniques such as MLC or MTMF may be easier and possible without hyperspectral data. *Tamarix* spp. has previously been successfully mapped using phenological differences – although this restricts data collection to relevant times (Carter et al., 2009; Everitt et al., 1996). Using hyperspectral profiles as a whole was shown to be more effective than optical traits at accurately differentiating oak populations (Cavender-Bares et al., 2016). Modelling classifiers such as Maxent have been used to classify target species using presence and absence data in a particular area, which have successfully predicted regional *Tamarix* spp. distributions using environmental predictors (Cord et al., 2010), but have also been used on a landscape scale with hyperspectral data (Skowronek et al., 2017).

Trait mapping in this form also overlooks two major factors in invasion – environmental change and propagule pressure. Alongside the use of plant optical traits, inclusion of RS environmental factors such as soil moisture, ground cover, and weather extremes could improve estimation of invasibility. *Parkinsonia* spp. diebacks for example occur with severe summer rain deficits (Bowers & Turner, 2001). Combining traits with modelling of propagule pressure, perhaps through neighbourhood density or the identification of pathways, could further increase the potential of the trait approach to highlight risk of invasion (Richardson & Pyšek, 2006).

Despite these issues, the potential for this method is great. Traits can be remotely detected over wide-scales, and linked to impacts on ecosystem functions and services. This can reduce the many uncertainties, and biases, surrounding the impacts of IAS to directly measure trait effects on the chosen ecosystem, rather than estimating them through presence or probable presence. The strength of traits can be used to show the degree of invasion, while stress traits can indicate invasibility, acting as an early warning system, or show the effect of understory invasives on canopy vegetation. Using expert local knowledge, optical traits can be converted into positive or negative impacts on ecosystem services, and hotspots mapped (Lavorel et al., 2011).

CONCLUSIONS

This study attempted to assess the effects of *Tamarix* spp. invasion on optical traits on a landscape scale. We firstly established that invasive *Tamarix* spp. could be spectrally separated from native *Parkinsonia* spp. species for visible and NIR spectral regions, and those over 1940 nm, for handheld and aerial spectrometry using a variety of different classification methods.

We linked this spectral separation to the ability of vegetation indices to measure plant traits using these spectral profiles. We showed that VIs from each trait – chlorophyll, LAI, leaf water content, lignin-cellulose and salinity could also be used to successfully differentiate the species. In the large majority of cases these indices showed the hypothesised results – that traits associated with invasiveness have higher values for *Tamarix* spp.

We then constructed indicators from these indices to more robustly assess the distribution of these traits on a landscape scale. These indicators had mixed results – for the combined MLC and MTMF vegetation map and the ground-truthed data the expected relationship was again found – *Tamarix* spp. was significantly associated with every indicator of invasiveness and summed invasiveness score. However, the more accurate MTMF map showed the opposite results. This illustrates the importance of the vegetation classification to any conclusions drawn.

Finally, we attempted to map the indicators to illustrate hotspots of invasive traits, both using total invasiveness score maps, and using indicators as RGB bands. While seeming promising techniques, little visible variation was present between the species – indicators increasing most clearly with vegetation density. This could be due to problems of weighting and scaling the indices, while the drought conditions and sparseness of vegetation also detracted from the strength of the optical traits shown. Such conditions also created large inaccuracies in the vegetation classifications used to create and map the indicators. This means that in the study area the method can only be used to make general, directional assessments of the impact of invasion on optical traits and in turn ecosystem services.

Nevertheless, there was a clear relationship between plant optical traits and IAS across a number of datasets. Using methods such as this will only become more important with global change, as non-species specific, wide-scale, transferable solutions become more urgently required. Areas where optical traits would be particularly useful would be to assess the change in native traits with invasion stress and density of invasion – many of the negative effects of *Tamarix* spp. occur with its homogeneity rather than presence in a mixed community. Expanding a similar study over time would increase the captured trait variability in both native and IAS, allowing a better estimation of their separability and the effectiveness of this method; as well as allowing the tracking of invasion effects. With the development of robust optical trait indicators for ecosystem health, this approach could be widely adopted, not only to show impacts of invasion, but a multiplicity of environmental changes.

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APPENDICES

APPENDIX 1. PREPROCESSING OF AVIRIS IMAGES

The preprocessed AVIRIS images available contained large numbers of bad bands (over 90), in regions important to trait classification. There was also spatial misalignment between bands. Therefore the raw AVIRIS flightlines were used, which did not share these issues. They were processed as follows using ENVI:

- Georeferencing - using the attached GLT (global lookup table) and IGM (input geometry) files created clear errors. Instead the images were georeferenced using a processed mosaic, which had been previously georectified to a digital orthophoto quad of the area. This was done using automatic image to image registration, using over 30 tie points per image, each with a root mean square error of below one per pixel.
- Mosaicking - the georeferenced flightlines were then combined into one image. Images were first masked to provide uniform background values. The seamless mosaicking tool required the images to be spectrally subset into layers of 10 bands, these were mosaicked one by one, then stacked to create the final image. Automatically generated seamlines were used to divide the overlapping sections of the flightpaths. Overlap based colour correction, using the larger eastern “yumasands3” flightline as a reference, was used to make the colour and tone consistent in the final image.
- AVIRIS wavelengths were added to the individual bands by editing the ENVI header file.
- Atmospheric correction - this was applied to change the data from radiance to reflectance, removing the scattering and absorption effects of the atmosphere to convert data into comparable units. The original FLAASH correction package used, with complex water and aerosol modelling, was unavailable. All other available methods were attempted – Flat Field, Internal Average Relative Reflectance, Log Residuals and automated and manual Dark Object Subtraction (DOS). Manual DOS was selected, as the only method which avoided large spikes in the produced reflectance while maintaining variation between cells. DOS assumes a stable minimum digital number (DN) value in the dark pixels selected, in this case from the tarmacked runways, which is then subtracted from all pixels in the image.
 - The darkest available pixels selected with the threshold tool had many bands of negative radiance, an error. However, the next darkest pixels were brighter than some areas of vegetation, meaning using these for DOS resulted in large areas of negative reflectance. Therefore, the darkest pixels were used for the subtraction, but in the two abrupt shifts to negatives the pattern of the next darkest pixels was followed, which did not share these drops. This was accomplished by calculating the percentage changes between each band in the next darkest pixels, then applying this to the radiance at the band before the darkest values fell sharply (Figure 24). The mean radiance of the darkest pixels was then calculated, and applied to the image using the manual Dark Subtraction tool .
- Bad band removal - noisy and zero bands were removed. Bands below 395 nm and above 2419 nm were excluded as not relevant to the traits identified, as were those where the AVIRIS sensors overlapped (665 and 1254 nm). Others were identified by visual inspection; bad bands demonstrating a consistent spiking across pixels covering different surface types, out of context with library and image spectra provided by the original survey (CSTARS, 2004; Ustin & Santos, 2010). These were removed at 655, 665, 722-732, 760-770, 818-827, 924, 1136, 1184, 1203, 1250-1254, 1263-1274, 1374-1394, 1454-1474, and 1822-1880 nm.
- Bad pixel removal - pixels with extreme values (orders of magnitude higher reflectances or negative values) were omitted to prevent their influence on further analysis. Reflectances of under -0.005 were excluded, as the DOS process will create some negative values; this preserved enough pixels for analysis, while eliminating clearly spurious pixels.

- Reflectance values - these were converted to between zero and one by firstly converting the images from integers to floating point, then dividing them by 10,000 using ENVI band math. This made them consistent with the ASD data, and also of the format that many vegetation indices require.
- The shapefiles for the vegetation regions of interest were slightly misaligned. The map was offset by altering the coordinate of the tie point to X = 0.567, Y = 0.929 to align them precisely over the map pixels. The ROIs and other classification images were also misaligned to the newly created mosaicked image – they were fit over these corrected shapefiles by offsetting each by X = -1 and Y = 19.

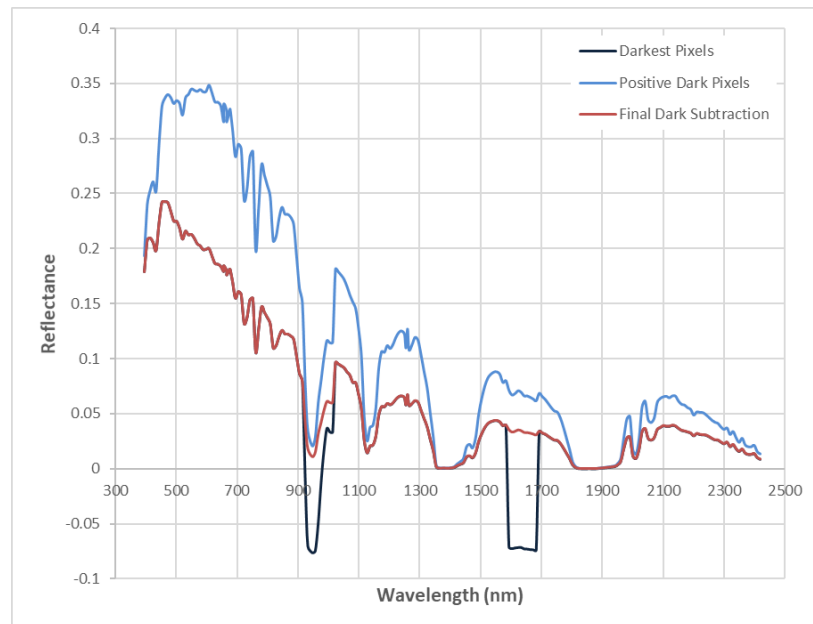
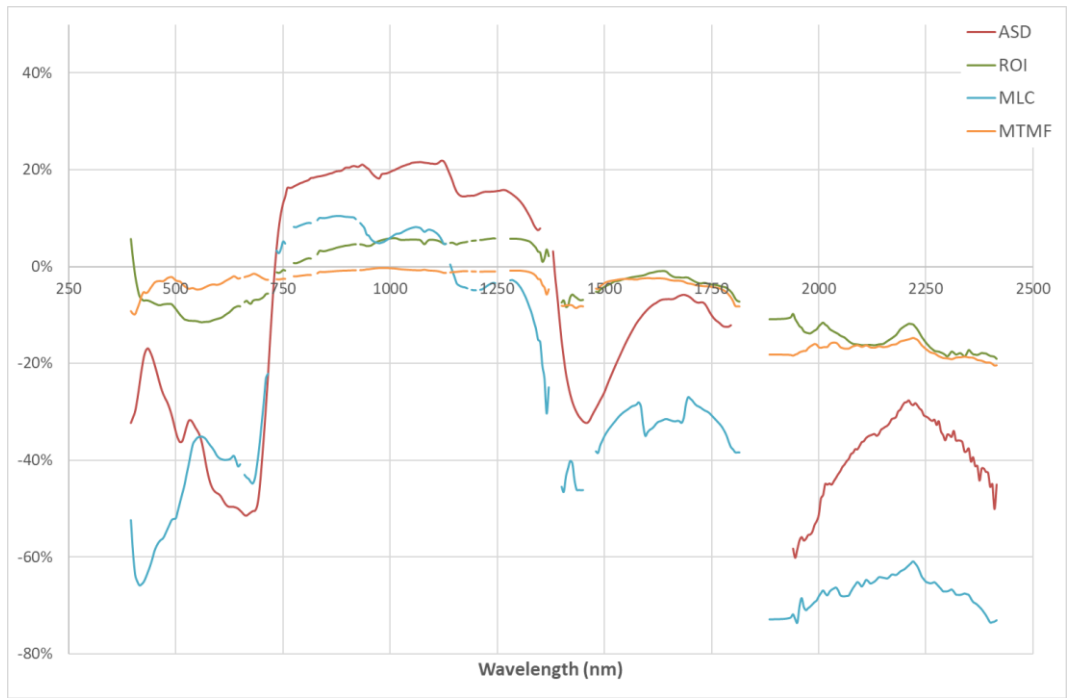


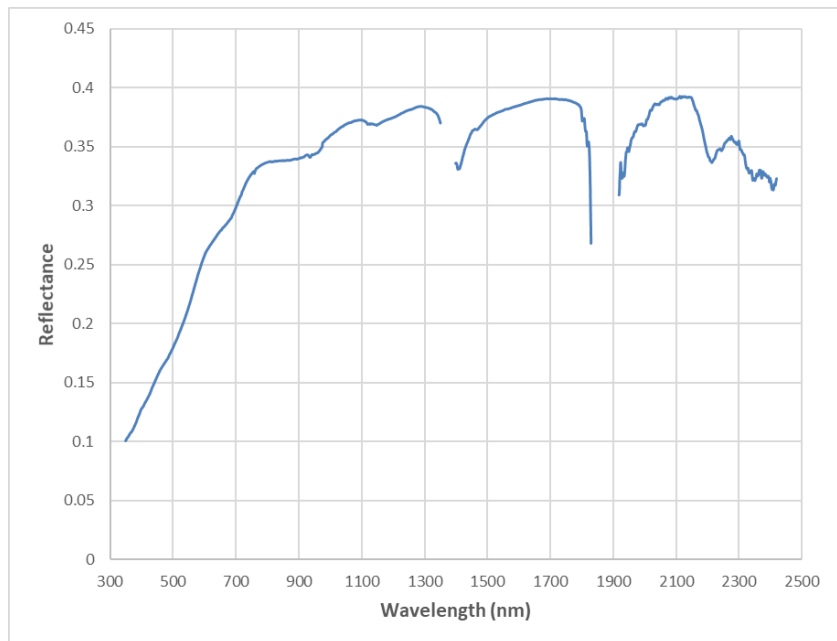
Figure 24. Creation of spectra for dark subtraction – negative areas of darkest pixels were adjusted using the percentage changes from the positive dark pixels (the next darkest set which didn't have negative values). This created the final dark subtraction spectra, which was applied to the dataset.

APPENDIX 2. PERCENTAGE DIFFERENCES BETWEEN REFLECTANCES

Percentage differences between the mean reflectances of *Tamarix* spp. and *Parkinsonia* spp. for each method.



APPENDIX 3. MEAN REFLECTANCE FROM ASD SOIL SAMPLES



APPENDIX 4. ROBUST INDICES U-TEST RESULTS

The mean values, effect size (r) and asymptotic significance (Sig.) for each of the methods used. $\alpha = 0.05$, highlighted red cells not significant.

Trait	Index	ASD			ASD P. microphylla			ROI			ROI P. microphylla			MLC			MTMF					
		Mean T	Mean P	Sig.	Mean	r	Sig.	Mean T	Mean P	r	Sig.	Mean	r	Sig.	Mean T	Mean P	r	Sig.				
Chl	DD	0.076	-0.011	0.000	-0.009	-0.790	0.000	0.053	0.043	-0.198	0.002	0.035	-0.440	0.000	0.082	0.034	-0.042	0.000	0.042	0.041	-0.023	0.001
	EGFN	0.682	0.562	0.000	0.594	-0.663	0.000	0.336	0.194	-0.240	0.000	0.186	-0.293	0.001	0.441	0.014	-0.034	0.000	0.083	0.061	-0.035	0.000
	Datt3	0.352	0.157	0.000	0.166	-0.790	0.000	0.500	0.356	-0.458	0.000	0.393	-0.390	0.000	0.586	0.309	-0.039	0.000	0.263	0.219	-0.208	0.000
	MCAR12	0.387	0.096	0.000	0.089	-0.742	0.000	0.074	0.057	-0.140	0.031	0.043	-0.255	0.004	0.167	0.021	-0.036	0.000	0.037	0.040	-0.021	0.004
	mND705	0.524	0.259	0.000	0.256	-0.782	0.000	0.214	0.166	-0.188	0.004	0.150	-0.282	0.001	0.294	0.099	-0.035	0.000	0.125	0.124	-0.015	0.036
	mNDVI	0.856	0.590	0.000	0.590	-0.775	0.000	0.268	0.187	-0.170	0.009	0.179	-0.202	0.022	0.418	0.041	-0.034	0.000	0.080	0.075	-0.032	0.000
	mSR	20.262	4.181	0.000	4.404	-0.775	0.000	2.093	1.670	-0.170	0.009	1.541	-0.202	0.022	-15.941	1.179	-0.026	0.000	1.429	1.377	-0.025	0.000
	MTCI	2.291	0.984	0.000	0.965	-0.788	0.000	2.365	3.641	-0.282	0.000	9.871	-0.249	0.005	0.708	2.657	-0.014	0.000	2.361	2.518	-0.059	0.000
	NDchl	0.415	0.200	0.000	0.200	-0.782	0.000	-0.239	-0.293	-0.291	0.000	-0.284	-0.264	0.003	-0.175	-0.333	-0.035	0.000	-0.321	-0.333	-0.072	0.000
	NDVI2	0.400	0.190	0.000	0.184	-0.782	0.000	0.148	0.116	-0.174	0.008	0.111	-0.212	0.016	0.229	0.059	-0.037	0.000	0.080	0.078	-0.014	0.042
LAI	OSAVI	0.554	0.352	0.000	0.342	-0.757	0.000	0.130	0.090	-0.158	0.015	0.086	-0.196	0.026	0.247	0.007	-0.036	0.000	0.036	0.035	-0.022	0.002
	Vogelmann3	1.175	0.767	0.000	0.762	-0.782	0.000	1.208	0.992	-0.248	0.000	1.015	-0.304	0.001	1.446	0.615	-0.040	0.000	2.286	0.558	-0.048	0.000
	REP_LE	714.811	700.677	0.000	699.156	-0.790	0.000	714.539	709.031	-0.257	0.000	708.822	-0.311	0.000	721.667	702.075	-0.041	0.000	704.709	703.767	-0.034	0.000
	SAVI664	0.452	0.278	0.000	0.266	-0.684	0.000	0.122	0.093	-0.131	0.044	0.083	-0.193	0.028	0.223	0.024	-0.037	0.000	0.052	0.052	-0.017	0.015
	SR705	2.389	1.478	0.000	1.466	-0.782	0.000	1.370	1.277	-0.174	0.008	1.261	-0.212	0.016	1.670	1.133	-0.037	0.000	1.188	1.184	-0.014	0.042
Water	MSAVI	0.461	0.272	0.000	0.260	-0.648	0.000	0.098	0.068	-0.157	0.016	0.062	-0.212	0.016	0.193	0.002	-0.036	0.000	0.025	0.024	-0.021	0.003
	mSR2	1.843	0.841	0.000	0.827	-0.782	0.000	0.718	0.613	-0.174	0.008	0.595	-0.212	0.016	1.051	0.448	-0.037	0.000	0.511	0.506	-0.014	0.042
	NDVI846	0.653	0.419	0.000	0.412	-0.775	0.000	0.113	0.059	-0.161	0.014	0.056	-0.191	0.030	0.253	-0.033	-0.036	0.000	0.004	-0.002	-0.036	0.000
	RdVI	0.442	0.277	0.000	0.265	-0.701	0.000	0.103	0.071	-0.159	0.015	0.066	-0.208	0.018	0.193	0.003	-0.036	0.000	0.026	0.025	-0.021	0.003
	RSR	2.132	1.072	0.000	1.067	-0.782	0.000	-0.001	-0.001	-0.165	0.012	-0.001	-0.184	0.037	-0.002	-0.001	-0.036	0.000	-0.001	-0.001	-0.028	0.000
	SAVI	0.466	0.292	0.000	0.280	-0.676	0.000	0.108	0.075	-0.157	0.016	0.070	-0.208	0.018	0.204	0.003	-0.036	0.000	0.028	0.027	-0.021	0.003
	GVMI	0.390	0.313	0.000	0.311	-0.303	0.002	0.682	0.675	-0.068	0.296	0.665	-0.163	0.065	0.709	0.623	-0.033	0.000	0.649	0.647	-0.032	0.000
	LWV11	0.062	0.054	0.040	0.057	-0.007	0.946	85.997	85.096	-0.015	0.824	75.139	-0.261	0.003	96.870	87.327	-0.010	0.004	96.001	98.256	-0.075	0.000
	MSI	0.505	0.616	0.000	0.630	-0.335	0.001	0.168	0.168	-0.017	0.793	0.163	-0.091	0.301	0.194	0.132	-0.034	0.000	0.147	0.147	-0.031	0.000
	LWCI	31.055	-5.609	0.000	-13.616	-0.388	0.000	0.177	0.182	-0.054	0.405	0.192	-0.150	0.088	0.152	0.233	-0.032	0.000	0.207	0.207	-0.016	0.028
Lignin	NDII2	0.314	0.222	0.000	0.216	-0.328	0.001	0.706	0.700	-0.054	0.408	0.684	-0.159	0.071	0.742	0.633	-0.033	0.000	0.669	0.668	-0.021	0.003
	SR820	0.503	0.614	0.000	0.628	-0.335	0.001	0.177	0.182	-0.054	0.407	0.191	-0.150	0.089	0.151	0.233	-0.032	0.000	0.207	0.207	-0.016	0.028
	CAI	-0.005	-0.004	0.001	-0.002	-0.474	0.000	-0.010	-0.012	-0.145	0.026	-0.011	-0.098	0.265	-0.009	-0.018	-0.027	0.000	-0.015	-0.018	-0.173	0.000
	Salinity GIR	1.795	2.168	0.000	2.058	-0.392	0.000	3.203	3.071	-0.113	0.082	3.590	-0.380	0.000	4.512	2.384	-0.026	0.000	2.495	2.424	-0.034	0.000
	SAS11	-0.005	0.008	0.000	0.008	-0.704	0.000	0.021	0.022	-0.077	0.238	0.024	-0.192	0.029	0.016	0.024	-0.018	0.000	0.022	0.020	-0.097	0.000
Salinity	SAS14	0.286	0.163	0.000	0.162	-0.790	0.000	-0.049	-0.081	-0.242	0.000	-0.071	-0.191	0.030	-0.010	-0.119	-0.034	0.000	-0.113	-0.120	-0.070	0.000
	WINDVI	2.445	5.475	0.000	6.083	-0.782	0.000	7.794	12.367	-0.161	0.014	9.369	-0.204	0.020	6.039	30.685	-0.036	0.000	-16.373	27.883	-0.019	0.007

APPENDIX 5. COMBINED VEGETATION CLASSIFICATION TRAIT IMAGES

Comparisons of *Tamarix* spp. (red) and *Parkinsonia* spp. (green) from locations around the study site (see Figure 23) for each trait indicator. Darker indicates greater indicator value.

