Spatial extent of invasiveness and invasion stage categorisation of established weeds of Queensland, Australia

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Abstract. The risk posed by invasive alien species is determined primarily by two factors: distribution (occupancy) and abundance (density). However, most ecological studies use distribution data for monitoring and assessment programs, but few incorporate abundance data due to financial and logistical constraints. Failure to take into account invaders' abundance may lead to imprecise pest risk assessments. Since 2003 as part of the Annual Pest Distribution Survey (APDS) exercise in the state of Queensland, Australia, government biosecurity officials have collected data on distribution and abundance of more than 100 established and emerging weeds. This data acquisition was done at spatial grid sizes of 17–50 × 17–50 km and across a very broad and varied geographical land area of ~2 × 10^6 km^2. The datasets provide an opportunity to compare weed dynamics at large-medium spatial scales. Analysis of the APDS datasets indicated that weed distributions were highest in regions along the southern and central, coastal parts of Queensland, and decreased in the less populated inland (i.e. western) and northern parts of the state. Weed abundance showed no discernible landscape or regional trends. Positive distribution–abundance relationships were also detected at multiple spatial scales. Using both traits of weed abundance and distribution, we derived a measure of invasion severity, and constructed, for several (64) weed species, 'space-for-time' invasion curves. State-wide and in each of Queensland's 10 regions, we also categorised the invasion stages of these weeds. At the grassroots of local government area or regional levels, the derived invasion curves and stage categories can provide policy direction for long-term management planning of Queensland's priority weeds.

Keywords: abundance–distribution relationship, invasion curve, life-history traits, pest risk assessment, spatial scale, Queensland, weeds.

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Introduction

Biological invasion is a key component of human-induced global change (Mack *et al.* 2000; Ehrenfeld 2010), and must be proactively and adaptively managed (Auld and Johnson 2014; Booy *et al.* 2017; Osunkoya *et al.* 2019*a*, 2019*b*). Successful management of invasions is influenced by knowledge of spatial extents or scales, impacts, and identification of the key drivers promoting invasiveness (Pyšek *et al.* 2008, 2009; Václavík and Meentemeyer 2012; Wilson *et al.* 2014; Osunkoya *et al.* 2019*a*). Invasiveness itself refers to the degree at which an invader has become established, spread and its impact in an ecosystem (Catford *et al.* 2012; Lacasella *et al.* 2017; Fan *et al.* 2018).

Understanding the scale-dependency and the contexts in which invasion processes operate is challenging. At large spatial scales (e.g. global, national or state-wide), the distributions of invasive species are thought to be best explained by climatic and historical factors (Sutherst 2003; Freckleton *et al.* 2005; Bradley 2013). At medium–low scales (e.g. regional, catchment, farm levels), local factors like land cover, topography, soil types or human activities (e.g. disturbance, population size, road networks) play greater roles in distributions of the invaders (Freckleton *et al.* 2005; Froese *et al.* 2019). Thus through consideration of multi-level spread patterns, it will be feasible to distinguish (for a given invader, say in a region) between invasiveness

factors that favour arrival and colonisation (i.e. distribution) and those that influence spread and establishment (i.e. increase in abundance or cover) (Brummer *et al.* 2013; Akin-Fajiye and Gurevitch 2018). For example, having many released individuals per introduction event favours distribution, whereas multiple introduction events allow environmental stochasticity to be overcome and hence tend to favour establishment (van Kleunen *et al.* 2018). Consequently, the use of simple occurrence data in species distribution models and in estimation of spatial spread may not reflect correctly an invader's population dynamics, and as such additional information relating to abundance or density (an indicator of propagule pressure) may improve our understanding of factors that influence a species' invasiveness (Bradley 2013; Lacasella *et al.* 2017).

Data for mapping weed spatio-temporal extent and abundance are drawn from a variety of sources. These include information from long-term depositories like herbaria, supplemented with information from local floristic surveys, published literature, and citizen science databases (Delisle *et al.* 2003; Antunes and Schamp 2017). Although these sources tend to contain substantial information on distribution, they rarely contain robust abundance data. Compared with using distribution data alone, the combination of both distribution and abundance data will generate a more robust invasion curve – an excellent bivariate indicator of invasiveness and the degree of disruption of ecosystem function and services (Standards Australia International Ltd 2006; Fleming *et al.* 2017).

Abundance data, especially on a medium–large spatial scale (such as at the regional, state and national levels) are rarely collected because of logistic and financial constraints (Bradley *et al.* 2018). Where such data are collected and integrated with spatial and temporal data of occupancy and climate or habitat suitability models, the ensuing distribution-abundance function is invaluable for mapping invasion stages, delineating the spatial extent of invasion severity, and quantification of invasiveness at multiple scales. For example, Ngugi and Neldner (2017) derived abundance data from systematic ecological plot data and combined this with distribution data from herbarium records to assess the invasive threats of non-native species in two bioregions of Queensland. Additionally, the two traits of invasiveness (i.e. abundance and distribution) have been shown to be correlated and hence one may reinforce or serve as a surrogate for the other, though the reliability of such a correlation at different spatial scale or in different types of organisms has often been questionable (Thompson *et al.* 1998; Buckley and Freckleton 2010).

Here we explore the Annual Pest Distribution Survey (APDS) data series – a qualitative medium-large scale dataset on distribution and abundance of priority weeds (established and new incursions) of the state of Queensland, Australia. The APDS data series, initiated in 2003, are consistent gridded spatial data (or cells), each on 17–50 × 17–50 km area and spanning the entire state. Periodically, the APDS captures local and regional expert knowledge of ~100 introduced pest plants and animals from on-the-ground local government and state biosecurity officers in a standardised form. Information from selected annual (mostly recent)

surveys can be accessed online from the Queensland Spatial Catalogue – BQ's Interactive Weed Map, or as PDF maps (https://www.daf.qld.gov.au/business-priorities/biosecurity/invasive-plants-animals/pest-mapping/distribution-maps, accessed 23 September 2020). Aggregate measures of weed invasions derived from the APDS have previously been used in State of the Environment reports (e.g. https://www.parliament.qld.gov.au/Documents/TableOffice/TabledPapers/2019/5619T2204.pdf, accessed 23 September 2020). In a recent pest risk assessment project, Osunkoya *et al.* (2019*a*) explored the distribution aspect of the APDS data and found a good agreement in weed spread between that generated by the datasets and that obtained from stakeholders' consultations. Indeed since its inception, the APDS has been a tool for documenting distribution and abundance of pests at the state level. We contend herein that there is also an opportunity to use the datasets to examine pest spatio-temporal trends and prioritisation at lower spatial scale levels of region or local government areas for policy or weed control decisions. Local and regional species inventories of invaders, such as that of the APDS, can provide useful information to identify multiple scale patterns of invader's presence or dominance, and to test alternative hypotheses explaining the invasion dynamics observed.

Our aims, using the weed datasets of the APDS series and taking into consideration the influence of survey period (year), regional variation, and differences in species' intrinsic traits (e.g. plant life form, life cycle) and historical factors (e.g. time since introduction, invasion pathway), are to:

(1) examine the patterns of variation (correlation relationship) between invasiveness traits of weed distribution and abundance, and the consistency of the trends at different spatial scales;

(2) construct state-wide and lower level (regional or local government area) invasion curves for 64 established and emerging weeds to classify weeds' invasion stages. Based on the invasion stage classifications, we then provide state-wide or regional control and mitigation measures for each of our focal weeds; and

(3) compare invasion scenarios (i.e. invaders' distribution) between a model that takes into account climate suitability and one that considers the entire landscape as potentially 'invadable' (i.e. open to occupancy or invasion). To do this, we integrated climate suitability–species distribution (henceforth the CS-SD) model into the dataset based on available 'Eco-climatic Index' values (EI) for 38 of our 64 test species (see Kriticos and Randall 2001; Sutherst 2003), and compared the model output with that generated from real dataset of spatial grid cell occurrence (henceforth, the GCO model) sourced from the APDS (see Gassó *et al.* 2012; Wilson *et al.* 2014 for a similar treatise). Climate suitability models can potentially predict areas where future spread is more or less likely, thus informing policy makers, including land managers, as to which areas are not currently occupied by an invader and how best to prepare or mitigate its arrival (e.g. Kriticos *et al.* 2018; https://www.agrifutures.com.au/wp-content/; https://www.daf.qld.gov.au/__data/assets/, accessed 13 June 2020).

Materials and methods

Study area

The study area (the state of Queensland) lies in north-eastern Australia (Fig. 1). The average minimum annual temperature varies from −10.6 to 5.4°C, and average maximum annual temperature varies from 36.0 to 49.7°C; mean precipitation ranges from 600 to 780 mm per year (Australia Bureau of Meteorology, http://www.bom.gov.au/, accessed 8 October 2020). Spanning an area of 1.73×10^6 km^2 (Fig. 1), the state of Queensland encompasses significant climatic and environmental gradients. Consequently, Queensland invasive flora, just like its native flora, varies considerably between regions, but is more similar across local government areas (LGA) within a given region (Osunkoya *et al*. 2019*a*). Established and widespread pest plants and animals are managed at a regional level in Queensland by local government authorities. Each of Queensland's 77 LGAs belongs to one of 10 regional organisations of councils (hereafter 'regions'), which are administrative groupings of nearby LGA councils that share relatively similar geographic and climatic features. These regional affiliations (south to

north) are: south-east (SEQld), Darling Downs (south-west) (DDSW), Wide Bay Burnett (WBB), Central Queensland (CQld), Remote Area Planning And Development (central west) (CWQld), Whitsunday (WHITS), North Queensland (NQld), North-West Queensland (NWQld), Far-North Queensland (FNQld), and Torres Strait Islands (TORRES) (see Fig. 1, and supplementary material table 1 in Osunkoya *et al*. 2019*a*; for LGA memberships of each Queensland region). In this study, to align with previous and sequel studies (Osunkoya *et al*. 2019*a*; O. O. Osunkoya, unpubl. data), we use regions and the entire state of Queensland to delineate the two spatial scales in which invasiveness of our focal invaders are explored.

Data compilation from Queensland APDS series

The oversight and management function of weeds and pest animals throughout Queensland is conducted by Biosecurity Queensland (BQ) – a statutory government agency within the Department of Agriculture and Fisheries. Since 2003 and at the LGA level, BQ carries out an APDS exercise to collect information on the distribution and abundance of the most important established and emerging invasive plant and animal species in Queensland (~100 species) (https://www.daf.qld.gov.au/business-priorities/biosecurity/invasive-plants-animals/pest-mapping/distribution-maps, accessed 13 September 2020). BQ, in collaboration with on-the-ground local government and state biosecurity officers, captures landscape, local and regional data on distribution and abundance of these introduced pests in a standardised form (Table 1). The biosecurity officers are very familiar with the locations, extent, and ecology of invaders in their LGAs and regions. Experts estimated qualitative abundance on a 7-point scale (Table 1) of each invader species on paper maps within 17–50 × 17–50 km grid cells that were overlaid on the maps of LGAs or regions they manage, and then digitised their assessments to create abundance estimates across the whole of Queensland.

Between 2003 and 2006, each APDS survey exercise mapped weed distribution and abundance using two grid sizes across Queensland: 0.167 × 0.167 degree (10 min) grids ('small grids', ~17 × 17 km in area) in coastal areas, and 0.5 × 0.5 degree (30 min) grids ('large grids', ~50 ×
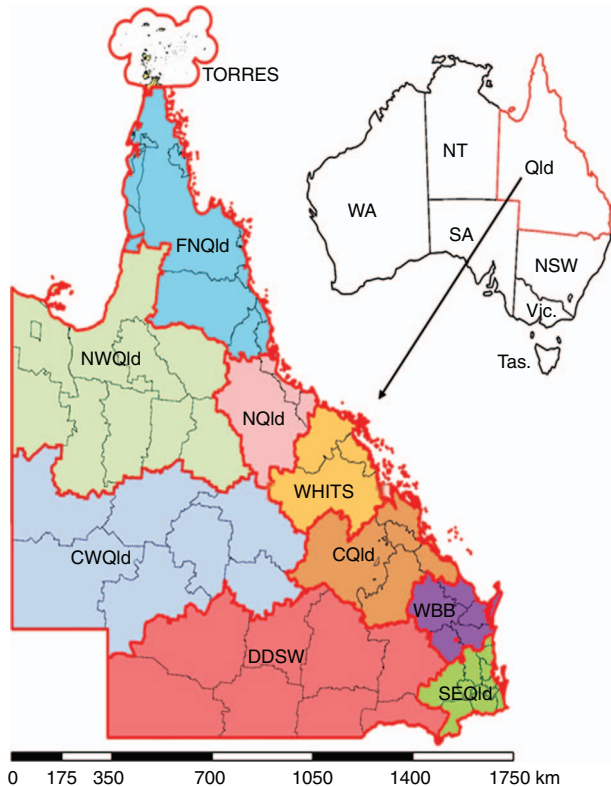

Fig. 1. Map of Australia (inset) and the state of Queensland showing the boundaries for all local governments (faint lines) and the 10 regions (bold lines) of the state. These regional affiliations (south to north) are: south-east (SEQld), Darling Downs (south-west) (DDSW), Wide Bay Burnett (WBB), Central Queensland (CQld), Remote Area Planning And Development (central west) (CWQld), Whitsunday (WHITS), North Queensland (NQld), North-west Queensland (NWQld), Far-North Queensland (FNQld), and Torres Strait Islands (TORRES).

Table 1. Density codes and range (%) used for assessment of abundance of established and emerging weeds of Queensland, Australia, by the Annual Pest Distribution Survey (APDS) series

Cover code	Probable range (%)	Explanation
0	–	Unsure if the weed exists in the grid cell
1	–	No infestation known in the grid cell
2	1–10	Weed occasionally found but localised within the grid cell
3	11–20	Weed occasionally found but widespread within the grid cell
4	21–30	Weed common but localised within the grid cell
5	31–50	Weed common and widespread within the grid cell
6	51–75	Weed abundant but localised within the grid cell
7	76–100	Weed abundant and widespread within the grid cell

50 km in area) in inland areas. From 2007 onward, weed distribution and abundance were mapped exclusively using the small grids across the entire state. This provided consistently finer resolution after 2007, but it created a divide in data between coastal and inland areas, as well as pre and post 2007 data, thereby limiting opportunities for data comparison both spatially and temporally. For this reason, for standardisation, data from the small grids were 'scaled-up' to match the format of the large grids. This was achieved by overlaying the small grids within the large grid template, with one large grid containing nine small grids. For each species, presence and abundance (cover scale: 0–7; see Table 1) values were assigned to large grids using the following rules: first, if a species was present in one or more of the nine small grids, then the large grid was listed as having that species present. Second, the abundance of that species in the large grid was based on the highest (maximum) cover value recorded in the nine small grids for that species. As a result, all APDS datasets included in this study used the large grids (50 × 50 km), making it possible to directly compare changes in weed invasiveness over time, across landscapes and at varying spatial scales. The choice of our spatial grid size also aligns with a sister study dealing with weed spread dynamics inferred from herbarium records (O. O. Osunkoya, unpubl. data). Data cleaning and conversions were conducted on ArcMap (ver. 10.7.1).

For the purpose of this study, we limited our interrogation of the APDS database to the period of 2006–2014. New data beyond 2014 are still being compiled and cleaned, and data custodians (B. Grey, M. Calvert, pers. comm.) advised that data from 2003 to 2005 lacked internal consistency as the APDS methodology was then still evolving. It was tempting to concentrate on the time range of 2007 and beyond as it allowed the use of only the small grid size of 17 × 17 km across the entire state. However, such a choice was discounted as it resulted in a much lower number of species and survey periods in the datasets, and may lead to low statistical power of many of the invasiveness traits being investigated. As highlighted earlier, the APDS record covers at best only the last 20 years, and hence it is difficult to infer the correctness of a species' invasion curve from the plot of time against distribution or abundance for such a limited time-specific dataset. Moser *et al.* (2016) and Fan *et al.* (2018) showed that by replacing 'time with space', the distribution and abundance data from a limited snap-shot series of years (like that of the APDS) when combined can infer invasion stage and invasiveness of any invader. This is the approach we have taken in this work. In the process, weed occupancy of spatial grid cells (in our case, ~50 × 50 km in size and spread over 1.73 × 10^6-km^2 area) was used as a surrogate for invasion time. In taking this approach, our notion is that a landscape of sparse or low weed occupancy implies an early stage of invasion whereas a landscape of high occupancy correlates with a later stage of invasion (Moser *et al.* 2016; Fan *et al.* 2018; Osunkoya *et al.* 2019a). Though not considered explicitly here, we acknowledge the influence of environmental conditions, especially moisture availability, as limiting factors on potential distribution of plant species.

Weed abundance, distribution, and invasion severity at regional and state levels

Note that not all the 64 focal weed species are surveyed each year due to logistic and time constraints. For each focal species and surveyed period (year), we aggregated its spatial (grid) distribution and abundance into LGAs, regional and state-wide datasets. We summarised and presented the analyses of invasiveness mostly at the regional and state-wide levels rather than at lower levels of LGAs or individual grids in view of the large dataset and number of species considered. In addition, LGAs within each region showed similarity in weed identity (Osunkoya *et al.* 2019a) – making management decisions across LGAs within regions to be all encompassing and effective.

Weed abundance

Grid weed density (abundance) estimate was based on a scale of 0–7 (Table 1), but truncated to a scale of 1–7 as 0 in the APDS means 'unsure if the weed exists in a particular grid cell'. The cover ('weed abundance') for each invader is the median density value of the APDS scale of 1–7 at a given survey year (t_i).

Weed distribution

At the state-wide, regional and LGAs levels, we estimated a focal weed's spread (distribution) in two ways: (i) using observed data as generated from the APDS (i.e. presence of a weed species in a spatial grid cell if cover code in the range of 1–7 is stated for that species), and (ii) using simulated data generated by climate suitability modelling from the CLIMEX software.

(i) Grid cell occupancy (GCO) model: We defined, for each weed species at survey time (year) t_i, the 'Probability of invasion' as a ratio of cumulative number of spatial grid cells infested (n_x) to total number of 'available' grid cells (N_x) (for our study and at the state-wide level, N_x is a total of 687 of ~50 × 50-km grids) (Table 2). At the regional level, the total number of 'available' grid cells refers to assigned total number of spatial grids for that particular region (Table 2). We referred to this approach

Table 2. Number of 50 × 50-km spatial grid cells in the 10 regions of Queensland, Australia

Number	Region	Region abbreviation	Number of grid cells
1	Central Queensland	CQld	49
2	Central West Queensland	CWQld	138
3	Darling Downs-South West	DDSW	144
4	Far North Queensland	FNQld	97
5	North Queensland	NQld	28
6	North West Queensland	NWQld	129
7	South East Queensland	SEQld	15
8	Torres Strait Islands	TORRES	20
9	Wide Bay Burnett	WBB	23
10	Whitsunday	WHITS	44
		Total	687

of using APDS dataset to estimate weed distribution as the grid cell occupancy (GCO) model. This metric, a crude but informative way to measure the weed's importance, describes the proportional area of a region or of the state actually infested with a weed;

(ii) Climate suitability–species distribution (CS-SD) model: BQ developed weed distributions models for ~60 weed species for Queensland in the early to mid-2000s using CSIRO CLIMEX software (https://www.daf.qld.gov.au/business-priorities/biosecurity/invasive-plants-animals/pest-risk-assessments, accessed 23 September 2020; Kriticos and Randall 2001; Sutherst 2003). The CLIMEX model is a simulation model that infers a species response to climate in a novel range from its known distribution in its native range. The model uses 'survival thresholds', which determine a species population growth and survival during adverse seasonal and inter-annual periods from its known distribution, then applies these limiting factors to meteorological data from other parts of the world to generate potential distribution in another (e.g. invaded) range (Kriticos and Randall 2001; Sutherst 2003). The model generates an 'Eco-climatic Index' (EI, scaled from 0 to 1) – an overall climatic suitability of a nominated location for a given organism. Thirty-eight of our 64 focal species have EI values that have been generated by the CS-SD CLIMEX modelling exercise. In this CS-SD model, climate suitability maps are created, consisting of spatial grid cells (or pixels) whose quantitative values range from 0 to 1. These values indicate how close the local environment in a novel range (i.e. Queensland) is to the invader optimal growth conditions, with higher values standing for the most suitable areas for invasion. The necessary step to model weed distribution using this approach generally consists of choosing a climate suitability threshold (often EI > 0.10) to separate unsuitable areas (EI below threshold) where the invader should be absent, from suitable areas (EI above threshold) where it should be present. For our focal invader species with hitherto modelled EI values, we chose a more conservative threshold of EI > 0.3 (equivalent to very suitable and suitable environmental envelopes for occupancy). We then estimated, for each of the 38 invader species with known EI values, a 'modelled' probability of invasion of a grid cell by the fraction of total grids potentially suitable for occupancy within a LGA, region or at the state level.

Weed severity – a product of distribution and abundance

We defined 'invasion severity' as the product of 'probability of invasion' (weed distribution) and 'weed abundance'. This index serves as a proxy to quantify the intensity of the occupation of an area by a given weed. This estimation was done only for the GCO model as the APDS provided real data to derive invasion severity measure. In estimating invasion severity, we considered both the distribution and the dominance of the weed in a particular area (grid, LGA, regional and state wide) (see also Catford *et al.* 2012; Pearson *et al.* 2016; Fan *et al.* 2018). To compare

the relative performance of each invader species in a pool of *S* species, we standardised the dataset across species by dividing each invader value with the global (overall) mean value followed by the log ratio of the estimate (see Colautti *et al.* 2014). The relative invasion severity values when plotted against distribution (i.e. proportion of grid cell infested) often gives a sigmoid or exponential curve, and can be viewed as a composite 'space-for-time' version of the hypothetical, temporal invasion process (stage) for a particular region or area (Fan *et al.* 2018). At the state-wide level, for each weed, points on the curve represent a region (with or without survey periods (years) in this study), with low invasion severity regions appearing on the left and high invasion severity regions on the right in a sequential order (i.e. from low to high probabilities).

Statistical analyses

Data were checked for heteroscedasticity of variance. Weed abundance and invasion severity were normally distributed. Spatial grid cell occupancy data were skewed and hence log-transformed; data presented are back-transformed values. A series of ANOVA and GLM were carried out to detect main and interaction effects of factors (survey year, region, and species) on traits of invasiveness. We used parametric and non-parametric correlation analyses to explore strength of bivariate relationships. We excluded the TORRES data from the CS-SD model analyses due to a difficulty in deriving a reliable estimate of EI index as the region is made up of series of islands some of which are smaller in size than our spatial grid cells.

To test for differences in the shape (i.e. frequency distribution) of the invasion severity between two species or between two regions, we explored various statistical procedures (including Q-Q (quantile) plots, Kolmogorov–Smirnov, interquartile range (IQR), Cramer-von Mises, GLM and permutation tests (Moser *et al.* 2016), and eventually settled on Kolmogorov–Smirnov test (a distribution free, non–parametric test-statistic that quantifies the maximum difference between two empirical curves or distributions).

Derivation of invasion stage categories through a proxy of grid cells infested (distribution) and invasion severity

As in Fan *et al.* 2018 and Pyšek *et al.* 2009, classification and regression tree (CART in SPSS version 25) analysis was invoked to segment invasion severity into invasion stage groups or categories. The CART analysis was done at region and at state-wide levels, and provided an objective way to classify the invasion severity into invasion stages both within and between species. The classifier uses the invasion severity as a response variable, whereas the invasion probability (weed distribution) and weed abundance, together with species-specific traits (plant growth form, life cycle) and species extrinsic traits of invasiveness (time since introduction (residence time), habitat invaded, origin, introduction pathway) were the predictor variables. The last two sets of data were sourced from herbarium records and from published literature (see Osunkoya *et al.* 2019*a*, 2019*b* for details).

At each node of a classification tree and using the CART tree-growing function of CHAID (Chi-Square automatic interaction detector), cases (i.e. species or region's invasion severity in this study) are split dichotomously to minimise an error criterion (Breiman *et al*. 1984; Fan *et al*. 2018). The optimal regression tree model is the one that minimises the relative cross-validation error-rate, and was generated with fives nodes, one depth and when the minimum number of cases (species × year × region) in parent and child nodes were 400 and 200 respectively. The classified outputs (species or regions) represent different levels of invasion stage at the survey year periods: species or regions with an invasion severity in Class I have low invasion stage; those of higher classes, say III–IV have higher levels of invasion stages. In other words, these classification outputs of invasion stages can be equated with weed management options: prevention or eradication (Stage I), eradication or control (Stage II), control or containment (Stage III), containment or asset protection (Stage IV), and asset protection (Stage V) (Standards Australia International Ltd 2006; Osunkoya *et al*. 2019*b*). CART also generates the importance value of the independent variables, reflecting the contribution of each variable stemming from both its role as a splitter and as a surrogate across all nodes of the tree.

Results

Invasion trend: effects of survey period, regional and species differences at varying spatial scale

Of the three main factors of species, region and survey year, the APDS dataset indicated that probability of invasion of spatial grid cells (i.e. distribution or occupancy), weed abundance and product of the two (invasion severity) were minimally (i.e. least) affected by year of survey (Table 3). In other words, these invasiveness indices varied more significantly among regions, even where data are analysed at the individual species level (see Table S1 of the Supplementary material). The direction of periodic variation (i.e. from year to year) in the above indices within regions are fairly consistent (mainly increase), as the interactions of survey year × region or survey year × species are often non-significant; also the *F*-ratio values of these interaction

effects were relatively low and made minimal contribution to the overall variation in the dataset (Table 3).

In all and using the APDS dataset, 50/64 species (78.1%) of our focal species showed regional differences in their distributions (i.e. in probability of a spatial grid cell invasion) (Table S1). Using observed grid cell occupancy as derived from the APDS dataset, the overall (state-wide) invasion was 18.40 ± 2.5% (Table S2). Grid cell occupancy values were highest in regions along the southern and central, coastal part of the state (in the order: WBB (30.1%) > NQld (25.1%) ≥ CQld (23.7%) ≥ WHITS (22.2%) > SEQld (21.1%), and decreased as one moves inland into the western regions (NWQld (15.6%) ≥ CWQld (13.0%) >> DDSW (7.0%)) and upwards into the northern (TORRES (12.6%) > FNQld (8.9%) parts of the state (Table S2). The proportion of Queensland suitable for invasion using the environmental envelop index (EI >30%) and generated by CLIMEX modelling (CS-SD model) was much higher (55.2%) than that derived from the APDS dataset (the GCO model: 18.4%). Using the CS-SD model, highest occupancy values were predicted for regions in the middle parts of the state. In general, the order of predicted weed occupancy at the regional level was WBB (68.1%) ≥ CQld (64.0%) ≥ CWQld (62.8%) > WHITS (55.2%) ≥ FNQld (51.2%) > NWQld (47.7%) ≥ SEQld (47.3%) ≥ NQld (46.9%) ≥ DDSW (45.6%) (Table S2). Using each region as an entity, a non-significant positive correlation for weed distribution was detected between actual counts of spatial grid cells invaded (The GCO model) and the count of simulated habitat (grid cells) available for occupation (The CS-SD model) ($r = 0.47$, $n = 9$, $P = 0.21$) (Fig. 2*a*). State-wide and across species, a non-significant positive correlation in grid cell occupancy (i.e. distribution) was detected between GCO and CS-SD models ($r = 0.28$, $n = 38$, $P = 0.22$, Fig. 2*b*), primarily due to three outlier species (water lettuce (*Pistia stratiotes*), Cabomba (*Cabomba caroliniana*) and mesquite (*Prosopis* spp.) with predicted CS-SD occupancy of >75%; removal of these outliers resulted in a significant trend ($r = 0.46$, $P = 0.007$; Fig. 2*b*).

In terms of weed abundance, 39/64 (61%) of species showed regional differences for the trait (Tables 3, S2). However, there were no discernible geographical trends like that observed for weed distribution: highest weed abundance

Table 3. Summary general linear model (GLM) table for influence of main factors of survey year, species, and region as well as their interactions on probability of weed invasion (distribution), abundance and invasion severity of a spatial grid cell

Databased on Annual Pest Distribution Survey (APDS) datasets of 2006–2014. Probability values of significant factors ($P \leq 0.05$) are in bold

| Source of variation	d.f.	Grid cell occurrence model (i.e. using the APDS dataset)					
		Weed distribution		Weed abundance		Invasion severity	
		F-ratio	Probability	*F*-ratio	Probability	*F*-ratio	Probability
Year	5	1.99	0.078	3.41	**0.005**	0.51	0.772
Region	9	605.73	**0**	18.68	**0**	474.85	**0**
Species	63	259.98	**0**	30.64	**0**	141.57	**0**
Region × species	265	102.7	**0**	17.75	**0**	54.34	**0**
Year × species	185	1.01	0.444	2.3	**0**	1.64	**0**
Year × region	45	0.86	0.736	1.25	0.136	1.53	**0.03**
Error	580	–	–	–	–	–	–
Total	1153	–	–	–	–	–	–
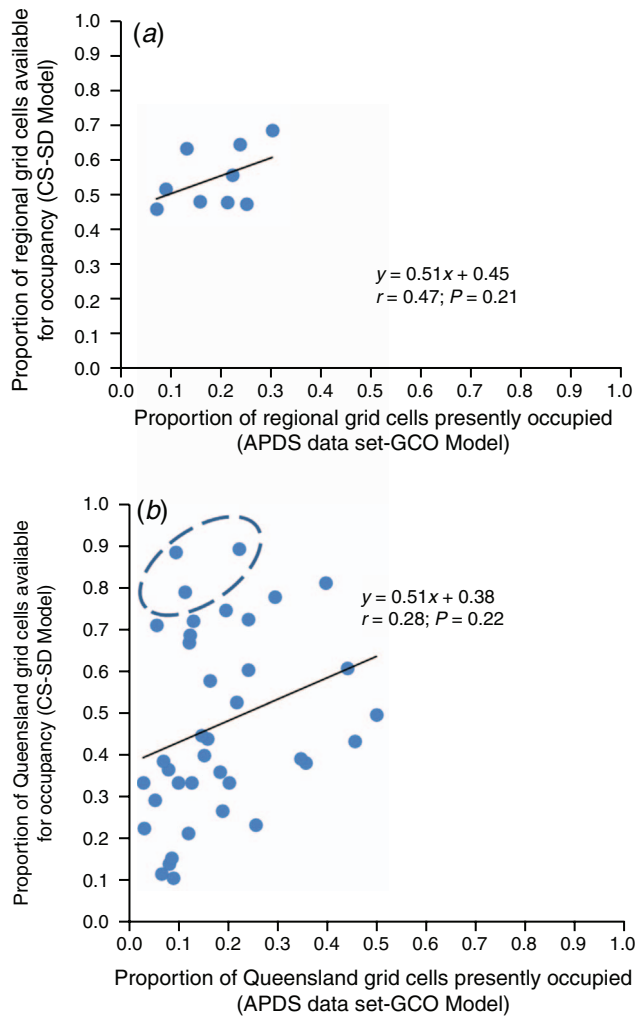
Fig. 2. Relationship between the grid cell occurrence (GCO) and climate suitability–species distribution (CS-SD) models in terms of grid cell occupancy (distribution) for established and emerging weeds of Queensland at (*a*) regional (*n* = 9), and (*b*) species levels (*n* = 38). For (*b*) only a subset of the 64 species investigated have available eco-climatic (environmental) index values (*n* = 35) and hence were considered; also dashed circle are around three species with predicted high invasion probability >0.75 by the CS-SD model whereas the observed occupancy level is <0.2; their removal from the dataset make the relationship to shift from non-significant (*P* = 0.22) to being significant (*P* < 0.05). APDS, Annual Pest Distribution Survey.
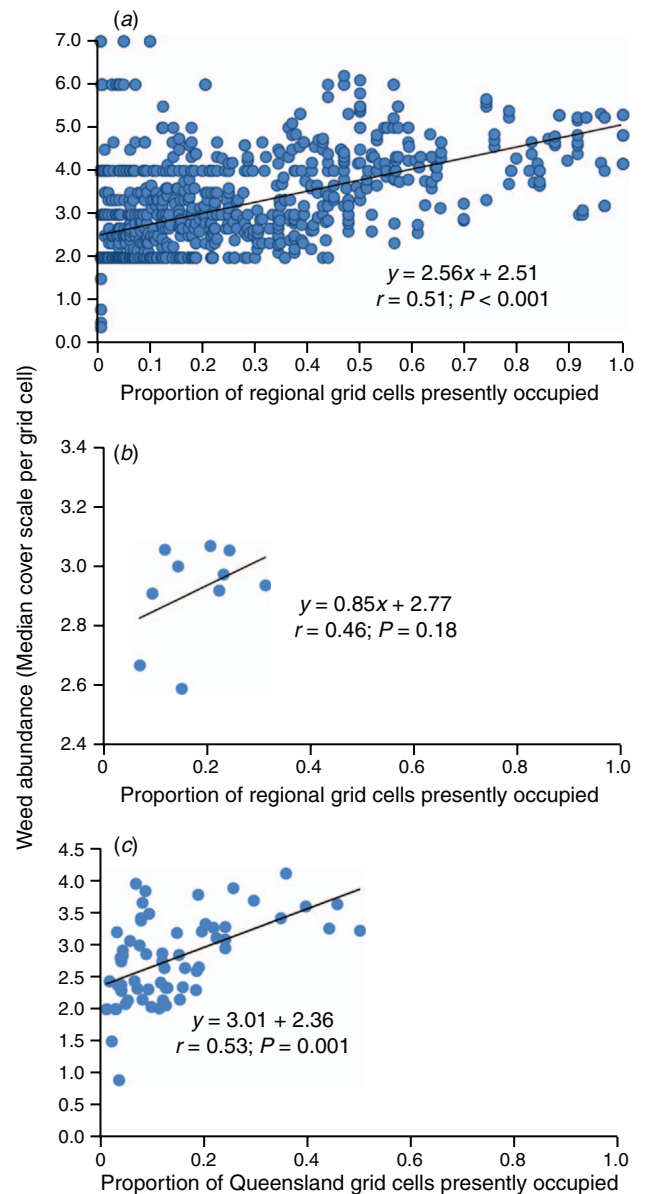

Fig. 3. Plots of weed invasion probability (distribution) as measured by the proportion of grid cells occupied against weed abundance at multiple spatial scales of (*a*) species × region, (*b*) region, and (*c*) across species at the state-wide levels.

estimates were in WHITS, CWQld, NQld, and lowest values in DDSW and NWQld (Table S2).

Weed distribution–abundance (D-A) relationships at multiple spatial scales are illustrated in Fig. 3 and Table 4. Positive D-A relationship was detected across species, year and regions (i.e. proportion of grid cells occupied by each species at each LGA and year plotted against their respective weed abundance data; Spearman rank correlation, r_s = 0.51, *n* = 1120, *P* = 0.001; Fig. 3*a*). Within individual region, significant positive D-A correlations also exist (range of r_s values = 0.210–0.75; range of *n* = 33–165, *P* ≤ 0.05, except for CWQld and TORRES where respectively marginally significant (*P* = 0.07) and no

trends (*P* = 0.35) were apparent) (Table 4). Across the 10 regions (i.e. using region as individual entity), the two invasiveness traits are also positively correlated, but non-significant (r_s = 0.46, *P* = 0.18, *n* = 10; Fig. 3*b*.). At the interspecific level, the positive D-A pattern was also apparent and significant (Fig. 3*c*). Within species (i.e. at the intra-specific level), 35 and 5 out of 64 species indicated significant r_s values for the D-A relationship at *P* < 0.05, and 0.10 < *P* > 0.05 respectively (*n* ranged from 8 to 44 grid cells per species). We note, however, that four species (bitou bush, *Chrysanthemoides monilifera* subsp. *rotundata*; Hygrophila, *Hygrophila costata*; blackberry, *Rubus anglocandicans*; and devils's rope pear, *Cylindropuntia*

Region name	Grid cell occurrence model		
	r	*n*	*P*-value
CQld	0.659	123	***
CWQld	0.212	69	†
DDSW	0.291	132	**
FNQld	0.606	165	***
NQld	0.573	112	***
NWQld	0.657	95	***
SEQld	0.673	168	***
WBB	0.552	136	***
WHITS	0.754	120	***
TORRES	0.151	33	NS
Overall	0.555	1120	***

imbricate), defy this positive trend and rather indicated negative significant trends (O. O. Osunkoya, unpubl. data).

Invasion trend: severity and stage categorisation

Plots of relative invasion severity against the fractions of grid cells that are presently occupied state-wide and in each region are respectively indicated in Fig. 4, 5 and S1 of the Supplementary material. The dynamics of the relationship varied between regions (test statistics: Kolmogorov–Smirnov test; Table S3).

At the state-wide level, CART (CHAID option) analysis splits relative invasion severity values into five nodes, and hence classification categories (Fig. 4*a, b*), with mean (s.d.) invasion severity values of 0.196 (0.09) (Stage I: prevention or eradication), 0.378 (0.06) (Stage II: eradication), 0.526 (0.07) (Stage III: control or containment), 0.676 (0.07) (Stage IV: containment or asset protection) and 0.86 (0.07) (Stage V: asset protection) (Fig. 4*a, b*). The division is driven mostly by grid cell occupancy (i.e. distribution) and to a limited extent by weed abundance, introduction pathway and time since invasion (Fig. 4*c*). These classifications (Stages I–V) respectively correspond to probability of Queensland spatial grid cell occupation in the range of <0.03, 0.031–0.07, 0.071–0.156, 0.157–0.371, and >0.371 (Fig. 4*a, b*). Using these classification intervals, the stages of invasion of 64 weed species (i) state-wide, and (ii) in each of the 10 regions of Queensland are indicated in Tables 5 and S4 respectively. Overall (i.e. state-wide) 3, 15, 30, 11 and 5 (of 64) species can be categorised being in invasion Stages I, II, III, IV and V respectively. The low species number in (final) Stage V (5/64 = 7.8%) will suggest that many of the established species are yet to fill all potential niches in their novel environment, and hence, further spreads are possible (see also Fig. 2*b*).

For our focal weed species, the dynamics of invasion stages state wide, and in each of the 10 regions of Queensland are

very instructive and can guide policy directions in terms of management options (Fig. 4*b*, 5, S1; Tables 6, S4). From Table 6, it can be seen that the inner, western regions of Queensland (NWQld, CWQld, and DDSW) have sizeable proportions of their weed species (53–65%) in early stages of invasion (classification Stages I and II). In contrast, most coastal regions, except FNQld and TORRES, have sizeable proportions of their weed species (50–65%) in the later Stages (IV and V) of invasion (Table 6). We use a couple of species within each of the five invasion stage categories to illustrate the variation in trends at the state and regional levels (Fig. 5).

(i) Stage I: The analysis suggests at the state level, Koster's curse (*Clidemia hirta*) (a shrub), Madras thorn (*Pithecellobium dulce*) (a tree) and snake cactus (*Cylindropuntia spinosior*) (a succulent), with mean invasion severity in the range of 0.09–0.19, are the only three invaders (3/64 species = 4.7%) in this early stage of invasion (Fig. 5*a, b*; Table 5); the first two species are limited currently in distribution to the WHITS and FNQld regions respectively. Snake cactus (*Cylindropuntia spinosior*) has scattered, isolated low populations in SEQld and western part of the state (CWQld, DDSW and NWQld); these isolated invasion foci are all in Stage I category (Fig. 5*b*).

(ii) Stage II: state-wide, athel pine (*Tamarix aphylla*) –a tree (mean (CI) invasive severity = 0.28 (0.26–0.31)) is a member of a stage classification group with the second largest membership (15/64 species = 23.5%). Like other weeds in this state-wide Stage II, athel pine (*T. aphylla*) invasion stage categories vary at the regional level (Fig. 5*c*; Table S4): Stage I (DDSW, FNQld), Stage II (SEQld, NWQld), and Stage III (CQld, WHITS). Other notable members include badhara bush (*Gmelina elliptica*), Mexican bean tree (*Cecropia* spp.), mikania vine (*Mikania micrantha*), Limnocharis (*Limnocharis flava*), Hudson pear (*Cylindropuntia rosea*), devil's rope pear (*Cylindropuntia imbricata*), and telegraphic weed (*Heterotheca grandiflora*).

(iii) Stage III: gamba grass (*Andropogon gayanus*), (mean (CI) invasion severity = 0.43 (0.41–0.46)) is typical of weeds in a stage classification group with the largest membership (30/64 species = 46.9%) (Table 5; Fig. 5*d*). For gamba grass (*A. gayanus*), its regional invasion stage categories ranges from Stage II (WHITS, NWQld), to Stage III (NQld), and Stage IV (FNQld, TORRES). Other prominent species in this group include African boxthorn (*Lycium ferocissimum*), African fountain grass (*Pennisetum setaceum*), alligator weed (*Alternanthera philoxeroides*), aleman grass (*Echinochloa polystachia*), bitou bush (*Chrysanthemoides monilifera* subsp. *rotundata*), fireweed (*Senecio madagascariensis*), madeira vine (*Anredera cordifolia*), mesquite (*Prosopis* spp.), Cabomba (*Cabomba caroliniana*), and coral cactus (*Cylindropuntia fulgida*). Regionally, this group's invasion stage categories vary widely, usually spanning Stages I–IV.

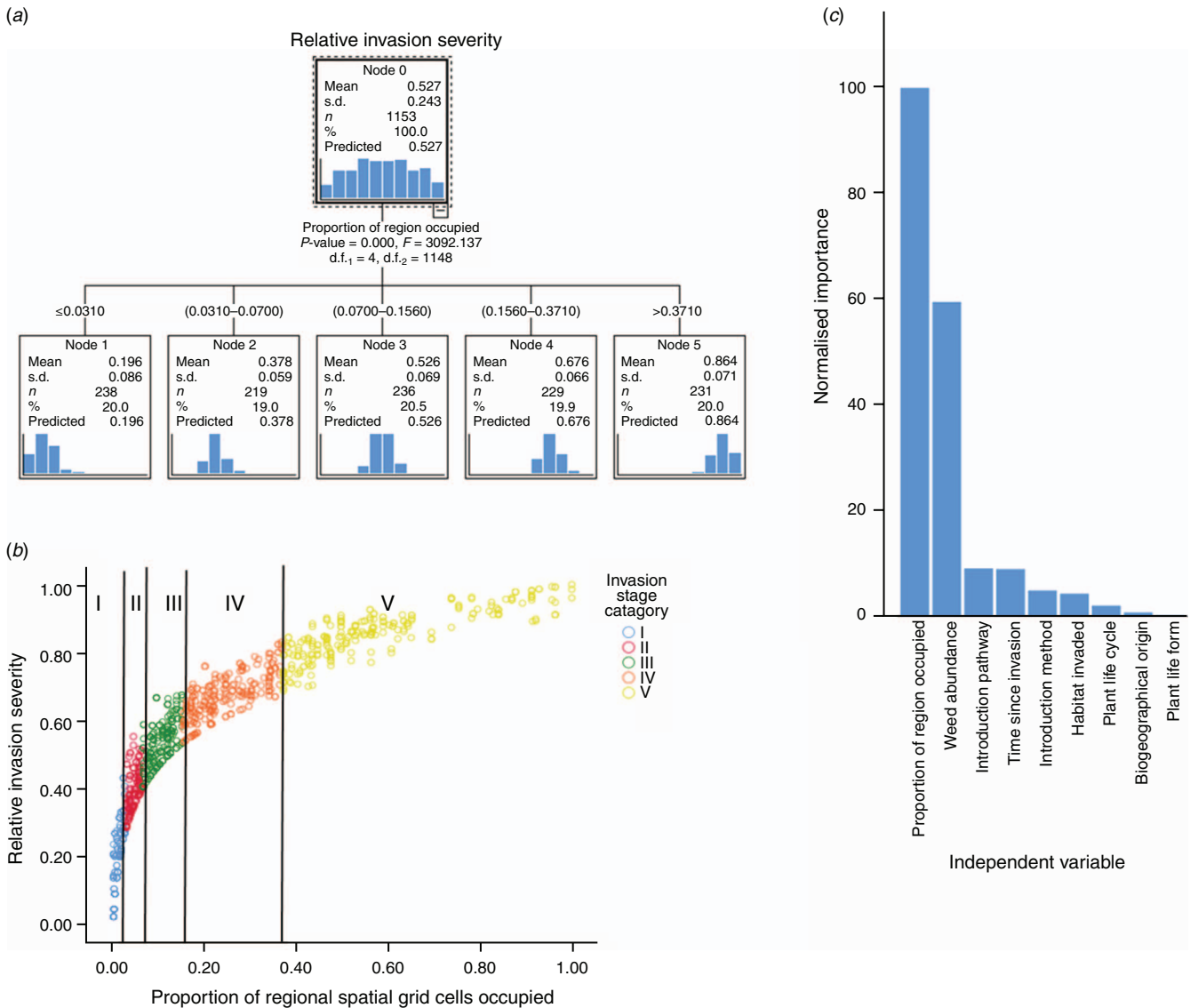(iv) Stage IV: state-wide, bellyache bush (*Jatropha gossypifolia*) – a small tree or shrub (mean (CI) invasion

Fig. 4. Classification of invasion stages of established and emerging weeds of Queensland, Australia: (*a*) the optimal regression tree model with five terminal nodes (labelled nodes 1–5) (corresponding to invasion Stages I, II, III, IV, and V) showing the cut off values of the relative invasion severity values – a product of weed distribution and abundance. The main splitter variable is probability of a region occupied (i.e. distribution data). (*b*) The relative invasion severity as a function of fraction of region occupied by the weed to map the established weed into five invasion stages (labelled I, II, III, IV and IV) based on the terminal nodes generated in 'a' (*c*) The relative contribution of factors to the relative invasion severity values

severity = 0.51 (0.48–0.53)) is typical of focal invader species in this classification stage (consisting of 11/64 = 17.2% species) (Table 5; Fig. 5*e*). Members in the group exhibit substantial amplitude in invasion stage categories at region level (Table S4). For bellyache bush (*J. gossypifolia*), its distribution spans the 10 regions of the state, with invasion stage categories ranging from Stage I (DDSW), Stage II (CWQld, SEQld), to Stage III (WBB, TORRES), to Stage IV (FNQld, CQld, NWQld, WHITS), and Stage V (NQld). Other prominent species in this group include, African love grass (*Eragrostis curvula*) cat's claw creeper (*Dolichandra unguis-cati*), calotrope

(*Calotropis procera*), Salvinia (*Salvina molesta*), prickly acacia (*Vachellia nilotica*), and rat tail grasses (*Sporobolus* spp.).

(v) Stage V: state-wide, Parkinsonia (*Parkinsonia aculeate*) – another small tree or shrub (mean (CI) invasion severity = 0.72 (0.71–0.73)) is illustrative of the few weed species in this late stage of invasion (5/64 = 7.8% species; Table 5; Fig. 5*f*). Their invasion stage categories at regional levels oscillate mainly in Stages III-V (Table S4). For *P. aculeate*, the classification ranges from Stage III (SEQld, WBB), to Stage IV (FNQld, DDSW) and Stage V (CQld, CWQld, NQld, NWQld and WHITS). Lantana (*Lantana camara*), mother-of-
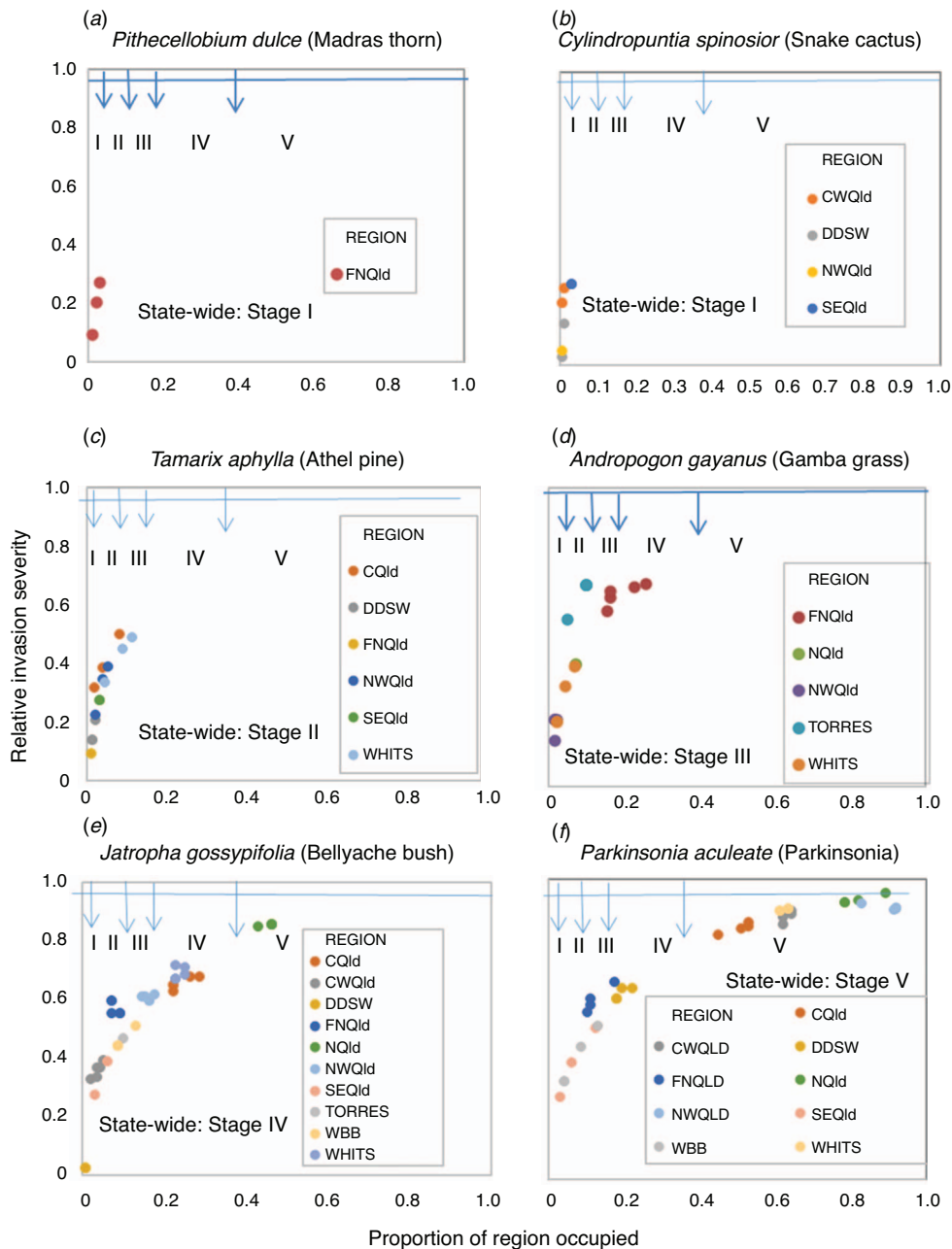
Fig. 5. Typical 'space for time' invasion curve for representative weed species of the five state-wide invasion stage categories based on invasion severity. In the graphs, each point is a regional data. Note that a species in a given region may have more than one data points where multiple survey periods (years) were conducted between 2006 and 2014. At the top of each graph is a line bar and arrows to depict the point of segmentation of the curve (trend) into invasion stage categories based on output from the regression tree (CART analyses). See Table 2 for a definition of abbreviations of region names.

millions (*Bryophyllum* spp.), parthenium weed (*Parthenium hysterophorus*) and rubber vine (*Cryptostegia grandiflora*) are also prominent members of this state-wide invasion category V.

Discussion

Across multiple spatial scales (state-wide, regional, across and within individual species levels) we have shown that abundance and distribution are not independent but are

frequently positively related to each other – a finding similar to other studies (Freckleton *et al.* 2005; Webb *et al.* 2007; Buckley and Freckleton 2010; Dallas *et al.* 2019). Several putative mechanisms exist to explain this relationship, including synchronous range expansion and population growth, temporal variation in resource (habitat) availability, and dispersal limitations (Gaston *et al.* 2000; Webb *et al.* 2007; Dallas *et al.* 2019). Thus it can be inferred that if the local abundance of an invader increases

Table 5. State-wide invasiveness trait values (mean or median ± 95% confidence interval, CI) for 64 established and emerging weeds of Queensland, Australia, using real data sourced from the Annual Pest Distribution Survey (APDS) dataset (the grid cell occurrence (GCO) model)

Species ordered by common names. For the purpose of comparison only, the fraction of the Queensland grid cells potentially suitable for occupation for 38 of the 64 species with eco-climatic (environmental index (EI) values based on climate suitability–species distribution simulation models from CLIMEX software are provided in the last but one column (for the climate suitability–species distribution (CS-SD) model). State-wide invasion stage categories based on the APDS dataset (i.e. the GCO model) and CART (regression tree) results are also given in the last column. Life form is abbreviated as: Grass (GR), Herb (HB), Shrub (SB), Tree (TR), Vine (VN) and Succulent (SU). See Table S4 of the Supplementary material for within-species variation of invasion stage categories at the regional levels

Number	Species scientific name	Species common name (and life form)	Weed abundance (cover scale)			GCO model Weed distribution (grid fraction invaded)			Relative invasion severity			CS–SD model Weed distribution (grid fraction available for invasion)	Invasion stage category based on the GCO model
			Median	Lower CI	Upper CI	Mean	Lower CI	Upper CI	Mean	Lower CI	Upper CI		
1	*Lycium ferocissimum*	African boxthorn (SB)	2.87	2.66	3.07	0.118	0.101	0.134	0.409	0.385	0.433	0.171	III
2	*Pennisetum setaceum*	African fountain grass (GR)	2.15	1.92	2.38	0.151	0.133	0.17	0.489	0.462	0.516	–	III
3	*Eragrostis curvula*	African love grass (GR)	3.42	3.23	3.62	0.345	0.33	0.361	0.677	0.654	0.7	0.355	IV
4	*Echinochloa polystachya*	Aleman grass (GR)	2.31	2.1	2.52	0.091	0.074	0.108	0.381	0.356	0.405	–	III
5	*Alternanthera philoxeroides*	Alligator weed (HB)	2.02	1.74	2.29	0.112	0.09	0.135	0.425	0.393	0.458	0.635	III
6	*Ambrosia artemisifolia*	Annual ragweed (HB)	2.64	2.46	2.82	0.161	0.146	0.176	0.39	0.369	0.411	0.576	III
7	*Tamarix aphylla*	Athel pine (TR)	2.28	2.06	2.51	0.038	0.02	0.057	0.281	0.255	0.307	–	II
8	*Gmelina elliptica*	Badhara bush (SB)	2.8	2.23	3.37	0.037	−0.009	0.083	0.312	0.245	0.379	–	II
9	*Jatropha gossypifolia*	Bellyache bush (TR)	2.85	2.68	3.03	0.15	0.136	0.164	0.505	0.484	0.525	0.481	III
10	*Chrysanthemoides monilifera* ssp. *rotundata*	Bitou bush (SB)	2.74	2.46	3.02	0.118	0.095	0.14	0.441	0.408	0.474	–	III
11	*Rubus anglocandicans*	Blackberry (SB)	2.33	2.01	2.66	0.124	0.098	0.15	0.463	0.426	0.501	–	III
12	*Thunbergia grandiflora*	Blue thunbergia (VN)	2.06	1.89	2.24	0.125	0.111	0.139	0.439	0.419	0.46	–	III
13	*Asparagus asparagoides*	Bridal creeper (HB)	2.3	1.72	2.87	0.039	−0.008	0.085	0.284	0.218	0.351	–	II
14	*Schinus terebinthifolius*	Broad–leaved pepper tree (TR)	2.3	2.11	2.48	0.182	0.167	0.197	0.443	0.422	0.465	0.379	III
15	*Cabomba caroliniana*	Cabomba (HB)	3.49	3.31	3.66	0.092	0.078	0.106	0.496	0.475	0.517	0.873	III
16	*Calotropis procera*	Calotrope (TR)	2.66	2.41	2.91	0.188	0.168	0.209	0.466	0.437	0.496	0.42	III
17	*Dolichandra unguis–cati*	Cat's claw creeper vine (VN)	2.95	2.76	3.13	0.239	0.224	0.254	0.534	0.512	0.555	0.42	IV
18	*Nassella neesiana*	Chilean needle grass (GR)	3.06	2.83	3.29	0.055	0.036	0.073	0.331	0.304	0.358	0.539	II
19	*Ziziphus mauritiana*	Chinee apple (TR)	3.22	3.05	3.38	0.193	0.179	0.206	0.586	0.567	0.606	0.597	IV
20	*Cylindropuntia fulgida*	Coral Cactus (SU)	2.32	2.09	2.56	0.069	0.05	0.088	0.391	0.364	0.418	–	III
21	*Cylindropuntia imbricata*	Devil's rope pear (SU)	3.2	2.92	3.48	0.03	0.008	0.053	0.289	0.256	0.321	–	II
22	*Pyracantha* spp.	Firethorn (SB)	2.91	2.54	3.28	0.042	0.012	0.072	0.368	0.326	0.411	–	II
23	*Senecio madagascariensis*	Fireweed (HB)	3.19	2.96	3.42	0.145	0.126	0.163	0.465	0.438	0.491	0.153	III
24	*Andropogon gayanus*	Gamba grass (GR)	3.39	3.19	3.59	0.077	0.061	0.093	0.434	0.411	0.457	0.352	III
25	*Mimosa diplotricha,* previously *M. invisa*	Giant sensitive plant (SB)	2.43	2.16	2.71	0.064	0.042	0.086	0.389	0.358	0.421	0.127	III
26	*Baccharis halimifolia*	Groundsel bush (SB)	3.88	3.69	4.07	0.254	0.238	0.269	0.53	0.508	0.553	0.218	IV
27	*Eriocereus* spp.	Harrisia cactus (SU)	3.28	3.14	3.43	0.238	0.227	0.25	0.589	0.572	0.606	–	IV
28	*Gleditsia triacanthos*	Honey locust (TR)	2.15	1.93	2.36	0.119	0.102	0.136	0.395	0.37	0.42	0.374	II
29	*Cylindropuntia pallida* (syn. *rosea*), *C. tunicata*	Hudson pear (SU)	2.38	2.05	2.71	0.031	0.005	0.058	0.273	0.235	0.312	–	II
30	*Hygrophila costata*	Hygrophila (HB)	3.95	3.72	4.19	0.067	0.048	0.086	0.437	0.409	0.465	0.424	III
31	*Hymenachne amplexicaulis*	Hymenachne (GR)	3.33	3.2	3.45	0.2	0.19	0.21	0.556	0.541	0.57	0.289	IV
32	*Heteranthera reniformis*	Kidneyleaf mudplantain (HB)	2.15	1.9	2.4	0.079	0.058	0.099	0.347	0.318	0.376	–	II
33	*Clidemia hirta*	Koster's curse (SB)	2	1.68	2.32	0.01	−0.016	0.036	0.091	0.053	0.129	0.088	I
34	*Pueraria lobata*	Kudzu (VN)	2.42	2.06	2.77	0.115	0.086	0.144	0.424	0.383	0.465	–	III
35	*Lantana camara*	Lantana (SB)	4.11	3.97	4.26	0.355	0.343	0.366	0.681	0.664	0.698	0.336	V
36	*Limnocharis flava*	Limnocharis (HB)	2	1.72	2.28	0.035	0.012	0.057	0.288	0.255	0.32	–	II
37	*Anredera cordifolia*	Madeira vine (VN)	2.35	2.16	2.53	0.157	0.142	0.172	0.428	0.407	0.45	0.4	III

Table 5. (*continued*)

Number	Species scientific name	Species common name (and life form)	Weed abundance (cover scale)			GCO model Weed distribution (grid fraction invaded)			Relative invasion severity			CS–SD model Weed distribution. (grid fraction available for invasion)	Invasion stage category based on the GCO model
			Median	Lower CI	Upper CI	Mean	Lower CI	Upper CI	Mean	Lower CI	Upper CI		
38	*Pithecellobium dulce*	Madras thorn (TR)	2	1.54	2.46	0.021	−0.016	0.058	0.188	0.135	0.241	–	I
39	*Prosopis pallida*	Mesquite (TR)	2.34	2.19	2.48	0.128	0.116	0.139	0.442	0.426	0.459	0.847	III
40	*Cecropia pachystachya, C. palmata* and *C. peltata*	Mexican bean tree (TR)	2.09	1.79	2.39	0.047	0.023	0.072	0.331	0.296	0.366	–	II
41	*Miconia calvescens*	Miconia (TR)	2.15	1.51	2.78	0.051	−0.001	0.102	0.356	0.282	0.43	0.378	II
42	*Mikania micrantha*	Mikania vine (VN)	2	1.68	2.32	0.029	0.003	0.055	0.259	0.221	0.297	0.288	II
43	*Mimosa pigra*	Mimosa pigra (SB)	2	1.65	2.35	0.027	−0.001	0.056	0.241	0.199	0.282	0.333	II
44	*Bryophyllum delagoense.*	Mother of a million (SU)	3.6	3.46	3.73	0.394	0.383	0.405	0.729	0.713	0.745	0.705	V
45	*Cyperus aromaticus*	Navua sedge (GR)	2.99	2.53	3.46	0.074	0.037	0.112	0.446	0.391	0.5	–	III
46	*Parkinsonia aculeata*	Parkinsonia (SB)	3.25	3.12	3.39	0.439	0.428	0.45	0.717	0.701	0.732	0.604	V
47	*Parthenium hysterophorus*	Parthenium (HB)	3.22	3.1	3.34	0.497	0.488	0.507	0.755	0.741	0.769	0.42	V
48	*Annona glabra*	Pond apple (TR)	2.86	2.66	3.06	0.087	0.07	0.103	0.43	0.406	0.453	0.139	III
49	*Vachellia nilotica*	Prickly Acacia (TR)	3.09	2.97	3.21	0.239	0.23	0.249	0.6	0.586	0.614	0.635	IV
50	*Sporobolus* spp.	Rat's tail grasses (GR)	3.7	3.54	3.86	0.293	0.28	0.306	0.623	0.605	0.642	–	IV
51	*Cryptostegia grandiflora*	Rubber vine (VN)	3.64	3.51	3.77	0.454	0.443	0.465	0.746	0.73	0.761	0.397	V
52	*Salvinia molesta*	Salvinia (HB)	3.27	3.13	3.41	0.216	0.204	0.227	0.589	0.573	0.605	0.496	IV
53	*Gymnocoronis spilanthoides*	Senegal tea (HB)	3.42	3.01	3.82	0.077	0.045	0.11	0.461	0.414	0.508	–	III
54	*Chromolaena odorata*	Siam weed (SB)	3.85	3.62	4.07	0.085	0.066	0.103	0.521	0.495	0.548	0.204	III
55	*Senna tora*	Sicklepod (SB)	3.79	3.57	4.01	0.186	0.168	0.204	0.612	0.586	0.637	0.617	IV
56	*Cylindropuntia spinosior*	Snake cactus (SU)	2.44	2.09	2.78	0.016	−0.012	0.044	0.169	0.128	0.209	–	I
57	*Hypericum perforatum*	Saint John's wort (HB)	2.38	2.1	2.65	0.039	0.017	0.062	0.296	0.264	0.329	–	II
58	*Florestina tripteris*	Sticky florestina (HB)	2.84	2.26	3.41	0.042	−0.004	0.088	0.391	0.324	0.457	–	III
59	*Heterotheca grandiflora*	Telegrapgh weed (HB)	2.75	2.35	3.15	0.039	0.007	0.071	0.347	0.301	0.393	–	II
60	*Thunbergia laurifolia*	Thunbergia spp. (VN)	2.04	1.81	2.27	0.097	0.079	0.116	0.417	0.391	0.444	0.41	III
61	*Elephantopus mollis*	Tobacco weed (HB)	3.65	3.37	3.93	0.08	0.057	0.102	0.521	0.489	0.554	0.089	III
62	*Eichhornia crassipes*	Water hyacinth (HB)	3.11	2.97	3.25	0.22	0.209	0.232	0.604	0.587	0.62	0.666	IV
63	*Pistia stratiotes*	Water lettuce (HB)	2.64	2.5	2.78	0.122	0.111	0.134	0.461	0.444	0.477	0.766	III
64	*Tecoma stans*	Yellow bells (TR)	2.6	2.37	2.82	0.183	0.166	0.201	0.468	0.442	0.494	–	III

Table 6. Regional variation in invasion stage classification of established and emerging weeds of Queensland, Australia, based on regression tree (CART model) output

Within each region and column, values are counts and percentages (in parentheses) of species in each invasion stage category. The invasion stage classifications are: Stage I: prevention or eradication), Stage II: eradication or control, Stage III: control or containment, Stage IV: containment or asset protection, and Stage V: asset protection

Invasion stage classification	Region										Overall (number of species)
	CQld	CWQld	DDSW	FNQld	NQld	NWQld	SEQld	TORRES	WBB	WHITS	
I	0	4	10	10	0	8	0	0	0	1	33
	(0%)	(21.1%)	(26.3%)	(21.7%)	(0%)	(30.8%)	(0%)	(0%)	(0%)	(2.9%)	(9.8%)
II	11	6	15	13	6	6	10	3	6	12	88
	(29.7%)	(31.6%)	(39.5%)	(28.3%)	(17.6%)	(23.1%)	(20.4%)	(21.4%)	(15%)	(34.3%)	(26%)
III	6	3	6	6	9	5	11	6	10	3	65
	(16.2%)	(15.8%)	(15.8%)	(13%)	(26.5%)	(19.2%)	(22.4%)	(42.9%)	(25%)	(8.6%)	(19.2%)
IV	6	3	4	12	5	2	8	3	10	7	60
	(16.2%)	(15.8%)	(10.5%)	(26.1%)	(14.7%)	(7.7%)	(16.3%)	(21.4%)	(25%)	(20%)	(17.8%)
V	14	3	3	5	14	5	20	2	14	12	92
	(37.8%)	(15.8%)	(7.9%)	(10.9%)	(41.2%)	(19.2%)	(40.8%)	(14.3%)	(35%)	(34.3%)	(27.2%)
Overall (number of species)	37	19	38	46	34	26	49	14	40	35	338
	(100%)	(100%)	(100%)	(100%)	(100%)	(100%)	(100%)	(100%)	(100%)	(100%)	(100%)

after establishment in a given area, so will its regional distribution – the so called double jeopardy or trouble hypothesis (Gaston 1999). Nonetheless, the negative correlation between distribution and abundance for bitou bush (*Chrysanthemoides. monilifera* subsp. *rotundata*), Hygrophila (*Hygrophila costata*), blackberry (*Rubus. anglocandicans*) and devil's rope pear (*Cylindropuntia imbricata*), in contrast to positive trends for many of the focal species investigated is worth commenting upon. The first three species have specialist habitat requirements (dunes, riparian areas) that limit their distributions. Based on the regression tree output, the above-named species were allotted a recommendation of eradication or control (Stage II category). We think eradication will be a more appropriate management option for these species. This is in line with the management objective of Queensland Government (for bitou bush (*Chrysanthemoides monilifera*, subsp. *rotundata*) see Behrendorff *et al*. 2019; https://www.daf.qld.gov.au/__data/assets/pdf_file/0006/72825/IPA-Bitou-Bush-PP10.pdf, accessed 23 September 2020), and with the generic belief that such species have established individuals in grid cells classified as having adequate habitat suitability (i.e. high probability of occupancy) but currently are limited in abundance and hence propagule supply (Osawa *et al*. 2019). Such grid cells are relatively less likely to be recolonised after a single (or few recurring) eradication activity due to limited propagule supply from surrounding grids. However, we concur that the presence of long-lived seed banks for bitou bush (*C. monilifera* subsp. *rotundata*) or blackberry (*R. anglocandicans*) might make the allotted recommendation challenging (Schoeman *et al*. 2010; Behrendorff *et al*. 2019; Scott *et al*. 2019).

Weed distribution rather than abundance was a better descriptor of invasion severity, and hence in the derivation of 'space for time' invasion curve (Fig. 4). Akin-Fajiye and Gurevitch (2018) also reported that overall, in modelling the spread of the invasive spotted knapweed (*Centaurea stoebe*),

the distribution models performed better than the abundance models across different spatial scales (see also Bradley 2013; Lacasella *et al*. 2017; Bradley *et al*. 2018). The lower predictive power of abundance could have resulted from the fact that most of our weed species are more dynamic along the abundance axis with varied (high and low) cover estimates at a given grid cell occupancy value compared with variation along the occupancy axis (Fig. 3), or that abundance is simply a difficult trait to comprehensively estimate. The finding also amplifies the fact that occurrence data alone can predict, to a great extent, the likely impact of an invader in its novel range (Václavík and Meentemeyer 2012). This, however, does not discount including invaders' abundance and effect data for improved model predictions, but we know they are often precluded as they are difficult to collect and parameterise due to logistic and financial constraints (Akin-Fajiye and Gurevitch 2018; Bradley *et al*. 2018), although for some weeds remote sensing can overcome these constraints. Additionally, collected abundance data are often, as in our case, only qualitative categorical estimates (Bradley 2013; Lacasella *et al*. 2017) and are thus prone to error.

Overall, the CS-SD model based on simulations suggested higher weed distribution (Fig. 2) than the observed data. In other words, the CS-SD model predicted much more land area at risk of invasion (i.e. higher weed distribution) than the GCO model based on the APDS datasets. A difference in prediction of CS-SD *v*. GCO models and as found in this work is not new (see Gassó *et al*. 2012; Václavík and Meentemeyer 2012), and may be due to a variety of reasons. The CS-SD model reflects the potential number of grids a focal weed is capable of invading assuming all conditions for spread and establishment are met, i.e. there are no limiting biotic and environmental conditions for filling available niches, which is not often the case (Bradley 2013). The CS-SD model uses CLIMEX predictions which often overestimate the likely potential occurrence of the species, given that distribution is only limited by average climate tolerance. It is well known that

when additional environmental parameters, like soil type or land zone, are incorporated into distribution models, a more realistic robust output is often produced (e.g. Taylor and Kumar 2013). In addition, our CS-SD model, like most other weed risk models, relied on herbarium occurrence records assembled from a variety of global herbaria (depicting natural and novel-range habitats of the invader) which have been shown to be good at predicting risk of spread (establishment niche) but are considered poor predictor of abundance or impact niche (Bradley *et al*. 2018). The discrepancy between the models has also been attributed to the stage of invasion and time lags between introduction and spread or impact – two important calibrators of the CS-SD model (Václavík and Meentemeyer 2012; Bradley 2013). These historical variables of invaders can influence CS-SD output, especially more so for species whose habitat or climate suitability model is based on data collected at early stages of invasion when all potential niches are yet to be filled. It is estimated that ~100–150 years after arrival in a novel environment are required by an invader to achieve habitat equilibrium or stability – i.e. full niche occupancy (Václavík and Meentemeyer 2012) – a condition not yet fulfilled by many of our focal species (O. O. Osunkoya, unpubl. data). The influence of climate change may mean that this equilibrium may never be achieved for many invader species.

The use of biological invasion curves to relate invader's population growth (based mainly on distribution) with time abounds in the ecological literature (e.g. Delisle *et al*. 2003; Crawford and Hoagland 2009; Antunes and Schamp 2017; Fleming *et al*. 2017; O. O. Osunkoya, unpubl. data). Based on this curve, policy recommendations are often inferred (Standards Australia International Ltd 2006; Auld and Johnson 2014; Antunes and Schamp 2017). In Australia, seldom have invasion curves been constructed for pest plants and animals of significant concerns (but see Sindel 2009; State of Victoria, see https://www.environment.vic. gov.au/__data/assets/, accessed 13 June 2020). This deficiency could be attributable to the fact that for many invader species, necessary data (especially abundance per unit area) are not recorded over a sufficiently long period of time. In this study, and exploring the spatially extensive but time-limited APDS datasets, we have replaced time with space (as in Fan *et al*. 2018). The approach provides an estimation of weed population changes and invasion status using a single or minimal number of points in space (distribution) within and across regions of Queensland.

Based on grid cell occupancy (distribution) and weed abundance, we have developed a workable framework that classifies the current conditions of many weeds in Queensland and its regions into invasion stage categories, which can then be related to standard weed management guidelines (Standards Australia International Ltd 2006). This approach closes the gap between the large spatial extent at the global and national levels of coarse grain plans (Wilson *et al*. 2014; Foxcroft *et al*. 2017; Froese *et al*. 2019; Osawa *et al*. 2019; Osunkoya *et al*. 2019*a*, 2019*b*) and that of the medium-finer scale necessary at the state or regional or LGA levels. For example for parthenium weed (*Parthenium hysterophorus*), one of the most aggressive invader weed in Queensland

(Dhileepan *et al*. 2018; Osunkoya *et al*. 2019*a*, 2019*b*), the regression tree (CART analysis) allocated an invasion category of Stage V at the state-wide level. This will suggest that overall, the relative invasion severity of the species is amongst the highest of the weeds examined. Parthenium weed (*P. hysterophorus*), just like Parkinsonia (*Parkinsonia aculeata*), is weed of state and national significance (van Klinken *et al*. 2016; Dhileepan *et al*. 2018; Osunkoya *et al*. 2019*a*; https://www.environment.gov. au/biodiversity/invasive/weeds/weeds/lists/index.html, accessed 8 October 2020). Nonetheless, drilling down to regional level, the 'space for time' invasion curve indicated that different regions have varying invasion stage categories for parthenium weed (*P. hysterophorus*), and as such different management options will need to be invoked. These options at the LGAs or regional level will range from monitoring or eradication if detected (TORRES), to the use of various control measures of integrated weed management, including chemical and biological controls and cultural practice of pasture manipulation (FNQld, CWQld), to the use of aforementioned actions coupled with protection of environmental and agricultural assets (CQld, NQld, WHITS, WBB, DDSW, SEQld). The control and asset protection options are in regions where parthenium weed (*P. hysterophorus*) has already taken footholds and eradication is no longer feasible. It is heartening that these varying management options are already in place for parthenium weed (*P. hysterophorus*) in different regions of Queensland (Bajwa *et al*. 2018; Dhileepan *et al*. 2018; Shabbir *et al*. 2018). Our finding thus confirms and validates 'on-the-ground' management, finer grain options for this particular weed. However, many of the 64 weed species investigated do not have realistic 'on the ground' policy and management actions either because they are low on the species prioritisation list (e.g. Aleman grass, *Echinochloa polystachia* – see Osunkoya *et al*. 2019*a*) are relatively new incursions (e.g. firethorn, *Pyracantha* spp.; Saint Johns's wort, *Hypericum perforatum*) or there are inconsistencies in legislation and lack of socio-political will to manage them (e.g. *Leucaeana leucocephala* though not investigated in this study; Margolis *et al*. 2005; Crowley *et al*. 2017; Mackay *et al*. 2017; Campbell *et al*. 2019). The last factor (i.e. a lack of socio-political will) is often a major consideration – implying that defining appropriate management option based solely on invasion stage may be insufficient.

Uncertainty might exist in our data acquisition and inputs (e.g. estimates of weed cover), and hence some level of errors is inevitable in data output. Thus the weeds stage categorisation scheme should be seen as a method to align weeds on a continuum (and hence compare and contrast), rather than give absolute values of their invasiveness or impact and management expediency (see also Auld and Johnson 2014; Osunkoya *et al*. 2019*b*). Consequently, the stage classification scheme presented here at best categorises species into fuzzy management action classes that can oscillate one-step down (except for Stage I category) or one-step up (except Stage V category) from the assigned stage category in terms of the realistic 'on the ground' management actions (Caton *et al*. 2018; Osunkoya *et al*. 2019*b*).

Conclusions

Using the spatially extensive, but time-limited APDS datasets, we showed that at multiple spatial scales, abundance and distribution are not independent but are frequently positively related to each other. The greater level of habitat modification caused by higher human populations, together with greater moisture environments, are likely to explain the higher weed spread and invasion severity in the coastal eastern regions (bar the far northern region and the Torres Strait Islands) (see also Osunkoya *et al.* 2019*a*). The use of models – one based on occurrence data from global herbaria and climate suitability (CS-SD) simulations, and the other on actual occurrence inferred from spatial grid records (GCO) extracted from the APDS – have provided the opportunity to show that most Queensland established weed species are yet to realise their full potential and hence further expansion is possible. We showed that invasion severity is driven mainly by distribution and abundance traits (in that order), though other factors (including environmental envelopes like moisture availability and species-specific and historical attributes) must be considered alongside these two traits (Pyšek *et al.* 2008; Václavík and Meentemeyer 2012; Osunkoya *et al.* 2019*a*; O. O. Osunkoya, unpubl. data).). We have used the APDS dataset to construct 'space for time' invasion curves, and have identified invasion stage categories of many Queensland weeds. This has led to the confirmation or development of region-specific control options for the weeds investigated. Hence, our findings can feed into policy and management. No doubt, like most pest prioritisation exercise (e.g. Booy *et al.* 2017; Osunkoya *et al.* 2019*a*, 2019*b*) as more spatial data at finer scale become available, it is imperative to review the invasion stage categories and offer appropriate adaptive management and policy options for the focal species presented in this work. Adding more environmental layers, e.g. soil types and land zones to the climate-based models of CLIMEX will also improve prediction of potential niche distributions. In conclusion, we advocate for continuing data gathering by the APDS (with improved accuracy and spatial grid-size standardisation) in view of its uniqueness of warehousing both spread and abundance data at multiple spatial scales. The APDS datasets will also complement herbarium records of invader species, and it will be interesting to compare model outputs from the two sources of data.

Conflict of interest

Olusegun O. Osunkoya is an Associate Editor for the *Australian Journal of Botany*. Despite this relationship, he did not at any stage have Associate Editor-level access to this manuscript while in peer review, as is the standard practice when handling manuscripts submitted by an editor to this journal. *Australian Journal of Botany* encourages its editors to publish in the journal and they are kept totally separate from the decision-making process for their manuscripts. The authors have no further conflicts of interest to declare.

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