

Tall-statured grasses: a useful functional group for invasion science

Susan Canavan  · Laura A. Meyerson  · Jasmin G. Packer  ·
Petr Pyšek  · Noëlie Maurel  · Vanessa Lozano  · David M. Richardson  ·
Giuseppe Brundu  · Kim Canavan  · Angela Ciccattelli  · Jan Čuda  ·
Wayne Dawson  · Franz Essl  · Francesco Guarino  · Wen-Yong Guo  ·
Mark van Kleunen  · Holger Kreft  · Carla Lambertini  · Jan Pergl ·
Hana Skálová  · Robert J. Soreng · Vernon Visser  · Maria S. Vorontsova  ·
Patrick Weigelt  · Marten Winter  · John R. U. Wilson 

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Abstract Species in the grass family (Poaceae) have caused some of the most damaging invasions in natural ecosystems, but plants in this family are also among the most widely used by humans. Therefore, it is important to be able to predict their likelihood of naturalisation and impact. We explore whether plant height is of particular importance in determining naturalisation success and impact in Poaceae by comparing naturalisation of tall-

statured grasses (TSGs; defined as grass species that maintain a self-supporting height of 2 m or greater) to non-TSGs using the Global Naturalised Alien Flora database. We review the competitive traits of TSGs and collate risk assessments conducted on TSGs. Of the c. 11,000 grass species globally, 929 qualify (c. 8.6%) as TSGs. 80.6% of TSGs are woody bamboos, with the remaining species scattered among 21 tribes in seven subfamilies. When all grass species were analysed, TSGs and non-TSGs did not differ significantly in the probability of naturalisation. However, when we analysed woody bamboos separately from the other grasses,

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S. Canavan (✉) · D. M. Richardson · J. R. U. Wilson
Centre for Invasion Biology, Department of Botany and
Zoology, Stellenbosch University, Matieland 7602, South
Africa
e-mail: sucanavan@gmail.com

S. Canavan · J. R. U. Wilson
South African National Biodiversity Institute,
Kirstenbosch Research Centre,
Private Bag X7, Claremont 7735, South Africa

L. A. Meyerson
Department of Natural Resources Science, The University
of Rhode Island, Kingston, RI 02881, USA

J. G. Packer
Environment Institute, The University of Adelaide,
Adelaide, SA 5005, Australia

P. Pyšek · J. Čuda · W.-Y. Guo · J. Pergl · H. Skálová
Department of Invasion Ecology, Institute of Botany, The
Czech Academy of Sciences, 252 43 Průhonice, Czech
Republic

P. Pyšek · J. Čuda
Department of Ecology, Faculty of Science, Charles
University, Viničná 7, 128 44 Prague, Czech Republic

N. Maurel · M. van Kleunen
Ecology, Department of Biology, University of Konstanz,
Universitätsstrasse 10, 78467 Constance, Germany

V. Lozano · G. Brundu
Department of Agriculture, University of Sassari, Viale
Italia 39, 07100 Sassari, Italy

the percentage of TSGs that have naturalised was 2–4 times greater than that of non-TSGs for both bamboos and non-bamboo groups. Our analyses suggest that woody bamboos should be analysed separately from other TSGs when considering naturalisation; within the ≥ 2 m height class they do not naturalise at the same rate as other TSGs. Rapid growth rate and the capacity to accumulate biomass (a function of height) give many TSGs a competitive advantage and allow them to form monospecific stands, accumulate dense and deep litter mats, reduce light availability at ground level, and alter fire and nutrient-cycling regimes, thereby driving rapid ecosystem transformation. While the height distribution in grasses is continuous (i.e. no obvious break is evident in heights), the 2 m designation for TSGs defines an important functional group in grasses that can improve predictive modelling for management and biosecurity.

Keywords *Arundo* · Bamboos · Biological invasions · Height · Invasive species · *Miscanthus* · *Phragmites* · Plant functional groups · Poaceae · Risk assessment

Introduction

A useful approach in studying alien plant invasions has been to identify broad patterns and correlates of

invasiveness and impacts, such as functional groups, and to use these to provide generalisations for management (Vilà and Pujadas 2001; Colautti et al. 2006; Pyšek and Richardson 2008; Novoa et al. 2015). Functional groups are sets of organisms that share attributes that confer similar morphological, physical, behavioural, biochemical or environmental responses to ecosystem processes (Lavorel et al. 1997; Pérez-Harguindeguy et al. 2016; Garnier et al. 2017). Functional groups can be used to identify species that respond similarly to environmental pressures and are therefore useful for predicting and managing impacts of alien species (Lavorel et al. 1997; Díaz and Cabido 1997).

Plant height is considered a key trait for ecological strategies (Grime et al. 1988; Westoby et al. 2002; Garnier and Navas 2012), and according to Tilman's (1982) resource competition theory, resource exploitation is proportional to individual biomass, with larger individuals exploiting a disproportionate amount of resources (DeMalach et al. 2016). Many studies have recognised the benefits of increased height for initial colonisation by alien plants, as it is associated with better light capture and competitive ability (Pyšek et al. 2012; Moodley et al. 2013; Gallagher et al. 2015). Among plants, invasions by tall-statured grasses (hereafter TSGs; Fig. 1) are particularly noted for their ability to dominate plant communities and alter ecosystem

K. Canavan
Department of Zoology and Entomology, Rhodes
University, PO Box 94, Grahamstown, South Africa

A. Cikatelli · F. Guarino
Department of Chemistry and Biology "A. Zambelli",
University of Salerno, 84084 Fisciano, SA, Italy

W. Dawson
Department of Biosciences, Durham University, South
Road, Durham DH1 3LE, UK

F. Essl
Division of Conservation, Vegetation and Landscape
Ecology, University of Vienna, Rennweg 14,
1030 Vienna, Austria

M. van Kleunen
Zhejiang Provincial Key Laboratory of Plant Evolutionary
Ecology and Conservation, Taizhou University,
Taizhou 318000, China

H. Kreft · P. Weigelt
Biodiversity, Macroecology and Biogeography,
University of Göttingen, 37077 Göttingen, Germany

H. Kreft
Centre of Biodiversity and Sustainable Land Use (CBL),
University of Göttingen, 37077 Göttingen, Germany

C. Lambertini
Department of Bioscience, Aarhus University, Ole Worms
Allé 1, 8000 Aarhus C, Denmark

R. J. Soreng
Department of Botany, National Museum of Natural
History, Smithsonian Institution, Washington, DC, USA

V. Visser
Department of Statistical Sciences, Statistics in Ecology,
Environment and Conservation, University of Cape Town,
Rondebosch 7701, South Africa

functioning (Meyerson et al. 1999; Lambert et al. 2010; Saltonstall et al. 2010). Recent studies have reviewed sub-groups of tall grasses such as invasive grasses that dominate aquatic ecosystems, and have argued that they are functionally similar and have generalizable impacts related to their competitive nature [e.g. Lambert et al. (2010) refer to “large-statured invasive grasses”].

More broadly, tall-statured grasses are potentially an important functional group in invasion science because (1) established populations of TSGs can cause significant negative ecological impacts (Pagad 2016; Canavan et al. 2017b); (2) large height and biomass contribute to specific environmental impacts, e.g. reduction in light availability, changes to fire regimes, and alteration of nutrient cycles (D’Antonio and Vitousek 1992; Meyerson et al. 1999; Brooks et al. 2004; Smith et al. 2013; Gaertner et al. 2014; Visser et al. 2016); (3) TSGs occur in grasslands, riparian areas and estuaries, as well as tropical and temperate forests, yet the abiotic and biotic impacts are often similar across ecosystems; (4) TSGs are increasingly cultivated for commercial purposes such as bioenergy production and phytoremediation and therefore present new risks (Mislevy and Fluck 1992; Czakó et al. 2005; Heaton et al. 2008; Jakob and Zhou 2009; Mirza et al. 2010; Chen et al. 2015); and (5) TSGs are often dominant components of the vegetation in their native ranges, providing biotic resistance to invasion (including against alien TSGs) (Sheley and James 2010). However, TSGs have not been fully explored as a distinct functional group until now.

Here, we review the usefulness of the TSG functional group for invasion science. We produce a preliminary list of TSGs, and test whether there is a

quantitative pattern in the naturalisation of grasses comparing TSGs with non-TSG grasses, for all grasses, only woody bamboo grasses, and all grasses other than woody bamboos. We identify which TSGs have been subject to risk assessments. We also discuss the invasion-science literature associated with TSGs, focussing on how competitive traits associated with increased height can affect the colonisation, invasion, and environmental impacts of alien grasses.

Methods

Defining and creating a list of tall-statured grasses

Height in grasses (defined here as average inflorescence height, as per Kew’s GrassBase; <http://www.kew.org/data/grasses-db.html>) varies across three orders of magnitude (2 cm–20 m; see Fig. 2). Efforts to classify vegetation into different height categories include Kùchler (1949) and Dansereau (1951) who proposed that “tall herbaceous plants”, including grasses, should have an average minimum height of 2 m; Edwards (1983) proposed four height categories for grasses, with tall grasses being 1 m and greater than 2 m to be the largest height category; Lambert et al. (2010) considered “large-statured invasive grasses” to be greater than 1.5 m in height. There are clearly important correlates between height and ecological processes, such as competition for light, e.g. light reduction to the soil surface decreases dramatically from 2 m down (Meyerson et al. 1999). However, previously proposed height classifications lack a clear ecological justification for their categories, and instead have been developed for practical purposes such as for vegetation inventories, descriptions and surveys (Edwards 1983). We propose 2 m as an ecologically relevant height threshold amongst grasses, and define TSGs as species that are ≥ 2 m. Grasses that maintain a height of ≥ 2 m experience a trade-off between other functional traits. Typical features associated with taller grasses include lignified culms, high growth rates, and abundant biomass (Table 1). For these reasons, and the common prior use of 2 m as the cut-off, we generated a preliminary list of “tall-statured grasses”.

We extracted data on inflorescence height for all grass species from Kew’s GrassBase. Our list of species was cleaned, updated and corrected; non-bamboo grasses were checked for synonyms using

V. Visser

African Climate and Development Initiative, University of Cape Town, Cape Town, Rondebosch 7701, South Africa

M. S. Vorontsova

Comparative Plant and Fungal Biology, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AE, UK

M. Winter

German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany

M. Winter

Leipzig University, Deutscher Platz 5e, 04109 Leipzig, Germany

Kew's World Checklist of Selected Plant Families (<http://apps.kew.org/wcsp/qsearch.do>) and bamboo species were checked using the International Network for Bamboo and Rattan's (INBAR) global checklist (Vorontsova et al. 2016). Species that do not maintain their height independently (i.e. those listed as 'climbing', 'scandent-', 'rambling', 'prostrate', 'liana' and or 'leaning' [on other vegetation]) were removed from the list of TSGs, and were considered non-TSGs along with shorter species.

Incidence and extent of naturalisation

If increased height is advantageous for colonisation, we expected that TSGs would have higher rates of

naturalisation compared to shorter grasses (i.e. non-TSGs). To test for this, we calculated whether: (1) TSGs are more likely to be naturalised in at least one region of the world (what we refer to as 'incidence of naturalisation'); and (2) for naturalised species, TSGs are more globally widespread outside their native range (which we refer to as 'extent of naturalization'; see e.g. Razanajatovo et al. (2016)). Data from the Global Naturalised Alien Flora (GloNAF) database were used for both analyses. The database covers 843 non-overlapping regions (countries, federal states, islands) covering around 83% of the Earth's land surface.

The effect of stature on the probability of a grass species becoming naturalised could simply mean that

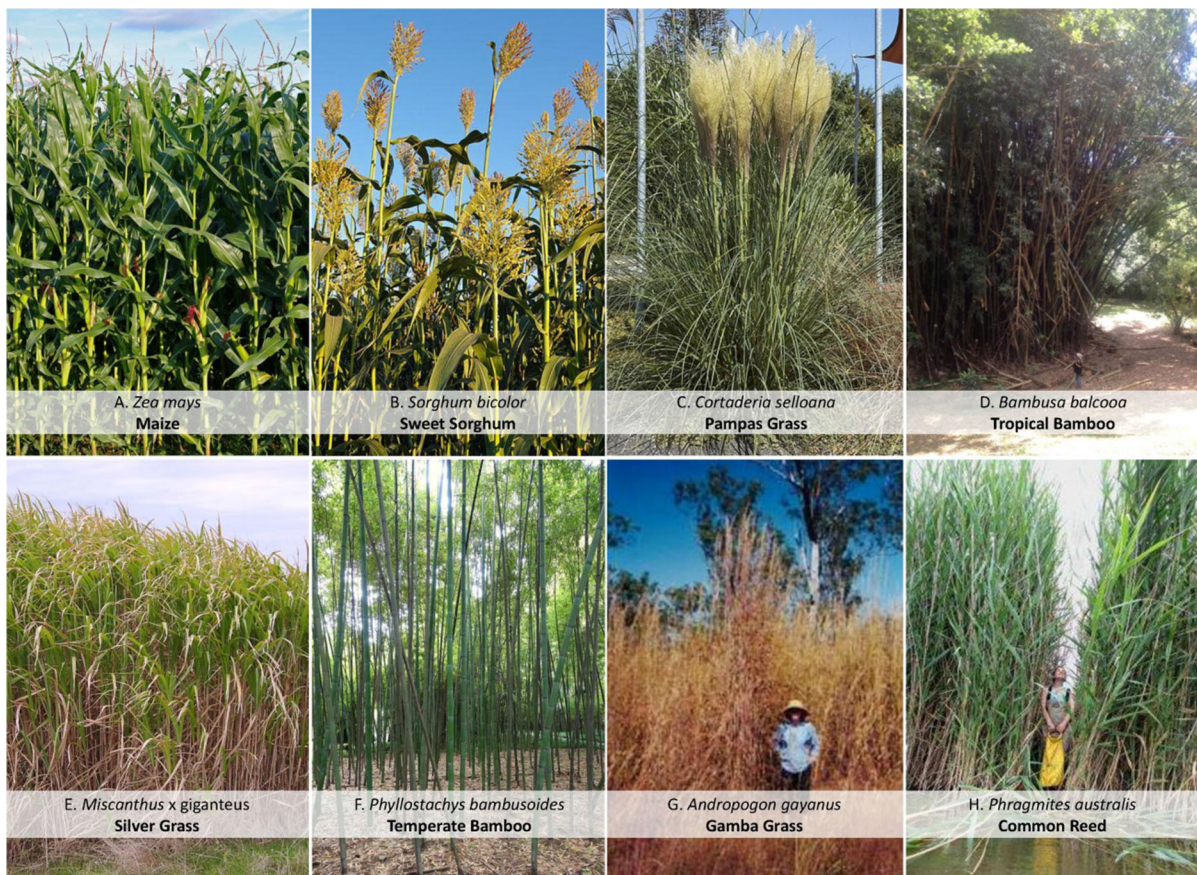


Fig. 1 Tall-statured grasses (TSGs) come in a variety of forms and occur in a range of different ecosystems (e.g. temperate forests, dry grasslands to tropical wetlands). They are useful to humans for food (**a** and **b**), ornamental horticulture (**c** and **d**), for biofuels (**e** and **f**) and other uses (**g** and **h**). Several TSGs are associated with environmental impacts in invaded ranges due to their ability to form monospecific communities that exclude

other vegetation types (**d**, **f**, **g** and **h**). Photographs: Wikimedia Commons (A: Christian Fischer (CC BY-SA 3.0 & CC0); B: Wouter Hagens (CC BY-SA 3.0); E: Bgabrielle (CC-BY-SA-3.0); F: Daderot (CC0)) and other sources (C: Kijktuinen Nunspeet -<http://www.kijktuinen.nl>); D: Susan Canavan; G: retrieved from Rossiter-Rachor et al. 2009; H: Michigan Technological University)

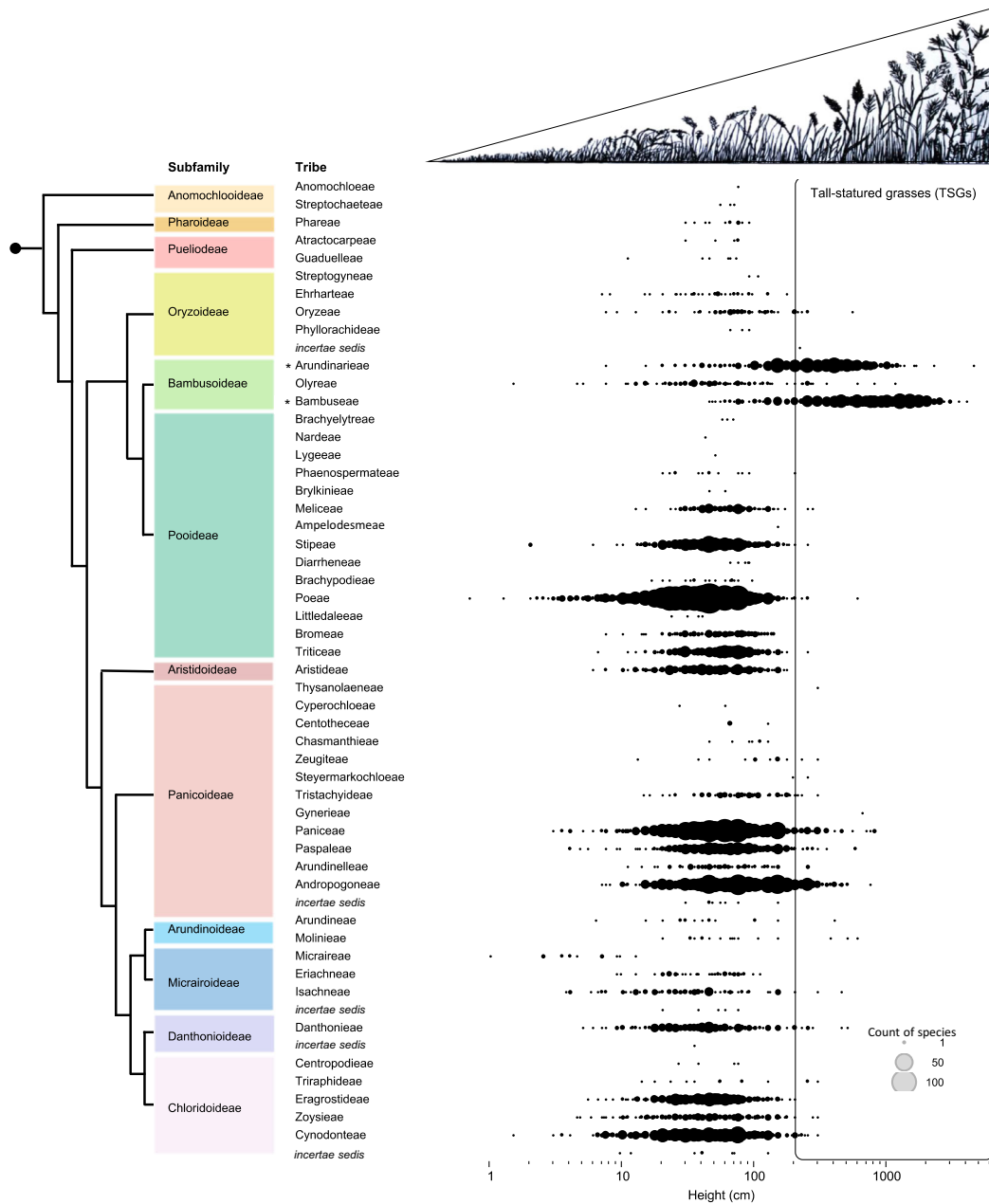


Fig. 2 Height distribution of grass species in subfamilies and tribes as per Soreng (2015)’s classification of Poaceae. Species within the black-outlined box have average bloom (inflorescence) heights of ≥ 2 m. Note that not all of these taxa are defined in this paper as tall-statured grasses (TSGs) as some taxa do not maintain their height independently (e.g. climbing species). The area of the black circles is proportional to the

number of species. Data were retrieved from Kew’s GrassBase (<http://www.kew.org/data/grasses-db.html>) for 10,818 species. Species that are unplaced in a tribe are shown as *incertae sedis* for that subfamily. Woody bamboos (tribes Arundinarieae and Bambuseae) are marked with an asterisk. Figure generated using Tableau V 10.0

TSGs are more likely to be traded because of their ornamental value. To test for this, we used data on the plant trade sourced from Dave’s Garden Plant Files

(<http://davesgarden.com/guides/pf>), arguably the most comprehensive global database of garden plants. While it would have been ideal to use quantitative sale

Table 1 Typical features of tall-statured grasses (TSGs) that confer a high likelihood of causing widespread invasions and severe environmental impact

	Features typical of TSGs	Implications for invasiveness/ impact	Examples
1. Biomass production	Statured architecture	High light capture, so likely to outcompete shorter vegetation	<i>Miscanthus sinensis</i> (Tang et al. 1990); <i>Phragmites australis</i> (Meyerson et al. 2000)
	Fast growth rates	Can outcompete neighbouring species	Bamboos (Montti et al. 2014)
2. Biomass accumulation	Leaf litter build-up	Suppress growth of neighbouring plants	<i>Cortaderia jubata</i> (Lambrinos 2000); <i>Cortaderia selloana</i> (Domènech et al. 2006); <i>Miscanthus × giganteus</i> (Amougou et al. 2012); <i>Phragmites australis</i> (Haslam 2010; Holdredge and Bertness 2011)
	Chemically distinct leaf litter	Reduced decomposition Alter nutrient cycling	<i>Bambusa</i> spp. (O'Connor et al. 2000); <i>Phragmites australis</i> (Meyerson et al. 2000) <i>Cortaderia selloana</i> (Domènech et al. 2006); <i>Phragmites australis</i> (Meyerson et al. 2000); <i>Phyllostachys edulis</i> (Song et al. 2017)
	Production of large quantities of highly flammable aboveground biomass	Alter the frequency and intensity of fires	<i>Arundo donax</i> (Herrera and Dudley 2003; McWilliams 2004; Lambert et al. 2010; Coffman et al. 2010); <i>Andropogon gayanus</i> (Rossiter et al. 2003); <i>Andropogon virginicus</i> , <i>Hyparrhenia rufa</i> , <i>Melinis minutiflora</i> , <i>Schizachyrium condensatum</i> (Brooks et al. 2004); bamboo (Jaiswal et al. 2002); <i>Cortaderia selloana</i> (Bossard et al. 2000)
3. Dual reproductive modes	Tall plants with seeds held high up	Long range dispersal of seeds	<i>Cortaderia selloana</i> (Drewitz and DiTomaso 2004); Generally in plants (Thompson et al. 1995); specifically for grasses (Linder et al. 2018)
	Dense root systems	Crowd out other vegetation	<i>Phragmites australis</i> (Meyerson 2000)
	Clonal networks leading to greater resource acquisition	Ability to survive high stress environments	<i>Gynerium sagittatum</i> (de Kroon and Kalliola 1995); clonal plants in general (Stueffer et al. 1996; van Kleunen and Stueffer 1999)
	Clonal networks leading to colonisation by juvenile ramets into low resource patches are supported by older ones	Ability to colonise stressful environments	<i>Phyllostachys edulis</i> (Wang et al. 2016)
	High belowground allocation/storage of resources	Ability to survive disturbance and regenerate quickly, out-competing neighbouring vegetation	<i>Dendrocalamus strictus</i> (Singh and Singh 1999); <i>Miscanthus</i> spp. (Amougou et al. 2011)
4. Anthropogenic interest	Use as biofuel	Increased dissemination, propagule pressure, often in large stands in climatically suitable areas close to the natural environment	<i>Arundo donax</i> (Cosentino et al. 2006); <i>Miscanthus × giganteus</i> (Schnitzler and Essl 2015); <i>Miscanthus sinensis</i> (Flory et al. 2012)
	Use in ornamental horticulture (particularly landscaping)	Increased dissemination, propagule pressure, and multiple foci for potential invasions	<i>Arundo donax</i> , <i>Cortaderia selloana</i> , <i>Cenchrus purpureus</i> (Foxcroft et al. 2008); <i>Cortaderia selloana</i> (Okada et al. 2007); bamboo (Canavan et al. 2017b); <i>Miscanthus sinensis</i> (Dougherty 2013)

and trade data from Dave's Garden as a proxy of propagule pressure, such data were only available for a small subset of species. We therefore confined the analyses to whether or not a species was present in Dave's Garden Plant Files.

When exploring the raw data, it was clear that the vast majority of TSGs were woody bamboos (tribes: Bambuseae and Arundinarieae; Fig. 2). Also, the percentage of TSGs that naturalised was greater than that of non-TSGs for woody bamboos and other grasses (i.e. non-bamboos and non-woody bamboos), although this pattern was not found when pooling all grasses together (a result of inequities in the proportions of the taxa which were TSGs; see Online Resource 4). For this reason, we conducted the remaining analyses on naturalisation incidence and extent (described below) separately for the set of woody bamboos and for the set of other grasses.

To assess whether naturalisation incidence was higher in TSGs than non-TSGs, we ran generalised linear mixed-effects models with a binomial error distribution (logistic regression), separately for woody bamboos and for other grasses, using the 'lme4' R package (Bates et al. 2015). The response variable was status (presence or absence) in the GloNAF database and the predictor variables were whether a species is a TSG or non-TSG, and whether a species was traded or not (as inferred from presence or absence in Dave's Garden Plant Files). To account for phylogenetic non-independence of the species, we included genus (in the case of woody bamboos) and genus nested within tribe (in the case of other grasses) as random factor(s). This also provided an opportunity to test whether the 2 m cut-off was appropriate. We ran similar models with height (standardised to a mean of 0 and standard deviation of 1) as a continuous explanatory variable instead of stature as a binary variable (TSG or non-TSG).

To analyse extent of naturalisation (i.e. number of regions in the GloNAF database) we ran generalised linear mixed-effects models with a negative binomial error distribution, due to high incidence of zeros, separately for woody bamboos and for other grasses, using the 'glmmADMB' R package (Fournier et al. 2012). We used the same predictor variables and random factors as in the analysis of naturalisation incidence. Finally, we looked at the global geographic pattern of numbers of naturalised TSGs and of the proportion of TSGs among all naturalised grass species.

Reviewing future risks

To explore the threats of TSGs introduced to new regions, we reviewed risk assessments that have been completed in different parts of the world for our list of TSGs (See Online Resource 2 for details). We did this by searching (from May to July 2016) for primary literature and fact sheets on Scopus, ISI Web of Science and Google Scholar using the specific names of the TSG species/"tall grass" AND "risk assessment"/"risk analysis" as keywords. We collated all the risks assessments and then summarised the species for which assessments have been reported.

Results

TSG species

From the lists extracted from Kew's GrassBase, we removed 18 species that did not have names matching the World Checklist of Selected Plant Families or INBAR's global 2016 checklist, four unplaced species were kept in the list, and synonyms ($n = 79$) were updated accordingly to reflect current nomenclature. Of the remaining 10,818 grass species for which height data were available, 1136 species reach heights of 2 m or more, although 207 of these do not maintain their height independently and were classified as non-TSGs. This left 929 species (8.6% of grass species) as TSGs for subsequent analysis (See Online Resource 1 for a complete list of species).

Among TSGs, the vast majority (80.6%) are woody bamboos (tribes Arundinarieae and Bambuseae). The remaining 180 species of TSGs come from 21 tribes in 7 subfamilies (Fig. 2), many of which are important reed species, such as Burma reed (*Neyraudia reynaudiana*; Triraphideae), common reed (*Phragmites australis*; Molinieae), and giant reed (*Arundo donax*; Arundineae). Other TSGs include popular horticultural and biofuel species such as pampas grass (*Cortaderia* spp.; Danthonieae) and silver grass (*Miscanthus sinensis*; Andropogoneae). The TSG group also contains important food crops, in particular maize (*Zea mays*; Andropogoneae), pearl millet (*Cenchrus americanus* = *Pennisetum glaucum*; Paniceae), sorghum (*Sorghum bicolor*; Andropogoneae), and sugarcane (*Saccharum* spp.; Andropogoneae) (Fischer et al. 2014). With the exception of woody bamboos, TSGs

are outliers in their respective tribes in terms of height, although the height distribution of all tribes appears to be roughly unimodal (Fig. 2).

Incidence and extent of naturalisation

The GloNAF database lists 1226 species in the grass family. We found overall a similar percentage of naturalised species among TSGs and among non-TSGs using the 2 m threshold, with 11.4 and 11.3% of species naturalised, respectively (Fig. 3). However, when considering woody bamboos alone, the percentage of naturalised TSGs is more than three times that of non-TSG bamboos, with 7.6 and 2.0% of species, respectively (Fisher's exact test: odds ratio = 4.1, 95% confidence interval of 1.9–9.9, $p < 0.001$). This is also the case among all other grasses (i.e. excluding woody bamboos), with 27.2 and 11.7%, respectively (Fisher's exact test: odds ratio = 2.8, 95% confidence interval of 2.0–4.0, $p < 0.001$). The lack of contrast overall between TSGs and non-TSGs is because most TSGs are woody bamboos but fewer woody bamboos than other grasses have naturalised (Online Resource 4).

Among both woody bamboos and other grasses, species that are traded for ornamental horticulture have naturalised more often than non-horticultural species. Of the 1233 grass species listed in Dave's Garden Plant Files, 53.4% are naturalised, while only 5.9% of the other 9585 grass species have naturalised. When the presence of a species in Dave's Garden Plant Files was accounted for in the analysis, tall stature had a significant, positive effect on naturalisation incidence of other grasses (Table 2a). This was not the case for woody bamboos. However, when a similar model was run with height as a continuous variable height had a significant, positive effect on naturalisation incidence for both woody bamboos and other tall grasses (Table 2a).

Of the subset of 1226 grass species (of all tribes) that have naturalised somewhere, 384 species have naturalised in only one region, whereas some species (e.g. *Eleusine indica*, a non-TSG) have naturalised in 309 regions according to the GloNAF database. On average, when considering grasses together, TSGs and non-TSGs have naturalised in similar numbers of regions (Online Resource 4; Wilcoxon test: $W = 56,274$, $p = 0.368$). When considering woody bamboos alone, and accounting for the strong positive effect of presence in the horticultural trade, the extent

of naturalisation was still significantly positively associated with tall stature (Table 2b). Indeed, woody bamboo TSGs have naturalised in up to 101 regions (e.g. *Bambusa vulgaris* being the most widespread species) whereas the 8 non-TSG woody bamboos have naturalised in at most five regions (Online Resource 1). However, this effect of stature on naturalisation extent was not found for other grasses.

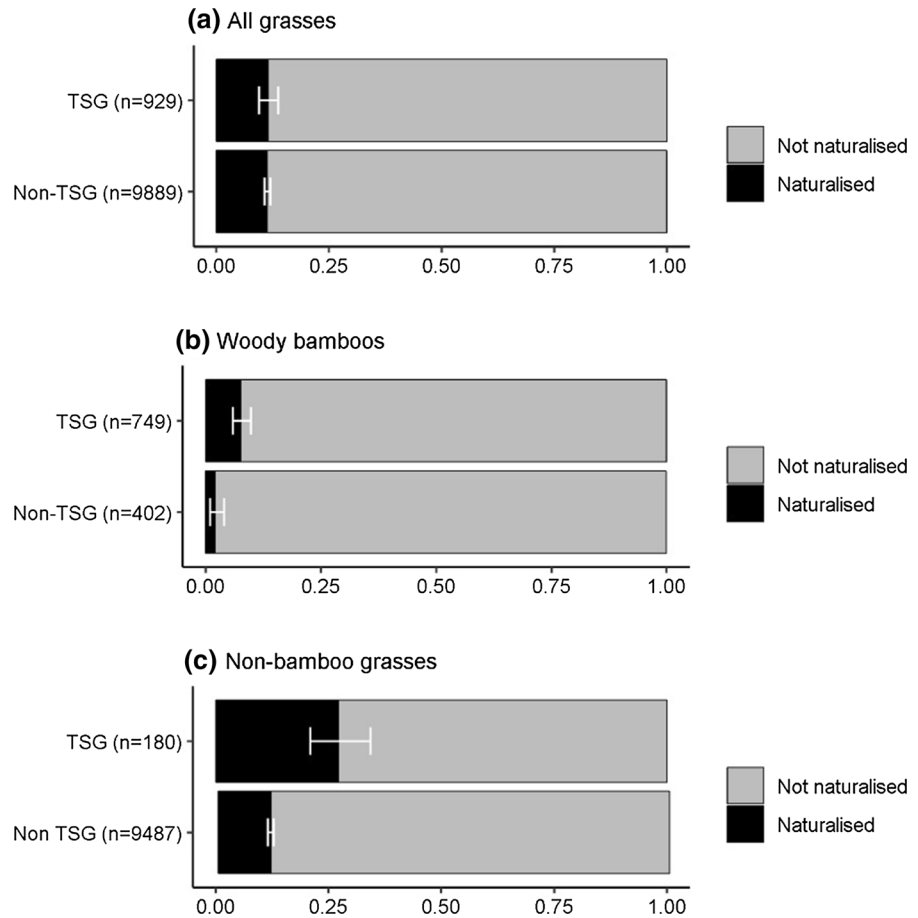
The regions with the highest number of recorded naturalised alien grasses (irrespective of whether they are a TSG or not) are the southern United States, tropical South America, Hawaii, parts of tropical Africa, Madagascar, Indonesia and New Zealand (Fig. 4a, Table 3). However, the pattern is strikingly different when using the proportion of TSGs among all naturalised grasses (in part because species richness is affected by differences in sizes of the regions). This relative measure identifies a marked hot spot of TSGs in tropical Africa (especially islands in the Western Indian Ocean), where the proportions in most countries range between 30–70% and even more (Fig. 4b). The Caribbean is a second hotspot (Fig. 4b).

Reviewing risks

We found 127 risk assessments that have been completed for 64 TSG species. Of these, 55 assessments (43%) on 23 species had an outcome indicating a high risk of invasion or recommended that further introductions should be rejected in the region evaluated (Table 4; See Online Resource 3 for full list). More than a third (38%) of the risk assessments were conducted on 32 woody bamboo species (all of which are TSGs). However, woody bamboos generally received lower risk scores than other TSGs, with only three risk assessments scoring high risk for two species, and five assessments called for an introduction to be rejected on five species.

The most widely used risk assessment scheme was the Hawaiian Weed Risk Assessment (H-WRA), which has been applied in 60 assessments, followed by the Australian Weed Risk Assessment (A-WRA) with nine assessments. Another 16 variant risk assessment frameworks were used. The following species had the greatest number of completed risk assessments: *Arundo donax* (12), *Miscanthus sinensis* (8), *Cortaderia jubata* (7), *Sorghum bicolor* (7) and *Cortaderia selloana* (7). Based on the results of the risk assessments, the species with a high potential to

Fig. 3 The proportion of grass species that have naturalised globally, by height group, for **a** all grasses, **b** woody bamboos only and **c** all grasses excluding woody bamboos. Data were retrieved from the GloNAF database [see van Kleunen et al. (2015)]. The proportion of tall-statured grasses (TSGs; those that are 2 m in height or greater) and non-TSGs (less than 2 m in height) that have naturalised vary between woody bamboos and other grasses. The white bars indicate 95% confidence intervals. There is a very large number of tall-statured non-naturalised bamboos. See Online Resource 4 for the raw data



cause negative impacts were *Arundo donax*, *Cortaderia jubata*, *Echinochloa pyramidalis* and *Phragmites australis* (Table 4).

Several intended uses for TSGs were identified as generating heightened risk due to the massive propagule pressure associated with such usage: of the risk assessments completed, 37% were for the introduction of ornamental horticulture and food crops species and 28% for biofuels and bioenergy purposes. The purpose of introduction was unspecified in 42% of assessments (see Online Resource 3 for more details).

Discussion

Tall-statured grass (TSG) groups with high impact

Woody bamboos (tribes Arundinarieae and Bambuseae) are among the tallest grasses and make up the majority of TSG species (Fig. 2). They have some of

the most varied uses of any plant group and are widely used in agroforestry, medicine, food, fodder, ornamentation and, more recently, phytoremediation and bioenergy, and for these reasons they have been distributed and cultivated around the world (Soderstrom and Calderon 1979; Farrelly 1984; Liese and Köhl 2015; Canavan et al. 2017b). According to Canavan et al. (2017b), at least 232 (14%) of all 1662 bamboo species have been introduced beyond their native range. However, only 12 species are recorded as invasive (i.e. spreading), fewer than other grass tribes and less than other TSGs. Although they have been widely introduced, bamboos have lower invasion rates but have high levels of environmental impacts in disturbed forests, both in the native and alien range (O'Connor et al. 2000; Teixeira and Oatham 2001; Lima et al. 2012; Xu et al. 2014; Rother et al. 2016; Canavan et al. 2018a). This is attributed to the high competitive ability of certain bamboo species and their capacity to rapidly colonise open space in disturbed

Table 2 The influence of plant stature and garden use status on global naturalisation of woody bamboos and other grasses. Plant height was analysed both as a factor (i.e. tall-statured grass (TSG) of stature $\geq 2\text{m}$ vs. non-TSGs) and as a continuous variable (results shown in italics). Garden-use status was binary (presence/absence in Dave's Garden Plant Files database; <http://davesgarden.com/guides/pf>). Global naturalisation was measured as (a) naturalisation incidence outside the native range (expressed as being naturalised in at least one region, yes or no), and (b) naturalisation extent (number of regions where the species is recorded as naturalised). To assess whether naturalisation incidence or naturalisation extent related to stature and to the presence in Dave's Garden database,

we ran generalised linear mixed-effects models with a binomial error distribution or a negative binomial error distribution, respectively. To account for phylogenetic non-independence of the species, we included genus (for woody bamboos) or genus nested within tribe (for other grasses) as random factor(s). For naturalisation incidence, we ran similar models with height (standardised to a mean of 0 and standard deviation of 1) as a continuous explanatory variable instead of stature, the results are shown in italics. Note that woody bamboos refers to species within the Bambuseae and Arundinarieae tribe, and non-bamboo grasses include all other species in the family Poaceae

Explanatory variable	Woody bamboos (n = 1162)				Other grasses (n = 9674)			
	Estimate	SE	z	p	Estimate	SE	z	p
<i>(a) Global naturalisation incidence (yes/no)</i>								
Intercept	– 5.365	0.533	– 10.06	< 0.001	– 3.026	0.181	– 16.74	< 0.001
	<i>– 5.101</i>	<i>0.422</i>	<i>– 12.087</i>	<i>< 0.001</i>	<i>– 3.023</i>	<i>0.187</i>	<i>– 16.15</i>	<i>< 0.001</i>
Stature (TSG/non-TSG)	0.4803	0.470	1.021	0.307	0.931	0.242	3.85	< 0.001
<i>Height (continuous)</i>	<i>0.431</i>	<i>0.143</i>	<i>3.021</i>	<i>0.0025</i>	<i>0.159</i>	<i>0.036</i>	<i>4.37</i>	<i>< 0.001</i>
Recorded in Dave's Garden (yes/no)	3.843	0.428	8.979	< 0.001	3.204	0.092	34.99	< 0.001
	<i>3.839</i>	<i>0.427</i>	<i>8.983</i>	<i>< 0.001</i>	<i>3.188</i>	<i>0.092</i>	<i>34.79</i>	<i>< 0.001</i>
Random factors	SD				SD			
Genus	0.6864				0.9504			
	<i>0.6854</i>				<i>0.9491</i>			
Tribe	not applicable				0.5826			
					<i>0.6278</i>			
Explanatory variable	Woody bamboos (n = 67)				Other grasses (n = 1162)			
	Estimate	SE	z	p	Estimate	SE	z	p
<i>(b) Global naturalisation extent (number of regions where naturalised)</i>								
Intercept	– 0.612	0.751	– 0.81	0.415	1.583	0.142	11.13	< 0.001
Stature (TSG/non-TSG)	1.139	0.511	2.23	0.026	– 0.147	0.242	– 0.61	0.54
Recorded in Dave's Garden (yes/no)	1.340	0.655	2.05	0.041	1.518	0.080	18.92	< 0.001
Random factors	SD				SD			
Genus	0.3947				0.7103			
Tribe	not applicable				0.4037			

forest canopies and take advantage of available light and resources. Due to their large size and robust stature, they often alter biotic and abiotic processes and compete with trees. The competitive interaction between bamboos and trees is unusual compared to species in other grass tribes. Tall bamboos are usually not perceived as 'invasive' given their low spread rates, but they should receive closer scrutiny with regard to their potentially large impacts on community

structure and ecosystem functioning (Canavan et al. 2018a). Recognising the dominance of bamboos and managing their biomass is an integral part of landscape management in many forest ecosystems (Suzaki and Nakatsubo 2001; Larpkern et al. 2011; Bai et al. 2013).

Large reeds form another important subgroup within TSGs and are often the dominant vegetation in riparian, lake and coastal ecosystems. Some of the most notorious invasive plants are reed TSGs

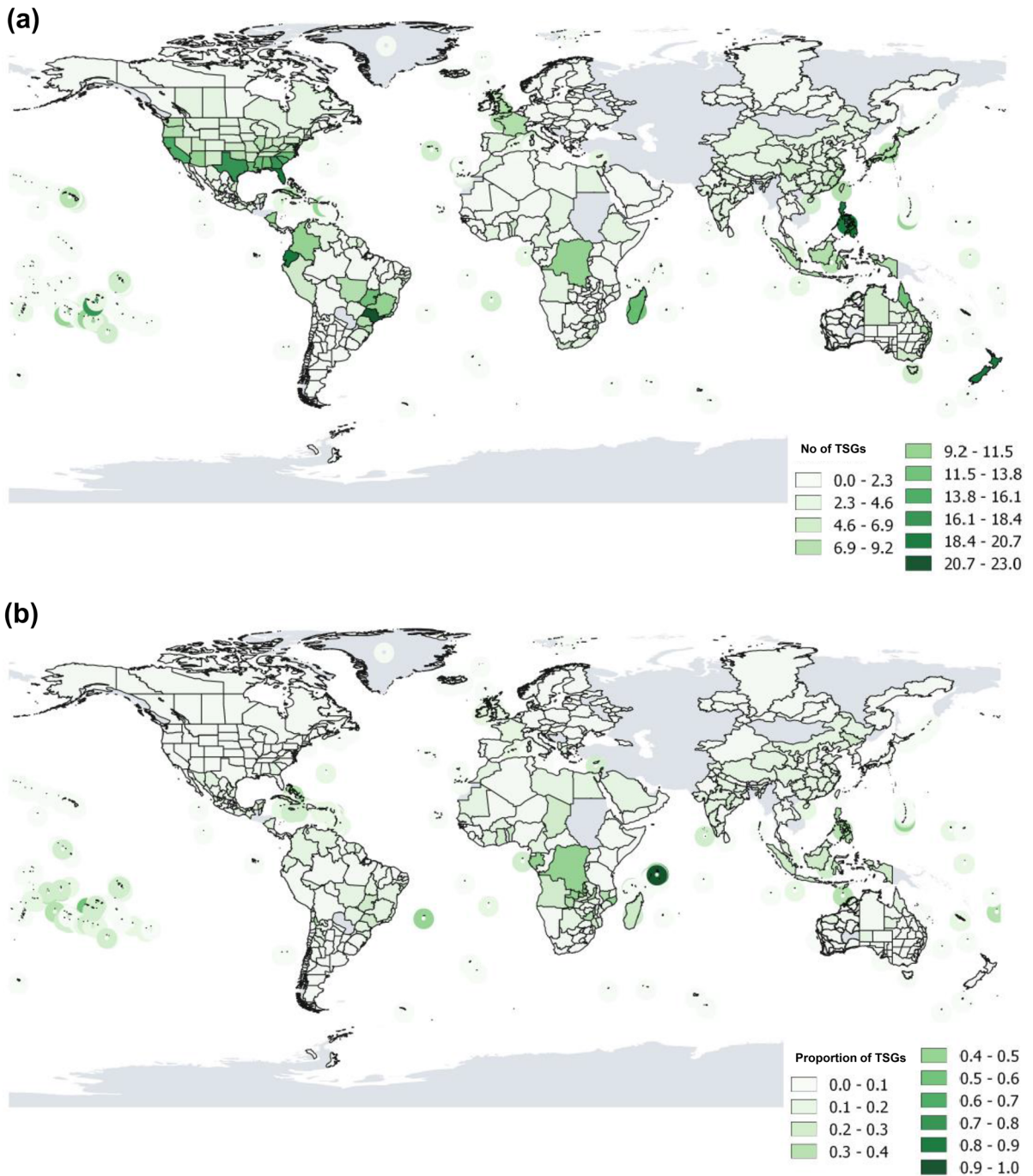


Fig. 4 **a** Numbers of naturalised tall-statured grass species (TSGs) and **b** their proportions among all naturalised grass species (**b**) in 843 GloNAF regions of the world (see van Kleunen et al. (2015) for description of regions and data

acquisition). Darker colours indicate a greater number of naturalised TSGs or that naturalised TSGs represent a greater proportion of all naturalised grasses, respectively. Regions in grey are missing data

Table 3 The twenty most widely distributed tall-statured grass species ranked according to the total number of regions in which they are naturalised. Height is in terms of the maximum inflorescence height. The broad continental regions (as per the Biodiversity Information Standards TDWG classification (see van Kleunen et al. (2015))) from which the grass is native are indicated with an asterisk, note species are often native and naturalised in a single TDWG region as there are many GloNAF regions per TDWG region

Taxon	Height (cm)	Tribe	Occurrence in regions (number of GloNAF regions)								
			Total	Africa	Asia (temperate)	Asia (tropical)	Australia	Europe	North America	Pacific Islands	South America
<i>Arundo donax</i>	400	Arundineae	220	26	12*	33*	33	7	46	15	48
<i>Cenchrus purpureus</i>	350	Panicaceae	175	38*	11	37	13	0	23	20	33
<i>Sorghum bicolor</i>	350	Andropogoneae	147	12*	2	5	34	8	57	9	20
<i>Cenchrus americanus</i>	225	Panicaceae	132	19*	33	33	9	0	21	6	11
<i>Zea mays</i>	250	Andropogoneae	120	18	0	2	2	6	52*	14	26*
<i>Saccharum officinarum</i>	450	Andropogoneae	113	23	0	2*	5	0	18	34	31
<i>Bambusa vulgaris</i>	1750	Bambuseae	101	23	0	10*	4	0	11	25	28
<i>Phragmites australis</i>	375	Arundineae	94	1*	0*	3*	3*	0*	85*	0	2*
<i>Cortaderia selloana</i>	200	Danthonieae	66	6	1	1	16	15	20	7	0*
<i>Sorghum alatum</i>	260	Andropogoneae	63	0	33	1	19	0	10	0	0*
<i>Zea mexicana</i>	300	Andropogoneae	41	1	33	2	0	0	4*	0	1*
<i>Phyllostachys aurea</i>	500	Arundinarieae	39	1	0*	1	7	2	15	1	12
<i>Chrysopogon zizanioides</i>	225	Andropogoneae	35	6	6	3*	0	0	2	13	5
<i>Sorghum arundinaceum</i>	215	Andropogoneae	33	10	0*	0	14	0	0	6	3
<i>Olyra latifolia</i>	230	Olyreae	30	30*	0	0	0	0	0*	0	0*
<i>Schizostachyum glaucifolium</i>	650	Bambuseae	28	0	0	0	0	0	0	28*	0
† <i>Pseudosasa japonica</i>	400	Arundinarieae	27	5	0	0	1	9	11	0	1
<i>Cortaderia jubata</i>	225	Danthonieae	24	8	0	0	7	0	4	1	4*
<i>Bambusa multiplex</i>	300	Bambuseae	23	2	8*	1	1	0	3	4	4
<i>Saccharum ravennae</i>	275	Andropogoneae	22	0*	0*	1*	0	0*	21	0	0

†*Pseudosasa japonica* originated from cultivation. Source of data: GloNAF (van Kleunen et al. 2015)

Table 4 Risk assessments completed for tall-statured grass species

Species	Common name	RAs	Reg	Accept	LR	IR	HR	Reject	EF	Other
<i>Andropogon bicornis</i> L.	West Indian foxtail grass	1	1				1			
<i>Andropogon gayanus</i> Kunth	Gamba grass	1	1					1		
<i>Arundo donax</i> L.	Giant reed	12	9				2	7		1
<i>Bambusa bambos</i> (L.) Voss	Thorny bamboo	1	1						1	
<i>Bambusa chungii</i> McClure	Emperor's blue bamboo	1	1		1					
<i>Bambusa glaucophylla</i> Widjaja	Malay dwarf bamboo	1	1		1					
<i>Bambusa lako</i> Widjaja	Timor black bamboo	2	1		1				1	
<i>Bambusa multiplex</i> (Lour.) Raeusch. ex Schult.	Chinese dwarf bamboo	3	2	1				1	1	
<i>Bambusa oldhamii</i> Munro	Oldhamii bamboo	2	1	1					1	
<i>Bambusa oliveriana</i> Gamble	Bush bamboo	1	1		1					
<i>Bambusa pervariabilis</i> McClure	Puntingpole bamboo	1	1		1					
<i>Bambusa textilis</i> McClure	Weaver's bamboo	1	1		1					
<i>Bambusa tuldoides</i> Munro	Buddha Belly bamboo	1	1						1	
<i>Bambusa vulgaris</i> Schrad.	Common bamboo	3	3		1				2	
<i>Schizostachyum pergracile</i> (Munro) R.B.Majumdar (= <i>Cephalostachyum pergracile</i> Munro)	Tinwa bamboo	1	1		1					
<i>Chimonobambusa quadrangularis</i> (Fenzi) Makino	Square bamboo	1	1					1		
<i>Chrysopogon zizanioides</i> (L.) Roberty	Vetiver grass	4	3	2	1		1			
<i>Cortaderia jubata</i> (Lem.) Stapf	Purple pampas grass	7	3				3	3		1
<i>Cortaderia selloana</i> (Schult.) Aschers. & Graebn.	Silver pampas grass	6	4		1		2	2		1
<i>Cymbopogon martini</i> (Roxb.) W.Watson	Ginger grass, Palmarosa	1	1		1					
<i>Dendrocalamus asper</i> (Schult.) Backer ex K.Heyne	Giant bamboo	2	2		1				1	
<i>Dendrocalamus brandisii</i> (Munro) Kurz	Velvetleaf bamboo	1	1						1	
<i>Dendrocalamus sikkimensis</i> Gamble ex Oliver	Philippine sweet shoot bamboo	1	1		1					
<i>Dendrocalamus strictus</i> (Roxb.) Nees	Male bamboo	1	1						1	
<i>Drepanostachyum falcatum</i> (Nees) P.C.Keng	Blue bamboo	1	1	1						
<i>Drepanostachyum khasianum</i> (Munro) P.C.Keng	Khasia bamboo	1	1		1					
<i>Echinochloa pyramidalis</i> (Lam.) Hitchc. & Chase	Antelope grass	2	1				1			1
<i>Fargesia fungosa</i> T.P.Yi	Chocolate bamboo	1	1		1					
<i>Fargesia nitida</i> (Mitford) Keng f. ex T.P.Yi	Blue Fountain bamboo	1	1	1						
<i>Gigantochloa apus</i> (Schult.) Kurz	Gigantochloa	2	2		1				1	
<i>Gigantochloa atroviolacea</i> Widjaja	Sweet bamboo, pring legi	1	1		1					

Table 4 continued

Species	Common name	RAs	Reg	Accept	LR	IR	HR	Reject	EF	Other
<i>Gigantochloa atter</i> (Hassk.) Kurz	Sweet bamboo	1	1		1					
<i>Gigantochloa robusta</i> Kurz	Robust bamboo	1	1		1					
<i>Guadua angustifolia</i> Kunth	Guadua, Columbian thorny bamboo	1	1						1	
<i>Hymenachne amplexicaulis</i> (Spreng.) Zuloaga	Hymenachne	1	1					1		
<i>Miscanthus floridulus</i> (Labill.) Warb. ex K.Schum. & Lauterb.	Giant miscanthus	1	1				1			
<i>Miscanthus sinensis</i> Andersson	Chinese silvergrass	8	7		1	1		3		3
<i>Miscanthus</i> × <i>giganteus</i> J.M.Greef & Deuter ex Hodk. & Renvoize	Giant miscanthus	3	1	3						
<i>Nastus elatus</i> Holttum	New Guinea edible bamboo	1	1		1					
<i>Neyraudia reynaudiana</i> (Kunth) Keng ex Hitchcock	Burma reed	3	1				2	1		
<i>Oatea acuminata</i> (Munro) C.E.Calderon & T.R.Soderstrom (= <i>Oatea aztecorum</i>)	Mexican weeping bamboo	1	1		1					
<i>Cenchrus americanus</i> (L.) Morrone (= <i>Pennisetum glaucum</i> (L.) R.Br.)	Pearl millet	1	1		1					
<i>Cenchrus macrourus</i> (Trin.) Morrone (= <i>Pennisetum macrourum</i> Trin.)	African feathergrass	1	1					1		
<i>Cenchrus purpureus</i> (Schumach.) Morrone (= <i>Pennisetum purpureum</i> Schumach.)	Elephant grass	5	3					5		
<i>Phragmites australis</i> (Cav.) Trin. ex Steud.	Common reed	4	3					1		3
<i>Phyllostachys aurea</i> Rivière & C.Rivière	Golden bamboo	4	3				2	1	1	
<i>Phyllostachys aureosulcata</i> McClure	Yellow groove bamboo	1	1						1	
<i>Phyllostachys nigra</i> (Lodd.) Munro	Black	2	2				1	1		
<i>Pseudosasa japonica</i> (Steud.) Makino	Arrow bamboo	1	1					1		
<i>Saccharum arundinaceum</i> Retz.	Plume Grass	1	1	1						
<i>Saccharum officinarum</i> L.	Sugarcane	3	2	2				2		
<i>Saccharum ravennae</i> (L.) Murr.	Ravenna Grass	1	1					1		
<i>Saccharum spontaneum</i> L.	Wild sugarcane	1	1				1			
<i>Schizostachyum brachycladum</i> (Kurz) Kurz	Sacred Bali bamboo	1	1		1					
<i>Schizostachyum glaucifolium</i> (Rupr.) Munro	Hawaiian bamboo	1	1		1					
<i>Sorghum bicolor</i> (L.) Moench	Sweet Sorghum	8	4	2	1		2	1		1
<i>Zea mays</i> L.	Corn	3	2	1						2

Number of risk assessments completed (RAs), number of regions evaluated (Reg), and the outcome of the evaluation are shown for each species; low risk (LR), intermediate risk (IR), high risk (HR), reject, evaluate further (EF) and other classification (e.g. prohibit for importation). See Online Resource 3 for a detailed list of all assessments

including *Arundo donax* and *Phragmites australis* (Lambert et al. 2010). Their presence and growth in ecosystems have important consequences for the structure and composition of their communities (Chambers et al. 1999; Meyerson et al. 2000;

Meyerson 2000; Holmes et al. 2005; Richardson et al. 2007a; Packer et al. 2017). In particular, invasive reeds efficiently exploit space and nutrients, allowing them to take advantage of natural and human-induced

disturbances (Meyerson et al. 1999; Canavan et al. 2018b).

Tall-statured grass species (e.g. *Cortaderia jubata*, *Cortaderia selloana*, *Miscanthus sinensis*, *Panicum virgatum*) are also widely used for ornamental horticulture and bioenergy production. Many species used for this purpose escape from cultivation and spread into natural areas (Lambrinos 2000; Quinn et al. 2010; Schnitzler and Essl 2015). Interestingly, food crop TSGs (e.g. maize, sugarcane, pearl millet, sorghum), tend not to be invaders although they are widely propagated making up a vast component of landscapes altered by humans for agricultural purposes around the world, and they are very commonly planted as hybrids.

Extent and incidence of naturalisation of TSGs

Although we did not find that all models yielded a significant effect of stature, we did show that TSG categorisation is relevant with respect to probability for naturalisation. Specifically, we found that stature is associated with naturalisation success in grasses, but only when woody bamboos are excluded (Table 2). While stature is unlikely the proximate factor driving naturalisation, naturalisation patterns support the notion that being a TSG contributes to invasion potential. In agreement with other studies, we also found that the presence in horticultural trade is an important correlate of both naturalisation incidence and extent (Dehnen-Schmutz et al. 2007; van Kleunen et al. 2007, 2018; Pyšek et al. 2010). We also found that TSGs seem to have naturalised more on islands, probably due to the long history of bamboos being widely introduced and cultivated on islands along early trade routes (Canavan et al. 2017b).

Competitive features of TSGs

The heights obtained by TSGs (including bamboos) result in unique traits that can confer a competitive advantage over other co-occurring vegetation, including lignified stalks, production of large amounts of biomass (often at a rate faster than woody shrubs and trees; Linder et al. (2018)), formation of dense monospecific stands and extensive root and rhizome systems (See Table 1). Although these traits are not unique to TSGs and are present in other plant groups including shorter grasses, the combination of these traits enables some TSGs to have increased impacts.

Tall-statured grasses are also often the dominant components of the vegetation communities in ecosystems where they occur and thus have a strong effect on ecosystem functioning. As such, they have impacts at different trophic levels when they become invasive (Gordon-Gray and Ward 1971; Onimaru and Yabe 1996; Larpkern et al. 2011; Pagad 2016; Maceda-Veiga et al. 2016). For example, the accumulation of dead biomass creates thick litter mats that can suppress the growth of emerging plants over time (Haslam 2010; Amougou et al. 2012; Rohani et al. 2014). The increase of litterfall, and therefore standing biomass, can also lead to changes in fire regimes through increased fuel loads which can inflict ecosystem-level changes, including transformed nutrient cycling and increased susceptibility of the ecosystem to further invasion (Rieger and Kreager 1989; Dwire and Kauffman 2003; Herrera and Dudley 2003; Brooks et al. 2004).

For most TSGs, vegetative growth is both a crucial competitive mechanism and a reproductive strategy for dispersal with tillers, shoots, ramets, rhizomes, stolons or fallen stems forming clonal networks (Wang et al. 2017). The connectivity of biomass between stands has many advantages: greater resource acquisition and sharing (de Kroon and Kalliola 1995; Stueffer et al. 1996; van Kleunen and Stuefer 1999); allowing invasion into closed canopies or low resource-patches (Welker and Briske 1992; Wang et al. 2016); and allowing the storage of resources (Grace 1993). The increased amount of below-ground vegetative biomass of TSGs, compared to shorter grasses and other plants like trees, likely gives populations added resilience to disturbances and provides a greater capacity for energy storage.

Sexual reproduction and seed dispersal is not a prerequisite for the spread of many TSGs (Ahmad et al. 2008; Hardion et al. 2012; Canavan et al. 2017a). Clonal TSGs use stem-derived spacers such as underground rhizomes or above-ground stolons to disperse which can be further aided by anthropogenic activities such as the movement of TSGs for ornamental horticulture and other purposes (SFAPRC 2006; Isagi et al. 2016). The ability of some TSGs to successfully colonise a wide variety of environmental gradients and yet have such low genetic diversity may also indicate that other important mechanisms are implicated, such as increased phenotypic plasticity in response to environmental changes (Canavan et al. 2017a).

Invasive clonal plants like *Arundo donax* may possess a ‘general-purpose-genotype’, i.e. a genotype that allows for phenotypic plasticity and thus adaptation to a wide range of conditions (Van Doninck et al. 2002). Further, many TSGs have an allopolyploid origin and incorporate high genetic diversity in their genomes (Soltis and Soltis 2000).

Although vegetative growth clearly carries several advantages for the establishment of TSGs, this mode of dispersal alone has limitations. When TSGs can also reproduce sexually they have the added advantage of being able to achieve long-range dispersal independently (e.g. without the need for disturbance or human-facilitation) into adventive ranges. Sexual reproduction also produces genetic diversity and increases the opportunities for naturalisation and eventually adaptation to new habitats and ranges (Colautti and Lau 2015). Increased height can also be a competitive advantage in seed dispersal by wind, as pollen and seeds can travel above the canopy and cover long distances (Thomson et al. 2011). A number of TSGs have been found to disperse widely via seed production (Quinn et al. 2010; Ecker et al. 2015), but can also invade new ranges through the distribution of seeds (Chambers et al. 1999; Belzile et al. 2010; McCormick et al. 2010; Kettenring et al. 2011; Bonnett et al. 2014).

Risks of invasion and impacts

We found that a majority of risk assessments that have evaluated TSGs have been for horticultural introductions and more recently for bioenergy projects (Scurlock et al. 2000; Blanchard et al. 2017; Lieurance et al. 2018). Since TSGs are the grasses most often selected for bioenergy and biofuel production, this usage category will probably continue to drive future introductions from the group (Cousens 2008; Gordon et al. 2011; Hartman et al. 2011; Amougou et al. 2011; Jung et al. 2015; Smith et al. 2015; Corneli et al. 2016). Potential bioenergy TSG crops tend to receive higher risk scores than TSGs selected for other uses (See Online Resource 3). The most commonly mentioned candidates for biofuels include *Arundo donax*, *Cenchrus purpureus* (= *Pennisetum purpureum*), *Miscanthus* × *giganteus* (importantly neither parental species grows to ≥ 2 m, indicating selection for greater height), *Saccharum* spp., as well as *Panicum virgatum*, (although just short of the 2 m threshold).

The high risk of biofuel-selected species is in line with previous studies; a comprehensive analysis by Budenhagen et al. (2009) found that biofuel species are two to four times more likely to establish and become invasive than species introduced to Hawaii for other purposes.

An additional risk associated with biofuel and bioenergy crops is the intention to develop more robust and vigorous cultivars through genetic manipulation to produce crops that yield more biomass (Bouton 2007). Many of the selected traits overlap with known weedy attributes, such as: (1) fast growth rates; (2) high seed production; (3) wide range of climatic tolerance; (4) adaptability to a wide range of environmental conditions; and (5) few herbivores, pests and diseases in receiving ecosystems (IUCN 2009; Richardson and Blanchard 2011; Flory et al. 2012). In general, the high levels of domestication and breeding of TSGs, both historically and currently, have likely increased invasion risks of some species, as more robust cultivars have been and continue to be developed. Concerns have been expressed that, in general, current risk assessment frameworks and policies are limited in their ability to evaluate subspecies or lower taxa (e.g. cultivars, genotypes) and hybrids (Meffin 2013). For example, a cultivar of a species may perform very differently to the wild type of the species as it occurs in nature. Greater intraspecific diversity of a species has been found to be associated with an increased likelihood of naturalisation or establishment [e.g. South African *Iridaceae* species; van Kleunen et al. (2007)] and invasion or spread [e.g. bamboos and lineages of *Phragmites*; further; Meyerson et al. (2010), Kettenring et al. (2011), Meyerson (2013), Canavan et al. (2017a)], highlighting the need for better understanding of intraspecific dynamics. Even natural variations within a species can be problematic in this regard; this has been the case with *P. australis* where a certain haplotype (Saltonstall 2002) and smaller genome sizes (Pyšek et al. 2018) are more invasive than others (e.g. displacement of native haplotypes in North America). Invasive genotypes likely exist within other TSGs and other plant taxa more generally [e.g., *Phalaris arundinacea*; Lavergne and Molofsky (2007)], although they go unrecognised due to the difficulty in identifying intraspecific diversity. Additional criteria are needed to evaluate the invasion risks of subspecific or lower taxa, particularly to keep pace

with the increasing selection and breeding of TSGs for biofuel and other uses surrounding high biomass yielding variations.

The TSG concept and future directions

While there is no clear break in the height distribution of grasses, TSGs are an important functional group as they cause distinct impacts and raise particular concerns for management and biosecurity. We suggest a number of directions that can be taken with the TSG group including: (1) studying subgroups of TSGs in particular biogeographical realms (e.g. Afrotropic TSGs), or habitat types in which they primarily occur (e.g. riparian, estuarine, or forest TSGs). Understanding the reasons for the differences between woody bamboos and other TSGs would be an important first step; (2) determining why different pathways and the traits selected in TSGs are associated with varying levels of risks. For example, trying to better understand why TSGs selected for biofuels are associated with high-risks, whereas food crops tend to be low-risk; (3) reviewing the importance of TSGs in their native range for resisting invasions. For example, the composition of dominant native grasses have been found to be mediators of invasions as well as important predictors of the ability of a system to resist invasion (Tilman et al. 1997; Pokorny et al. 2005; Richardson et al. 2007b; Young et al. 2009; Wang et al. 2013); and (4) reviewing whether there is merit in expanding the functional group to encompass tall Poales [order of monocotyledons that include grasses, bromeliads and sedges] more generally, as many sedges and rushes employ similar mechanisms to disrupt and produce ecosystem-level changes through biomass production and accumulation [e.g. the removal of invasive *Typha × glauca* biomass increased native plant diversity along Great Lake coastal wetlands; Angeloni et al. (2006), Farrer and Goldberg (2009), Lishawa et al. (2015)].

In summary, we believe that the group of TSGs, including bamboos, are a useful functional group both for invasion science and management and that further research on the group, on both the biological reasons and the socio-economic imperatives that drive invasions, is warranted. Tall-statured grasses also provide an important counter-point to other analyses as to when generalisations can be made in invasion science (Kueffer et al. 2013).

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