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ORIGINAL PAPER

The 'lawnification' of Australia's eastern grassy woodlands: the past, current and likely future spread of an invasive perennial grass, *Bothriochloa pertusa*

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Abstract Many of today's damaging invasive plants were intentionally introduced for pasture development and amenity. By examining the introduction history and consequent spread of these species, we can identify factors associated with their successful establishment and dominance. Using collated presence/absence and cover data, alongside a review of the literature and discussions with land managers, we present a comprehensive analysis of the introduction history and spread of the environmental and agricultural grassy weed, *Bothriochloa pertusa* (L.) A.Camus (Indian couch) throughout Queensland, Australia. Using this data, we also perform habitat suitability models to predict its potential distribution and local-scale cover across Queensland in relation to key environmental variables. We found that *B. pertusa* was introduced on multiple occasions and across a large area of Queensland, despite re-occurring doubts and poor evidence for its benefit to livestock production. Livestock grazing, associated disturbances (i.e. land clearing, soil erosion) and climatic extremes were commonly associated with its spread throughout the landscape. In 2020 the main area of *B. pertusa* invasion as indicated by occurrence records spanned 28,537,600 ha. Results from the habitat suitability models suggest the occurrence and local-scale cover of *B. pertusa* is largely determined by climate variables and the foliage projective cover of trees. Based on these results *B. pertusa* still has considerable capacity to spread and increase in dominance across many areas of Queensland, particularly further west and south of its current range. The introduction and spread history of *B. pertusa* suggests propagule pressure, traits, climate, land management and cultural perceptions are all key factors implicated in the spread of *B. pertusa*. Where *B. pertusa* has become dominant there has been a major shift in lifeform from native perennial tussock species to a grazing tolerant stoloniferous species. To slow this process of 'lawnification' we recommend more conservative grazing strategies and strategically selected protected areas to maintain cover of grazing sensitive native tussock grass species.

Keywords Grazing · Habitat suitability model · Pasture · Propagule pressure · Species introductions

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Introduction

The introduction of non-native plant species for the purpose of forage and browse is a pervasive

agricultural practice across the globe (Cook and Dias 2006; Jank et al. 2014; McAlpine et al. 2009; McGill 2015; Walker and Weston 1990). Many of these species become invasive, replacing native pasture species, expanding into natural areas and sometimes transforming ecosystems (Keane and Crawley 2002). Invasive pasture species can lead to changes in plant community composition and diversity either directly, through altered competitive interactions (Firn et al. 2010) or indirectly through changes to ecosystem functions, such as nutrient cycling (Rossiter-Rachor et al. 2009) or fire regimes (Butler and Fairfax 2003; Setterfield et al. 2010). Although the introduction of these species has sometimes improved pasture productivity and led to economic gain (Brenner 2010; Friedel et al. 2011), their success has been variable, with many species achieving negligible benefits for production and instead becoming problematic invasive species (Cook and Dias 2006; Driscoll et al. 2014; Firn and Buckley 2010; Grice 2006; Setterfield et al. 2010).

Despite the impacts of invasive pasture species often being well studied, their introduction history and initial spread is often overlooked or understated within the invasion biology literature (Cook and Dias 2006; Puth and Post 2005) [but see (Adams et al. 2015)]. This is concerning as the introduction and early spread of invaders provide important insights into the mechanisms that drive their expansion and are essential for developing strategies to reduce their spread and impact (Lonsdale 1999). Further, given the pressure to meet global food demands and the potential intensification of pasture development across the globe (Driscoll et al. 2014; McAlpine et al. 2009), having a thorough understanding of historical plant introductions is important for developing appropriate risk assessments for future plant introduction programs. This study presents a comprehensive analysis of the introduction history, spread and potential future distribution of the invasive non-native pasture species, *Bothriochloa pertusa* (L.) A.Camus (Indian couch) in Queensland, Australia.

Bothriochloa pertusa was first introduced to northern Queensland, Australia in 1939 for pasture and lawn trials. Since its introduction in 1939, the perennial grass species, *B. pertusa* has spread widely and has been observed forming apparent monospecific stands across large areas of Queensland. The continued spread of the species poses a significant threat to native flora and fauna and ecosystem function (Bartley et al. 2014, Koci et al. 2020; Kutt and Fisher 2011; Kutt and Kemp 2012; Lebbink et al. 2021a), in a region already under threat from other invasive species, widespread habitat clearance and other anthropogenic disturbances (McAlpine et al. 2009; Reside et al. 2017). Using plfots from 1 to 1000 m^2, Lebbink et al. 2021a found the negative effect of *B. pertusa* on floristic diversity was maintained both at small and large spatial scales, which is a pattern contrary to some other invaders (Powell et al. 2013) and suggests large scale diversity loss where this species is dominant. Further, findings from Bartley et al. (2014), find that the invasion of *B. pertusa* may be associated with increased sediment load into The Great Barrier Reef on the east coast of Australia, due to its shallower roots than native perennial grasses. Understanding the past and current extent of *B. pertusa* is crucial for predicting and managing its ongoing spread and impacts on native biota.

By examining historic introduction and spread patterns, this study proposes key modes of spread, predicts future spread, and suggests management options for *B. pertusa*. Although the findings presented here are specific to Australia, the methods and concepts are relevant for evaluating and understanding the spread and impact of invaders across the globe.

Methods

Study species

Bothriochloa pertusa is a perennial stoloniferous grass species native to south-east Asia and India. *B. pertusa* possesses high fecundity and rapid growth rates (Howden 1988; McIvor et al. 1996) (Fig. 1). *Bothriochloa pertusa* does not produce high aboveground biomass but forms a dense mat of stolons that allows for a much more continuous ground cover of culms than is typical of tussock grasses. The network of stolons renders *B. pertusa* resistant to grazing, and it typically increases under heavy stocking rates after colonizing bare ground (McIvor 2007; McIvor et al. 1982). *Bothriochloa pertusa* is palatable to cattle, however, provides less feed than larger tussock grass species which are generally preferred.

Bothriochloa pertusa can invade a variety of both wooded and grassland habitats. Where it is observed



Fig. 1 *Bothriochloa pertusa*; **a** seed heads, **b** stoloniferous life-form, **c** example of invasion front in central Queensland. The bright green prostrate grass is *B. pertusa* and the taller tussock is the native *Bothriochloa ewartiana*. **d** A woodland heavily invaded by the *B. pertusa* and an example of '*lawnification*', the process by which native tussock grass species are replaced by grazing tolerant stoloniferous species

most dominant however is in tropical and sub-tropical grassy woodlands on sandy loam soils, which are wide-spread in the sub-coastal areas of central and northern Queensland. Key wooded species within invaded areas include narrow leafed Iron bark (*Eucalyptus crebra*), Mountain coolabah (*Eucalyptus orgadophila*) and Poplar Box (*Eucalyptus popalnea*). Key native grass species within invaded areas include Desert bluegrass (*Bothriochoa ewartiana*), Queensland bluegrass (*Dicanthium sericeum*) and Black spear grass (*Heteropogon contortus*). Areas invaded by *B. pertusa* often appear as a manicured lawn (Fig. 1d), with low diversity or structural complexity. This process of 'lawnification' reflects a major shift in growth form from native perennial tussock grasses to a grazing resistant stoloniferous grass species.

Data sources

Bothriochloa pertusa presence/absence records were collated from multiple data sources and used to describe and analyse the introduction history and spread of *B. pertusa*, and to predict its future distribution throughout the north-eastern Australian state of Queensland. Data included both publicly available records and records collated from field surveys (Table 1, Appendix 1). Once collated, the data was checked, and duplicate records removed. In total we collated 1449 presence records spanning 1939–2019.

Table 1 Total number of *B. pertusa* presence, absence and cover records collated from a variety of data sources between 1941 and 2019

Source	Presence/absence	Cover	Date range
Detailed floristic surveys			
Queensland Herbarium CORVEG	774	738	1984–2019
Other Queensland Herbarium survey sites	411		1950–2019
Department of Agriculture and Fisheries Q-graze	79		1992–2001
Bothriochloa pertusa impact and spread surveys*	130	130	2017–2020
Online sources			
Australian Virtual Herbarium	271		1941–2018
Other			
Bothriochloa pertusa spread surveys*	390	357	2017–2020
Property evaluation vegetation maps**	153		1950–1997
Total	2208	1225	

Contemporary absence records were collated from where *B. pertusa* was not recorded during floristic surveys conducted between 2017 and 2020. Further information on data collection methods can be found in Appendix 1

*Conducted by the author (G. Lebbink) (methods Appendix 1)

**Sourced from the Queensland Department of Natural Resources, Mines and Energy

In addition, 759 contemporary absence records were collated from where *B. pertusa* was not recorded during comprehensive floristic surveys conducted between 2017 and 2020.

For 1262 of the 2208 total presence/absence records, a measure of *B. pertusa* cover was also recorded, either as a percentage or within the broad cover categories (1 = absent, 2 ≤ 1%, 3 = 1–10%, 4 = 10–20%, 5 = 20–50%, 6 ≥ 50%). We converted all records to broad cover categories for use in the habitat suitability model described below.

Introduction history and spread

We used only the *B. pertusa* presence records, alongside information obtained from within the literature, and discussions with land managers to assess and describe the introduction history and spread of *B. pertusa* throughout Queensland. To illustrate its spread, we mapped the change in the total number of presence records (within 30 km grid cells) over time. We calculate the approximate area of invasion using a polygon around the main centroid of occurrence points. This is likely an underestimate of its true range but highlights the area it is most likely to occur.

We acknowledge that there are limitations to using species presence records to discuss trends in a species' spread. In particular, the rate of species collections is not consistent over time and space. However, the trends in this data were verified by information obtained from the literature and discussions with long-term land holders who have witnessed the spread of *B. pertusa*.

Habitat suitability and predicted future spread

To assess the relationship between *B. pertusa* and key environmental predictors, and to predict its future spread, we performed two habitat suitability models (HSM); one with presence/absence (occurrence) and another with cover as the dependent variable. These models predict the potential distribution of *B. pertusa* based on its current occurrence and environmental preferences. For Queensland, the environmental predictors that were consistently mapped and appropriate for inclusion in a HSM were as follows: land-zones (12 classes which summarise soil and geology), rainfall variability, wet-season rainfall, mean temperature during the growing-season (October to April), distance to a waterway, soil clay content, foliage projective cover (FPC) of trees and vegetation clearing index (2 classes; uncleared and high-valued regrowth or cleared) (Table 2). Gridded climate data (rainfall variability, wet-season rainfall and mean temperature during the growing season) were obtained from Bureau of Meteorology, 2020. Spatial land-zone information (Christian et al. 1953; Gunn et al. 1967; Story et al. 1967; Speck et al. 1968; Galloway et al. 1970, 1974; Nix and Gunn 1977) and other environmental data were obtained from the Queensland Government Spatial Catalogue 2020. Land zone 1 which represents tidal flats and beaches was not well represented by the data and was excluded from both the cover and occurrence models. To ensure the cover models were representative of the current invasion potential, only records (both presence and absence) from the last 5 years (2015–2020) and those with a cover value > 20% (as this still reflects vulnerable habitat), were included (1226 records in total). After these data checks, 1433 presence records and 740 absence records (2174) were used in the occurrence models, and 466 presence (with broad cover 2–6) and 760 absence (with broad cover = 1) records were used in the cover model.

A boosted regression tree approach with tenfold cross validation of training data (Elith et al. 2008) was used to build the HSMs. The resulting occurrence model explained 45% of cross-validated deviance, while the cover model explained 38%. The fitted HSM was used alongside the mapped grids of environmental conditions to predict the probability of occurrence and likely cover of *B. pertusa* within Queensland. Analyses were conducted in R (version 2.10.0, R development Core Team, 2009) using the "gbm" library supplemented with functions from Elith et al. (2008) (see Appendix 2 for full modelling methods).

Results

Introduction history

Key sources of *B. pertusa* introduction were associated with pasture development, rehabilitation, and amenity.

Table 2 Details of environmental predictors used in habitat suitability models (HSM) to predict *B. pertusa* cover and occupancy

Variable	Abbreviation	Source	Details
Mean growing season temperature (°C)	MGST (°C)	Bureau of Meteorology (2018)	The mean temperature between October and March based on the standard 30-year period 1961–1990. Data accuracy dependent on available station data. Station data has an accuracy of the order of 0.01 degrees
Foliage protective cover (%)	FPC (%)	State of Queensland (2021a)	Foliage projective cover is a metric of vegetation cover from the mid- and over-story measured using remotely sensed data sourced from Sentinel2
Distance to watercourse (m)	DTW (m)	State of Queensland (2021b)	The definition of a watercourse here is any natural channel along which water may flow from time to time, so included both permanent and ephemeral streams
Rainfall variability index (0 − > 2)	RVI	Bureau of Meteorology (2018)	Rainfall variability determined using the percentile analysis method. The index of variability is defined as the 90th rainfall percentile minus the 10th rainfall percentile divided by the 50th percentile. Data accuracy dependent on available station data. Station data has an accuracy of the order of 0.01 degrees
Mean growing season rainfall (mm)	MGSR (mm)	Bureau of Meteorology (2018)	The mean rainfall between October and March based on the standard 30-year period 1981–2010. Data accuracy dependent on available station data. Station data has an accuracy of the order of 0.01 degrees
Land-zone	Land-zone	Queensland Herbarium (2020)	Land-zones 1–12 describe the major geologies and associated landforms and geomorphic processes in Queensland. Refer to Wilson et al. 2012 for specific details. Land zone 1 is associated with deposits subject to periodic tidal inundation. Due to poor representation of data points within this area this was excluded from the model
Clay content (%)	Clay content (%)	CSIRO Land & Water (2011)	Clay content 0–30 cm (250 m raster). Data sourced from state and federal soil surveys
Clearing score (1 or 0)	Clearing score	Queensland Herbarium (2020)	Allocates polygons as uncleared and high-value regrowth or cleared using a combination of satellite imagery (Sentinel2) and ground truthing surveys

Pasture development

The first Australian Herbarium samples of *B. pertusa* are from Queensland and date back to 1939, where it was introduced to the Commonwealth Scientific and Industrial Research Organisation (CSIRO) Fitzroy Vale research facility, in Rockhampton (See Fig. 2 for place names), and to the agricultural college facility in Gatton. At Fitzroy Vale, *B. pertusa* was trialled within five 40 m^2 plots; two sown with only *B. pertusa* and three with a mixture of *B. pertusa*, six other non-native grass species and the

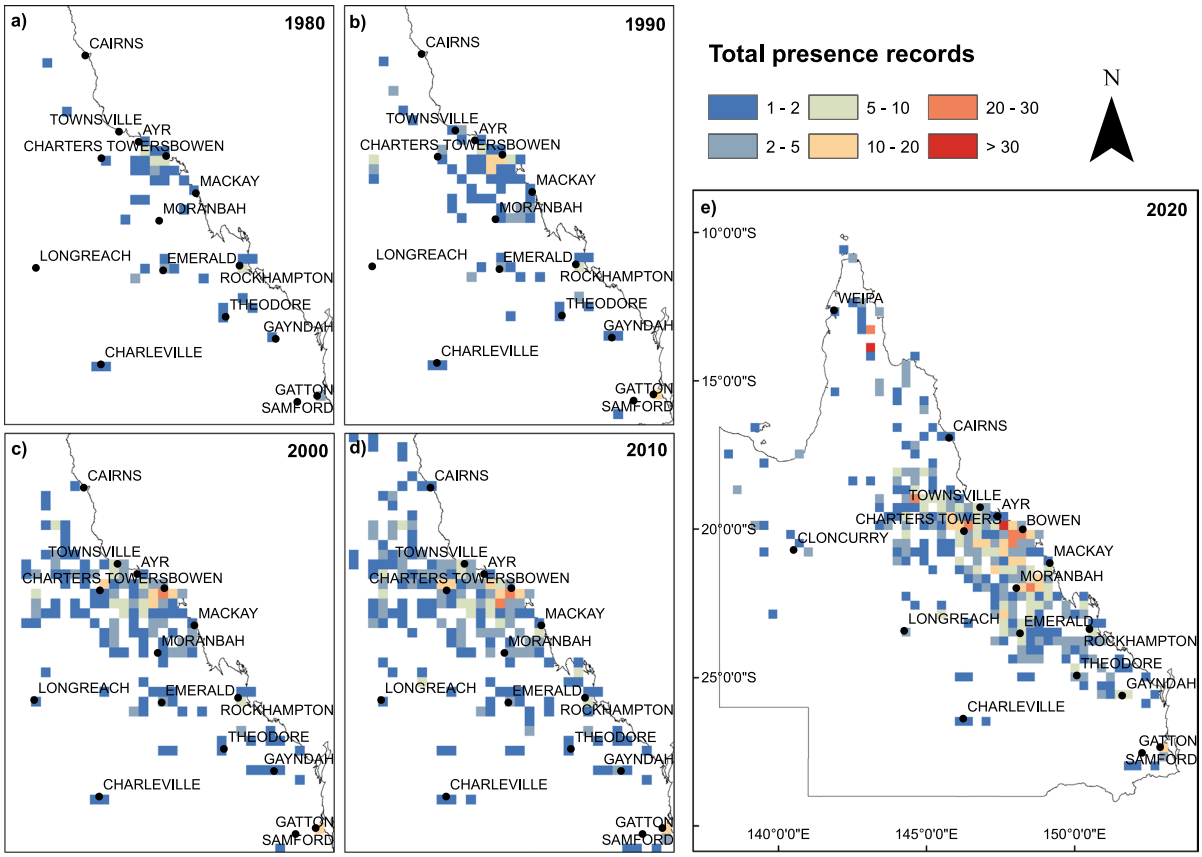


Fig. 2 Total *B. pertusa* presence records within 30 km^2 raster grid cells in 1980 (**a**), 1990 (**b**) 2000 (**c**), 2010 (**d**) and 2020 (**e**), within Queensland. Records were collated from a number of different data sources which are detailed in Appendix 1

non-native leguminous shrub *Stylosanthes gracilis* (Miles 1949). At conclusion of the trial in 1942, *B. pertusa* was not included amongst the promising species enlisted for wider regional testing. Among the species considered promising were a number that have since spread widely and had substantial negative environmental impacts; namely *Andropogon gayanus* (Rossiter-Rachor et al. 2009; Setterfield et al. 2010), *Chloris gayana*, *Cenchrus ciliaris* (Fairfax and Fensham 2000; Jackson 2005), *Melinis multiflora* (van Klinken and Friedel 2017) and *Panicum maximum* (van Klinken and Friedel 2017).

Despite its poor performance in initial trials, *B. pertusa* continued to be introduced and tested across a number of different research facilities across the state. In the early 1950s, *B. pertusa* was being grown for seed at the CSIRO research facilities in Samford and nearby Strathpine, in South-East Queensland. In 1955, the species was introduced at the Department of Agriculture and Fisheries (DAF) research stations in Emerald and Biloela (92 km NE of Theodore on map), in central Queensland. In Emerald, *B. pertusa* was noted as "unimpressive for pastures because of its low productivity" (Bisset 1980). In 1978 *B. pertusa* was introduced to the DAF Brian Pastures research facility, near Gayndah, and in the early 1990s *B. pertusa* was included in pasture trials at CSIRO Landsdown station in Townsville (Jones 1997).

Although its value as fodder was contested, during the late 1980s and into the 1990s the species was recommended as a useful fodder crop, particularly in low fertility soils and to sustain high grazing pressure (Partridge and Miller 1991). A survey of 297 commercial beef producers in Queensland during 1996–97, found *B. pertusa* was used for pasture improvement across some properties in central and northern Queensland (Bortolussi et al. 2005).

Rehabilitation

During the 1970s, *B. pertusa* was introduced to a number of regions across Queensland during trials to assess its value for soil conservation (Bisset 1980; Truong and McDowell 1985). *Bothriochloa pertusa* was initially trialled for this purpose in research facilities near Gatton in south-eastern Queensland (Truong and McDowell 1985). This trial led to a series of larger trials in 1979 and 1980 in south, central and northern Queensland, to evaluate the effectiveness of *B. pertusa* in stabilising farm waterways (Truong and McDowell 1985). *Bothriochloa pertusa* was quick to germinate and establish high cover and deemed useful for stabilising the riverbanks and reducing water erosion. Its use for other stabilising works such as mining overburden and road and railway embankments was also promoted in this study.

During the 1980s the species was sown for mine rehabilitation at Blackwater, Theodore and Callide coal mines near Emerald (Truong and McDowell 1985) and was observed spreading naturally onto mine spoils at the Collinsville coal mine, near Mackay. The abundance of *B. pertusa* on gem-mine spoils in inland from Emerald (near Rubyvale) is also likely associated with the rehabilitation of these mines in the late 1990s. It is difficult to determine how frequently the species was used for rehabilitation projects as detailed records were often not kept or were not made available (Silcock 1991). The Queensland Government's Soil Conservation Guidelines (2015), however, suggest that *B. pertusa*, along with *C. ciliaris* (buffel grass) were used widely for rehabilitation projects on the lighter arid inland soils but "were no longer recommended due their weed potential".

Amenity

The final major source of *B. pertusa* introductions was for amenity purposes, such as lawns, airstrips and along road verges. It was particularly advocated as a lawn species in the drier parts of the state and as such most lawns in central and western Queensland are *B. pertusa* dominant (personal observation, March 4, 2020). Known plantings of *B. pertusa* for amenity in Queensland date to the 1950s with the species recorded as the lawn for the Bowen showgrounds and the airstrips at Cloncurry, Charleville and Bowen aerodromes (Bisset 1980). Sowing of the species for amenity purposes was also occurring in the Northern Territory throughout the late 1980s (Cowie and Werner 1993). Its presence was recorded on the neighbouring Tiwi islands during this time (Fensham and Cowie 1998). The species is now common throughout the Northern Territory and its dominance is increasing in some grazed ecosystems (Robyn Cowley pers. comm. 2019).

Spread

It wasn't until the mid-1960s that the number of *B. pertusa* herbarium records in Queensland started to increase, and its spread discussed within the literature. During the 1960s *B. pertusa* mostly occurred within the Bowen area, where the species was described to have 'spread like wildfire', during the 1960s and 1970s (Fig. 2a) (Bisset 1980). The landholders of Salisbury Plains, near Bowen first saw the species in 1964 and were 'initially concerned by its aggression' but noted an 'improvement in management and production' in comparison to pastures previously dominated by *H. contortus* (black spear grass) (Partridge and Miller 1991). Vegetation maps used for property evaluations in the 1960s and 1970s (Table 1, Appendix 1), also suggest the species was dominant across several properties in the Bowen region during this time.

By 1980 the species was observed forming solid stands over whole paddocks inland of Ayr (Bisset 1980). The species was also noted as abundant and spreading along roadsides inland from Bowen and up towards Townsville. Transport of hay and cattle from the Bowen region is thought to have facilitated its spread into these regions (Bisset 1980). It was also during the 1980s when *B. pertusa* started to increase in occurrence inland of Mackay, and it is within this region today that *B. pertusa* is particularly abundant (Fig. 2b, e). Coal mining is an extensive enterprise in this region, and the use of *B. pertusa* to rehabilitate mine spoils during this time (Truong and McDowell 1985) is plausibly associated with this spike in occurrences.

Throughout the 1990s the number of records in the Charters Towers region increased considerably (Fig. 2c). *Bothriochloa pertusa* was observed naturally spreading onto several properties during this time, often from the edge of roads or from neighbouring sown pastures (Bortolussi et al. 2005; O'Reagain

and Bushell 2015). A grazing trial initiated in the region in 1992, found a steady increase in *B. pertusa* after the mid-1990s, particularly on heavily grazed sites (Ash et al. 2011). Its increase after this time was suggested to be associated with a series of below average rainfall years prior to 1996, followed by a run of higher rainfall years leading up to the 2000s (Ash et al. 2011). Also, during the 1990s, *B. pertusa* was observed replacing substantial areas of *H. contortus* grasslands in central and northern Queensland, with Walker and Weston (1990) suggesting 800,0000 ha had been colonised by *B. pertusa* by the early 1990s.

During the 2000s the species appeared to expand between Mackay and Charters Towers (Fig. 2d). On a long-term (1998 to current) grazing trial near Charters Towers, the species was very infrequently recorded up until 2007, when it increased exponentially across all grazing treatments, but particularly on the heavily grazed treatments in the poplar box (*Eucalyptus populnea*) woodland (O'Reagain et al. 2022). Similar to the initial spike in the region in the 1990s, this increase on the trial was thought to be associated with the few years of above average rainfall following drought culminating in 2007. The significant increase in *B. pertusa* across the trial was coupled with significant declines in native perennial grass species, particularly of its native congener *Bothriochloa ewartiana*. Also, during the 2000s, *B. pertusa* appeared to increase within the northern tip of Queensland (Cape York Peninsula), which aligns with findings from Bortolussi, et al. (2005) who suggest the species was naturally spreading onto several pastoral properties in this region during this time.

In the 10 years between 2010 and 2020 *B. pertusa* continued to spread and increase in dominance in northern and central Queensland, and more recently has spread into southern parts of the state, near Gayndah (Fig. 2e). A producer survey conducted in this region in 2016 suggests that only in the last 5–10 years has *B. pertusa* become particularly noticeable and problematic (Spiegel 2016). Surveys conducted throughout Queensland's grassy woodland ecosystem in 1995–6 across the southern and central Queensland found *B. pertusa* in only 1 of 207 survey sites. We resurveyed 92 of these sites in 2018 and found *B. pertusa* in 43 sites and at greater than 20% cover in nine sites (Lebbink et al. 2022). It's spread within the Gayndah area has likely been even more recent with two producers here suggesting that although it has been present for ~ 25 years (mostly along roadsides) its dominance within the pasture has only become noticeable in the last five years (Pers. comm., Les and Don. 7 July 2019). Since its introduction to the Brian Pastures research station, near Gayndah, in 1978, *B. pertusa* has also spread considerably, replacing native *Bothriochloa ewartiana* pastures in some areas. In 2020 the key invasion area (centroid around main occurrence points) spanned 28,537,600 ha.

Habitat suitability and predicted spread

The occurrence and cover of *B. pertusa* across Queensland was largely predicted by climate [particularly mean temperature during the growing season (October to April)] and FPC of trees (Table 3, Figs. 3, 4). *Bothriochloa pertusa* mostly occurred in areas with a mean growing season temperature between 23 and 27 °C and in areas with low tree cover (< 40% FPC). Outside of these thresholds *B. pertusa* was very infrequently recorded. This temperature range is typical of most sub-humid and semi-arid regions of Queensland; as well as in India and south-east Asia, where *B. pertusa* is native.

Where *B. pertusa* was most likely to achieve high cover, was in areas with a mean growing season temperature of 25 °C and in areas with < 10% FPC. Its

Table 3 Relative importance of environmental variable to models predicting *B. pertusa* occurrence (presence/absence) and cover

Variable	Relative importance (%)	
	Occupancy	Cover
MGST (°C)	36.6	29.4
FPC (%)	15.3	15.4
DTW (m)	12.5	10.1
RVI	11.6	17.7
MGSR (mm)	9.5	11.5
Land-zone	9.0	9.1
Clay content (%)	3.6	4.5
Clearing score	1.9	1.3

Variables are ordered in decreasing order of importance to the occupancy model. Variables assessed were mean growing season temperature (MGST), foliage protective cover (FPC), distance to waterway (DTW), rainfall variability index (RVI), mean growing season rainfall (MGSR), land-zone, clay content (%) and clearing score

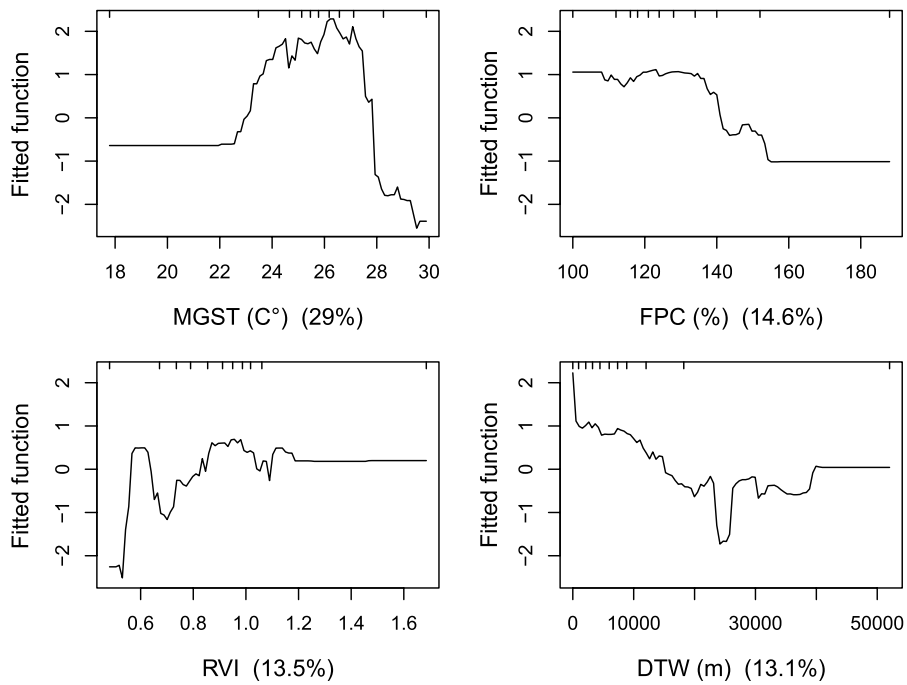


Fig. 3 Partial dependence plots for the four most influential variables in the model for *B. pertusa* occurance (presence/absence). Variables are as follows; mean growing season temperature (MGST), foliage projective cover (FPC), rainfall variability index (RVI) and distance to waterway (DTW). Y-axes are on the logit scale and centred to have zero mean over the data distribution. Rug plots at inside top of plots show distribution of sites across that variable, in deciles. See Table 3 for the full list of environmental variables and their relative importance

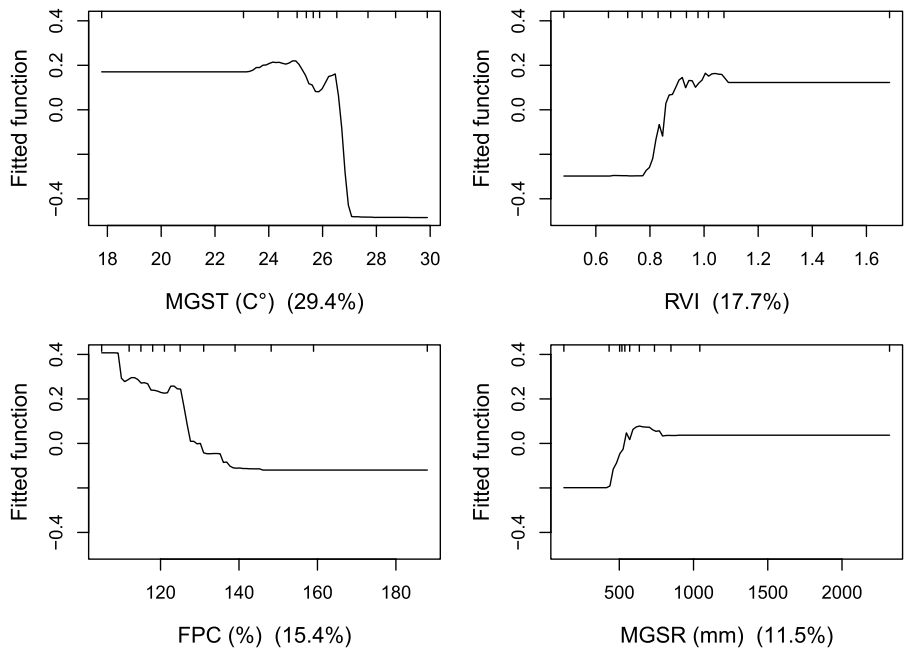


Fig. 4 Partial dependence plots for the four most influential variables in the model for *B. pertusa* cover. Variable are as follows; mean growing season temperature (MGST), rainfall variability index (RVI), foliage protective cover (FPC) and mean growing season rainfall (MGSR). Y-axes are on the logit scale and centred to have zero mean over the data distribution. Rug plots at inside top of plots show distribution of sites across that variable, in deciles. See Table 3 for the full list of environmental variables and their relative importance

dominance at this temperature may be in part associated with high germination success, with Howden (1988) finding 80% germination at 25 °C, compared to only 10% at 20 °C and 30 °C. These results align with most other plant species distribution models, which find climate rather than soil or terrain variables, are the most important predictors of plant species occupancy (Syphard and Franklin 2009). This follows that landzone was not highly influential in predicting the occurrence of *B. pertusa*. *Bothriochloa pertusa* can indeed occur across a wide range of land zones including clay to sandy soils. Although,

it is not likely to occur across extremely weathered infertile substrates such as those which occur in the far west of the state. It is also well established that competition from trees (for light and nutrients) limits grass growth, particularly for shade intolerant species, such as *B. pertusa* (Jackson and Ash 1998; Setterfield et al. 2005).

For *B. pertusa* cover, rainfall variability was also a strong predictor, with high cover associated with moderate to high rainfall variability (index of variability ~ 1.0) (Table 3, Fig. 4). This response aligns with anecdotal reports suggesting *B. pertusa* increases after cycles of drought, followed by a period of above average rainfall. Although *B. pertusa* is not considered particularly drought tolerant, its stoloniferous growth strategy and large seed bank enables it to quickly regain space and resources in response to improved growing conditions (Ash et al. 2011; Howden 1988). Conversely, many co-occurring native perennial grass species are considered drought tolerant. Livestock grazing severely compromises this tolerance however, with many studies finding a decline in basal area and survival of native grass species during drought, particularly on intensely grazed sites (Ash et al. 2011; McIvor 2007; Orr and Reagain 2011). Even in response to improved growing conditions, the rate of recovery and recruitment of native grass species was low, and they were often replaced by *B. pertusa* (Ash et al. 2011). Thus, drought and grazing-induced competitive release, combined with the colonising ability and high grazing tolerance of *B. pertusa*, provides the ideal conditions for its proliferation.

Based on habitat suitability, *B. pertusa* still has considerable capacity to spread into new areas of Queensland and to increase in dominance within the coastal and sub-coastal regions where it already proliferates. In particular, it may become more prevalent in the western (towards Longreach and Charleville) and south-western (west from Gayndah), where it has not commonly naturalised (Fig. 5). It is not predicted to reach high cover in these areas however, because these regions are mostly outside the optimal temperature and rainfall range for high *B. pertusa* cover (Fig. 5). Where it already occurs in western Queensland, these limitations to growth have been observed; for instance, on a conservation property near Longreach, *B. pertusa* is common but restricted to seasonally inundated and water run-on areas, suggesting the moister and perhaps cooler microclimates of these habitats allow for its establishment. Results from the HSMs also suggest *B. pertusa* is more likely to occur and achieve high cover closer to waterways (Table 3, Fig. 5.). In southern eastern areas of Queensland, a combination of lower and less variable rainfall and high FPC in many areas has resulted in smaller and more dispersed patches of predicted suitable habitat, and lower predicted cover, than in northern Queensland. Predicted increases to temperature and rainfall variability under future climate change scenarios (IPCC, 2019) may change these range predictions for *B. pertusa*. Likewise, *C. ciliaris* (Martin et al. 2015) and other tropical non-native grass species (Gallagher et al. 2013), are expected to move southwards with the warmer winter temperatures predicted under climate change.

The predicted extent of *B. pertusa* presented here is based on environmental variables alone. As this paper has highlighted however land management, particularly grazing management is also a very important predictor of spread and dominance in this species. These habitat suitability models should be used in conjunction with information on land management to predict invasion risk more accurately. Overall, considering the influence of land management on invasion is crucial when assessing environmental weed risk for all introduced species.

Five proposed drivers of *B. pertusa* spread

Using a combination of empirical and anecdotal data this paper describes the introduction and spread of a damaging invasive species *Bothriochloa pertusa* into Australia. By taking this approach we have gleamed important insights into both the environmental and societal factors involved in the spread of invasive plant species. We have distilled these learnings and propose five key factors associated with the spread for *B. pertusa*: propagule pressure, species traits, land management, climate, and cultural perception. Briefly we discuss each of these factors in turn before providing recommendations for their management.

1. *Propagule pressure* As this paper highlights, *B. pertusa* was repeatedly introduced across Queensland, sometimes with significant propagule load per dispersal event (such as where it was deliberately sown for pasture or lawn). As a

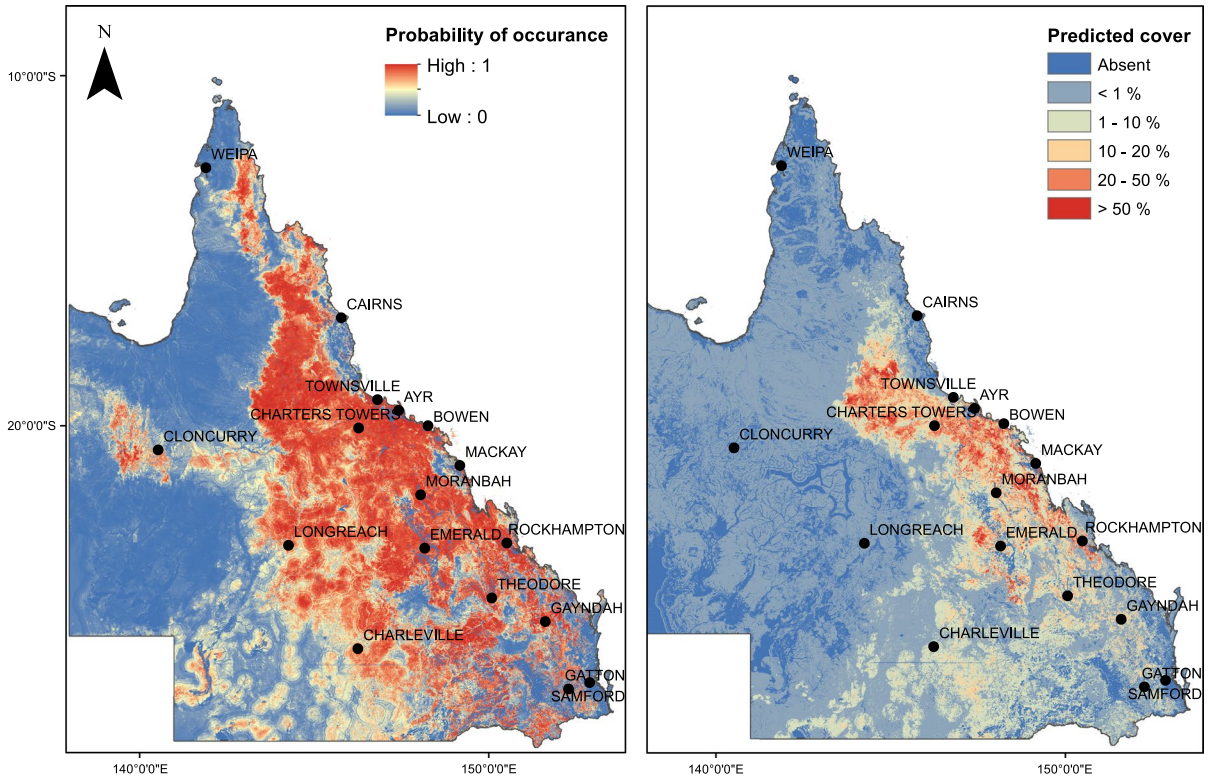


Fig. 5 Probability of occurrence (presence/absence) (left) and predicted broad cover (right) of *B. pertusa* in Queensland, as predicted by habitat suitability models, built using boosted regression trees. The resulting occurrence model explained 45% of cross-validated deviance, while the cover model predicted 38%

result, propagule load for this species has been far greater than what could have been achieved by natural processes of dispersal. *Bothriochloa pertusa* is also far more fecund than common co-occurring native species (Howden 1988). High propagule load is a key factor attributed to the success of many invasive plants (Eschtruth and Battles 2009; Fensham et al. 2013; Warren et al. 2013) and it improves the likelihood of a species surviving demographic and environmental stochastic events which threaten small populations (Lockwood et al. 2005).

2. *Species traits* The physiological traits of *B. pertusa* have potentially provided it an advantage over native species in some contexts. Very few native grasses in Australia are stoloniferous, with most perennial species forming tussocks. Clonality is a trait often associated with invader success as it increases the species capacity to colonise, with options for sexual and asexual reproduction and can provide access to a wider resource pool (Hollingsworth and Bailey 2000; Keser et al. 2014; Wilfried et al. 2012). There is also evidence to suggest *B. pertusa* roots are more resource acquisitive than co-occurring native species (Lebbink et al. 2021a). Indeed, *B. pertusa* recovers rapidly after heavy grazing and drought and this is perhaps associated with these efficient resource acquisition strategies
3. *Land management* By opening up space and resources, disturbance, such as grazing, can make a 'weed shaped hole' for opportunistic invaders to establish (Buckley et al. 2007). The movement of *B. pertusa* across the landscape has been in close association with commercial grazing land uses and associated management practices (including land clearing and fragmentation) (Jones 1997; McIvor et al. 1996; Scanlan et al. 1996). There is also research to suggest the abundance of *B. pertusa* in protected areas, free from domestic graz-

ing, is considerably lower than in adjoining lands grazed by cattle (Lebbink et al. 2021b). The pervasive and wide-spread use of land for intensive grazing systems in Queensland has shifted natural disturbance regimes in favour of *B. pertusa* invasion. Grazing intensity also appears to be important with less *B. pertusa* in areas conservatively grazed (O'Reagain et al. 2022).

4. *Climate* The anecdotal and empirical data collated in this paper point to climate and particularly the cycles of drought and heavy rainfall often associated with El Nino and La Nina respectively, as important drivers of *B. pertusa* spread. Drought can reduce the cover of native understorey species and similar to other disturbances creates space and resources for opportunistic species such as *B. pertusa* to monopolise when conditions improve (Diez et al. 2012; Shea and Chesson 2002). Climate has also been associated with the spread of other non-native grasses in Australia including *C. ciliaris* (Buffel Grass) (Fensham et al. 2013) and *Eragrostis curvula* (African Lovegrass) (Roberts et al. 2021). Extreme climatic events can facilitate invasion by (a) causing significant and widespread mortality of individuals increasing the available resources for invaders and/or (b) reducing the resilience of resident species to respond to improved growing conditions (Diez et al. 2012). Invasion attributed to climate is therefore a factor of the species resilience (both native and invasive), as well as the duration, magnitude and timing of the climatic event (Diez et al. 2012). Understanding how global climate cycles such as La Nina and El Nino affect invasion success is an important area of future research, particularly under an uncertain climatic future.
5. *Cultural perceptions*: The early introductions of *B. pertusa* were mostly occurring during a post-war era when there was a big push for pastoralism in Australia (Clements and Henzell 2010; Cook and Dias 2006). Research into the productivity of native pastures was overrun by a campaign for 'greener pastures', non-native species bred for high fecundity, productivity and resilience (Cook and Dias 2006; Driscoll et al. 2014). The aim of some influential agronomists of this time was indeed to replace all existing native pasture species with non-native pasture (Davies 1953). As such, effort to control escaped non-native pasture populations was likely negligible, particularly as this adventive behaviour was considered a good trait of productive pasture (Miles 1949). Thus, non-native pasture species such as *B. pertusa* were given a free pass to invade. Despite their environmental impacts being well known today, these species are in many cases still not considered or managed as 'weeds' under government legislations (Department of Agriculture and Water Resource 2017). Exceptions includes species such as *E. curvula* (African lovegrass) and *A. gayanus* (gamba grass) which are mostly recognised as detrimental to the agricultural industry as well as the environment (Department of Agriculture and Water Resource 2017). Due to their potential importance economically, non-native pasture species such a *B. pertusa* are 'taboo weeds', and this has and continues to stifle attempts to reduce their spread and impact.

Propagule pressure, traits, climate, land management and cultural perceptions are all key factors implicated in the spread of *B. pertusa*. Changing approaches to land management and shifting cultural perceptions may help to improve the management of this species and its consequential spread and impact into the future. Disturbance, whether it be from grazing or drought, and the consequential opening of niche space seems to be an important driver of *B. pertusa* invasion. Ensuring niche gaps are minimal by managing for consistent ground cover may help to reduce the establishment and spread of this stoloniferous species (Buckley et al. 2007). Improving grazing management practices to allow adequate rest and rotation of pastures and increasing grazing-protected areas may help to achieve this (O'Reagain et al. 2018; O'Reagain and Bushell 2015). This will encourage the persistence of native ground cover and improve the resistance and resilience of ecosystems to stochastic climatic events, and invasion by opportunistic invaders like *B. pertusa*. These approaches may also help to reduce the establishment of monospecific stands and reduce landscape scale propagule load. Acknowledging environmentally invasive pastures species, such as *B. pertusa* within key state and federal weed legislation is important to both improve public education around these species and to help channel resources into their management.

Conclusion

By detailing the introduction and spread story of the non-native invasive pasture species, *Bothriochloa pertusa* we have consolidated and improved our understanding of this species past, current and future distribution and the environmental and cultural factors associated with its spread. Propagule pressure, species traits, land management, climate and cultural perceptions were key factors driving the spread of *B. pertusa* and the 'lawnification' of Queensland's grassy woodlands. *Bothriochloa pertusa*, along with many other invasive pasture species were introduced on multiple occasions and across a large area of Queensland, despite re-occurring doubts and limited evidence of benefit. Its continued spread has been perpetuated by livestock grazing and associated disturbances (i.e., land clearing, soil erosion) and climatic extremes. Results from the HSMs suggest *B. pertusa* will spread and increase in dominance across Queensland particularly in the southern and western parts of the state. We suggest that the use of both empirical and anecdotal information, as has been done in this study, provides a greater depth of understanding than either source alone and we encourage this approach in future invasion research.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare no competing interests.

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