Historical legacies and ecological determinants of grass naturalizations worldwide
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The global distribution of exotic species is the result of abiotic, biotic and dispersal filtering processes that shape the movement and success of species outside their native range. In this study we aim to understand how these filtering processes drive the fluxes of grass species among regions, the factors that influence which species establish outside of their native range, and where they do so.

We used national and subnational checklists of native and introduced grass species to determine the extent to which each region was a source or recipient of exotic species. We asked how species traits may distinguish those grass species that have naturalized outside their native range from those that have not, and how environmental conditions are related to the distribution of exotic grass species.

We found that exotic grass establishment is shaped by an array of factors including characteristics of regions, traits of species and their interactions. Regions with a longer history of human occupation and larger numbers of native grass species were generally the most important sources of exotic species. Global flows of species were mostly driven by a climate match between the native and exotic ranges, but were also highly asymmetric, with regions with recent human arrival being the major hosts of exotic grass species. Tall, annual and C4 grass species exhibited particularly high probabilities of establishment outside their native range.

Despite the idiosyncrasy and stochasticity characteristic of exotic species establishment, this biogeographical analysis revealed important generalities across this large plant group. Our results suggest that grass species that have co-occurred with humans for a longer time may be better adapted to living in anthropogenic landscapes, explaining the global asymmetry in species introductions.

Keywords: alien species, biological invasions, functional traits, invasibility, invasiveness, Poaceae
Introduction

Human activities have broken down biogeographic barriers that previously maintained distinct regional species assemblages (Capinha et al. 2015). As a result, many species have been introduced to and become invasive in new regions. Invasive species can have large economic and ecological consequences (Bradshaw et al. 2016), and can be very difficult to eradicate (Rejmánek and Pitcairn 2002). Thus, predicting which areas are likely to be susceptible to the establishment of new species (‘invasibility’) and which species are likely to become invasive (‘invasiveness’) are important applied problems in ecology. Flows of exotic plants among continents vary markedly and are often asymmetrical (van Kleunen et al. 2015), but the underlying mechanisms are still poorly understood.

Our goal here is to test a range of hypothesized mechanisms for plant introductions at a global scale for a large phylogenetic group, the grass family (Poaceae, 11,361 species). Grasses are among the most ecologically important plant groups, are overrepresented among invasive taxa and have transformed many ecosystems along their evolutionary history (D’Antonio and Vitousek 1992, Strömberg 2011, Linder et al. 2017). In this study we used checklists that report the native and exotic presences of grass species at national or sub-national level (hereafter called ‘regions’) as the basis of a comprehensive analysis of the invasiveness of grass species and the invasibility of the recipient regions. The process of naturalization involves passing through multiple filters, from the original dispersal event to successful germination and growth in the new environment, to persisting in the face of local climate variation, competitors, herbivores and diseases (Catford et al. 2009). For each of these filtering processes, success depends upon the characteristics of regions, the characteristics of grass species, and how they interact, as traits that are associated with invasiveness in one environment might not be in another (Richardson and Pyšek 2006). This interaction is particularly important for understanding the distribution of species introduction and establishment at a global scale (Catford et al. 2009).

To overcome the dispersal filter, at least one propagule of a species must arrive in a new region. Connectivity of regions due to geographic proximity (Minaya et al. 2017) or international trade (Westphal et al. 2008) is likely to promote the transfer of exotic species. Certain species traits, such as propagule characteristics and life history features are associated with increased naturalization in new regions, likely due at least partially to their role in overcoming the dispersal filter (Rejmanek and Richardson 1996, Cadotte et al. 2006, Grotkopp and Rejmanek 2007, Pyšek and Richardson 2008, van Wilgen and Richardson 2014).

Once a propagule has arrived in a new region and begun to reproduce, the population must be able to survive the abiotic conditions. In general, species are likely to establish in regions that are climatically similar to their native range, a pattern called ‘climate matching’ (Bomford et al. 2009).

In the past, for instance, the historical dispersal events of the grass subfamily Danthonioideae can partly be explained by range-filling due to climate similarity but are also constrained by geographic distance (Linder et al. 2013). In many situations, disturbance intensity or rate is an important predictor of invasibility (Burke and Grime 1996, Davis et al. 2000, Fenn et al. 2003). Many grass species are adapted to fire, can benefit from establishing a positive feedback loop with fire frequency, as is the case with cheatgrass Bromus tectorum in the western United States (D’Antonio and Vitousek 1992), and alter fire regimes over large spatial scales (Fusco et al. 2019). Environmental factors in a region may also influence the number of species native to that region that naturalize elsewhere. There are various mechanisms possible – first, the climate may select for certain values of a trait (hereafter, trait states), which promote or inhibit establishment elsewhere, thereby exerting an indirect effect. Alternatively, climatic states that are regionally unusual but replicated in other areas of the world may be important sources of species establishment (for example, Mediterranean climates around the world, which share many exotic species, Fox 1990). Long-term climate stability may also play an important role, in part because stability increases the time available to adapt to the environmental conditions (Fridley and Sax 2014). Finally, there is also marked global variation in the degree and duration of human impacts (Ellis et al. 2013). We hypothesize that the potential for a plant species to adapt to anthropogenic landscapes should increase with the duration of co-occurrence with humans (following Buckley and Catford 2016). We therefore predict that regions with a longer history of human occupation should be more important sources of exotic species (e.g. Africa and Eurasia are more likely to contribute exotic species to North America than vice versa, MacDougall et al. 2018). This prediction is likely to be especially true for economically important groups such as grasses.

The biotic community within a region, together with the characteristics of the potentially naturalizing species, influences the establishment success of that species (Pearson et al. 2018). On one hand, a species functionally similar to the native community might be generally well-adapted for that environment. On the other hand, taking a very different functional strategy may reduce competition with the native community, thereby increasing naturalization success. In a phylogenetic context, close phylogenetic relatives in the native community may indicate greater or lesser probability of establishment depending on the relative strengths of these two mechanisms and the scale of observation (Carboni et al. 2015).

Species traits associated with fast life cycles, acquisitive resource strategies and rapid spread rates are often linked to successful naturalization or invasiveness in the face of biotic interactions. For grasses, these traits include high specific leaf area (SLA), Grotkopp and Rejmanek 2007, Pyšek and Richardson 2008, Sandel and Dangremond 2012) and tall stature (Sandel and Dangremond 2012, Canavan et al. 2016, Visser et al. 2016). While there is considerable variation
around these generalities, some trait states are clearly related to the propensity for a grass species to naturalize in a new region. At the same time, environmental conditions apply a strong filter to grass traits (for example, warmer climates support taller grass species, Sandel et al. 2016). Thus, the set of functional traits observed among exotic grass species in a region is expected to reflect the interplay of filtering by climate conditions and selection for traits associated with successful naturalization.

In this study, we test a range of hypotheses relating to abiotic, biotic and dispersal filtering processes on the exotic distribution of grasses. We explore the current and historical factors that influence the propensity for a region to be a source of exotic grass species, the species traits that are related to a successful establishment in new environments, and the anthropogenic, biotic and abiotic characteristics of regions that make them susceptible to the establishment of new grass species. Then, we ask how grass species differ in their dependence on these factors with respect to their functional traits.

**Material and methods**

**Distributions**

We used the World Checklist of Selected Plant Families (WCSP; Royal Botanic Gardens Kew 2015) which provides national or subnational lists of all native and alien grass species. Because the environmental and anthropogenic processes that drive their distributions are likely to be different from those of uncultivated species, we discarded cultigens and widely cultivated species among the 11 361 Poaceae species, following the classification of Pyšek et al. (2004) of alien species occurring outside cultivation. Cultigens are plants that have been altered by humans through a process of selective breeding (Plants of World online). The list of species we excluded for our analysis is available in the data repository. We obtained the presence of 11 332 species in their native range in each geographic unit. The geographic units, hereafter called ‘regions’, are the TDWG level 3 units defined by Biodiversity Information Standards (historically known as the Taxonomic Databases Working Group (TDWG), Brummitt 2001) and mostly correspond to countries or a subnational level for the larger countries. We also used the TDWG level 1 units corresponding to nine continents (Brummitt 2001). Among these species, the World Checklist of Selected Plant Families also recorded the naturalization or casual introduction of 1134 species outside their native range. This status was determined in each region from the distribution maps and from the local floras, especially for isolated occurrences and regions on the fringes. The list of exotic species is available in the data repository.

For each region, we counted both the number of species donated to other regions and the number of exotic species received from other regions. For each continent, we visualized its connections to other continents using an approach similar to that of van Kleunen et al. (2015). We described the flows of exotic species by summing the flow of species from their native continent(s) to the continent(s) where they have naturalized (hereafter the ‘donor’ and the ‘recipient’ continent(s), respectively). If one species is native to more than one continent, we divided the flow by the number of donor continents. We plotted the observed and expected flows using circular plots of directional bilateral migration flows using the ‘circlize’ package (Abel and Sander 2014, Gu et al. 2014).

**Functional traits**

We considered functional traits of grasses in two capacities: first, as predictors of which species would be donated to other regions from a focal region, and second, as predictors of variation in where a particular species will naturalize.

In both cases, we used five functional traits. Three are quantitative traits corresponding to Westoby’s (1998) leaf–height–seed (LHS) plant strategy scheme: specific leaf area (SLA), maximum height and seed mass. SLA describes a plant’s position along a leaf economic spectrum ranging from leaves that obtain rapid returns on investment but suffer short lifespans, to leaves with high longevity but high construction costs (Wright et al. 2004). Maximum height relates to a species’ light competition strategy and seed mass indicates a species’ strategy along an axis of low investment in many seeds and high investment in few seeds. SLA data were obtained from the TRY plant trait database (Kattge et al. 2011) and an extensive literature review of published trait values for grasses (see Supplementary material Appendix 1 for full references). Maximum height in this case was measured as the maximum culm length of a species, which among grasses is highly correlated to field-measured height while being available for many more species. Seed mass data came primarily from the Kew SID, with some additional values from TRY and literature review (Supplementary material Appendix 1).

In the main analyses presented here, we imputed missing values for quantitative traits by taking the mean value for the trait among congeners. Trait data were available at the species level for 89.7% of species for height, 15.6% of species for seed mass and 7.9% of species for SLA. After imputing missing values with generic means, their coverage increased to 98.7, 82.1 and 79.4%, respectively. Among species with measured trait values, 63% of the variation in height was captured at the genus level, while these numbers were 77% for seed mass and 46% for SLA. We also repeated the analyses by using only species with directly measured trait values. The results, mostly similar, are presented in Supplementary material Appendix 2 Fig. A1, A2. For example, mean trait values of native grasses within regions with or without imputation of missing values were highly correlated (height $r=0.999$, seed mass $r=0.847$, SLA $r=0.849$).

Finally, we also considered two categorical traits: C4 or C3 photosynthetic pathway, and annual or perennial lifespan. Both are known to be very important descriptors for grass species’ strategies, and are strongly related to their distribution and abundance along climate gradients (Sandel et al. 2016). Lifespan and photosynthetic pathway information...
were available for 91.3% and 91.6% of species, respectively. No imputation of missing values was performed for these traits: we used only species with directly measured trait values.

**Phylogeny**

To assess how phylogenetic relatedness in the native community is associated with the establishment outside their native range, we built a super-tree from the phylogenetic relationships established by Edwards et al. (2010) among 2684 grass species. Interior nodes were dated using the phylogeny of Christin et al. (2014). Missing species in the phylogeny were iteratively grafted in a random position next to a randomly selected congener (Sandel and Tsirogiannis 2016). We repeated the procedure 100 times to get 100 dated and ultrametric trees for 10 113 species (89% of the family Poaceae). The World Checklist of Selected Plant Families for Poaceae was used as a taxonomic backbone (WCSP; Royal Botanic Gardens Kew 2015).

**Environmental predictors**

We used information on the current and past climate in each region and the degree and duration of human impact on natural systems to assess how they are related to the number of grass species native to a region but naturalizing elsewhere. We extracted major descriptors of current climate from the Worldclim database at a 10 arc-minute resolution (Hijmans et al. 2005) and calculated their average values for each region. These variables were mean annual, minimum and maximum temperature and precipitation, temperature seasonality and precipitation seasonality. We calculated the climate change velocity from the Last Glacial Maximum (21 000 yr ago) to the present following the method by Sandel et al. (2011).

For each region, we calculated the mean Human Influence Index (HII) from Wildlife Conservation Society – WCS – and Center for International Earth Science Information Network – CIESIN – Columbia Univ. (2005). This index summarizes anthropogenic environmental impacts and was derived from nine global data layers covering human population pressure, human land use and infrastructure, and accessiblity. We also measured, as another surrogate of the human influence on the environment, socio-economic activity using the per capita Gross Domestic Product at Purchasing Power Parity in US dollars (hereafter ‘GDP’) at the national level or at the subnational level for Canada, China, the United States, Russia and South Africa (see data and sources in Supplementary material Appendix 2 Table A1). For each region, we calculated the mean fire frequency, excluding cropland and built-up areas from GloCover (2009) land cover data (Bontemps et al. 2011). We used the Moderate Resolution Imaging Spectroradiometer (MODIS) product providing monthly burn area dates for the years 2000–2016 (Giglio et al. 2015).

We described the length of co-occurrence with humans using the time period of first hominin colonization in the region. Regions were classified into five categories, following Sandom et al. (2014): the region of origin for the genus *Homo* (roughly, sub-Saharan Africa), regions in southern Europe and Asia colonized by *Homo erectus* (and related taxa) as early as the Late Pliocene or Early Pleistocene (Archaic-early), a region of further expansion in Europe and Asia by *Homo neanderthalensis* and Denisovan humans (Archaic-late), peripheral regions of northern Europe and Asia that may have been occasionally used by these early hominins (Archaic-peripheral), and finally the rest of the world for which modern *Homo sapiens* was the first hominin to arrive. We also calculated the mean area covered by cropland and grazing at different time intervals from 8000 BCE to 2017 CE. Grazing was divided into intensively used pasture and extensively managed rangeland. We extracted the data at a 5 arc minutes resolution from HYDE database ver. 3.2.1 (Klein Goldewijk et al. 2017).

**Distance metrics for each exotic species**

For each exotic species, we extracted the minimum climatic and geographic distances between each region in the world outside its native range and any region within its native range to assess the role of climate match and geographic distance in determining the exotic range of species. We calculated two climate distances – one based on the four temperature variables, and one based on the four precipitation variables. In each case, the distance measure was the minimum of the Euclidean distances between a region and any region in the native range. We calculated the geographic distance on the WGS ellipsoid between the centroids of each pair of regions using the function ‘pointDistance’ of the spatial package (Venables and Ripley 2002). This measure slightly overestimates the distance between the native and exotic range of the species but does so consistently for all species.

We also used two metrics to measure the phylogenetic distance of each exotic species to the native assemblage species. We computed the standardized value of the community distance measure and the value of the directed Community Distance Nearest Taxon measure in the ‘PhyloMeasures’ package (Tsirogiannis and Sandel 2015) to calculate respectively for each exotic species: 1) its average phylogenetic distance to the native assemblage species in each native region (hereafter, MPD), and 2) its phylogenetic distance to their nearest native species in each native region (hereafter MNTD).

**Statistical analysis**

We began by considering the factors that influence which regions are major donors and recipients of exotic grass species. For each region, we computed the total number of grass species native to that region that have naturalized elsewhere and the number of non-native grass species occurring there. For each region, we also computed the mean value of each functional trait of the native grass flora. We fit an ordinary linear model to explain each of these two response variables, based on a range of descriptors of the anthropic,
abiotic and biotic context of the region. These explanatory variables were: four climate variables (mean annual temperature and precipitation, temperature seasonality and precipitation seasonality), the current and past human influence on environment (Human Influence Index, GDP, time period of hominin colonization and grazing area), the past climate change velocity, the native grass species richness and the average traits of the native grass flora. All variables were centred and scaled. Velocity was log-transformed; and mean annual precipitation, and temperature and precipitation seasonality, were square-root transformed. We further tested how the correlation between the percentages of each land cover category across different time points (from 8000 BCE to 2017 CE) and the current richness in leaving species (i.e. species native to one region that have naturalized elsewhere) and exotic species changed over time (Supplementary material Appendix 2 Fig. A3).

Next, we considered how well species traits may distinguish those species that have naturalized elsewhere from those that have not. For each region, we fit pairwise and multiple logistic regressions (GLM with logit link) to predict which species had or had not naturalized elsewhere based on the five functional traits (SLA, height, seed mass, photosynthetic pathway, lifespan). Further, we sought to understand whether the trait states most likely to confer naturalization success differ when species originate in different environments. For each trait, we had obtained one regression coefficient from each region. We then treated these as response variables and attempted to explain their variation based on the environmental characteristics of the region using ordinary linear regression. The environmental predictors were four climate variables (mean annual temperature and precipitation, temperature seasonality and precipitation seasonality), the Human Influence Index, GDP and the past climate change velocity. Quantitative trait values were log-transformed before analysis; and mean annual precipitation, and temperature and precipitation seasonality, were square-root transformed.

Finally, we took a similar approach to understand where leaving species established. For each of 214 species with sufficiently large exotic ranges (at least twenty regions), we fit pairwise and multiple regression models to explain which regions were in the exotic range or were unoccupied (regions in the native range were excluded). For each region outside the native range, we used nine predictors: minimum climatic and geographic distances from the native range (defined above), the two metrics of phylogenetic distances (MPD and MNTD), magnitude of human influence (Human Influence Index and GDP), fire frequency and past climate change velocity. Geographic distance, GDP and MNTD variables were square root-transformed prior to analysis. We then examined how species traits were associated with the importance of each predictor of their exotic distribution. We fit linear models predicting the coefficient values for a predictor using SLA, seed mass, maximum culm length, lifespan (annual/perennial), photosynthetic pathway (C3/C4) of a species, and the native range size. All data analyses and statistical analyses were performed with R, ver. 3.2.3 (R Core Team).

Results

Source areas for exotic grass species

The major source regions for exotic grasses occurred in a belt from the Mediterranean through Turkey, Iran, India and into southeast Asia, with an additional hotspot in eastern Africa (Fig. 1a, b). We related the number of species that have left their native range with anthropogenic, abiotic and biotic variables (Table 1, Fig. 2a). Large numbers of leaving species were most strongly associated with high native species richness, high temperature seasonality, low precipitation seasonality, largely annual, short-statured native grass floras, large current human impacts and a long association with hominins (Fig. 2a, all p < 0.03). Recent grazing areas had relatively weak effects on richness in leaving species, though grazing area at 0 CE was significantly positively associated with leaving species richness (p = 0.04). Detailed analyses showed that the percentages of land in crops and grazing (pasture and rangeland) across all time periods were positive indicators of richness in species naturalizing elsewhere, though the strongest correlations were for cropland (Supplementary material Appendix 2 Fig. A3). The linear models captured the variation in leaving species richness well (R² = 0.88).

Trait characteristics of exotic grass species

Among the grasses in a region, those that established elsewhere were a non-random subset of the native species. In particular, they had higher SLA (on average, 12% higher), had longer culms (27% longer) and had smaller seeds (10% smaller) than non-leaving native species, and were more likely to use C4 photosynthesis and be annuals (Table 1, all p < 0.05). The importance of lifespan and photosynthetic pathway in influencing which species did or did not naturalize elsewhere declined with increasing mean annual temperature of the region (Fig. 3), while the influence of culm length declined with increasing annual precipitation. Generally, results from single and multiple predictor models were similar. When the analysis was performed without trait imputation, the results were also mostly similar (Supplementary material Appendix 2 Fig. A1).

Recipient areas for exotic grass species

There was pronounced variation among continents in their exotic species richness. North and South America, Australia and New Zealand had high exotic grass richness (Fig. 1c), with much lower richness in Africa, Asia and, to a lesser extent, Europe. By relating the number of exotic species to the environmental and anthropogenic variables and traits composition of the native assemblages (Table 1, Fig. 2b), we
found that the highest richness of exotic species occurred in areas with high native richness, warm, seasonal climates, low climate change velocity, native grass floras with low SLA and seed mass, high current human impacts, recent settlement by early hominins or modern Homo sapiens, and recent distribution of grazing area. The percentages of land in crops or grazing across various time points in history were all negatively correlated with exotic richness, except for the most recent time point (2017) when all but rangeland became positive predictors (Supplementary material Appendix 2 Fig. A3).

The presences of the most widespread exotic species (n = 214) outside their native range were predominantly negatively correlated with temperature and precipitation distances and positively to geographic distances (Fig. 4). That is, a species was most likely to naturalize in regions that were climatically similar to, but geographically distant from, its native range. In general, temperature distance was a more important predictor of a species’ exotic distribution than precipitation distance. This was particularly true for C4 species, which as a group exhibited strong temperature constraints, but nearly no precipitation constraint. The results are illustrated for one species in Supplementary material Appendix 2 Fig. A3.

Grasses were most likely to establish in a region if there were close relatives in the native flora – both MPD (mean pairwise phylogenetic distance) and MNTD (mean nearest taxon distance) exerted a negative influence on naturalization probability. However, this effect disappeared in the multiple regression models that also account for climate distance, suggesting that this reflects an environmental filtering effect. Considered alone, the Human Influence Index, GDP and climate change velocity had relatively minor influences, while fire frequency reduced the naturalization probability for C3, but not C4 species. When accounting for other factors in multiple regressions, the Human Influence Index had a weak negative influence, and GDP a strong negative influence on naturalization probability (Fig. 4, Supplementary material Appendix 2 Table A2). We found mostly similar results when performing the analysis without trait imputation procedure (Supplementary material Appendix 2 Fig. A2).

Discussion

This study presents the first attempt to document human-driven grass species establishment worldwide. Recently, some efforts have been made to document patterns of global plant naturalizations and invasions (van Kleunen et al. 2015). Among them, grasses are one set of invading species that in the aggregate may be sufficiently widespread and abundant to alter regional and even global aspects of ecosystem function (D’Antonio and Vitousek 1992). We estimate that roughly 10% of grass species have established outside their native range. This rate is higher than the total proportion for vascular plants (3.5%, van Kleunen et al. 2015), and also higher than birds, mammals, reptiles and amphibians, as reviewed by Capinha et al. (2017). Thus, the family Poaceae is characterized by a long history of colonization.
Transfers of exotic grass species were highly asymmetrical, and dominated by flows from Africa, the Mediterranean and southern Asia to the Americas, Australia and New Zealand. This result is consistent with the idea that longer co-occurrence with humans allows more time for grass species to adapt to living in anthropogenic landscapes. The expansion of grasslands in Africa is thought to have strongly influenced hominin evolution (Uno et al. 2016), and it is possible that the expansion of hominins similarly influenced grass evolution. Selective agents are likely to include human-modified fire frequencies (Archibald et al. 2012), altered large mammal communities (Sandom et al. 2014), increasing populations of domesticated livestock, and in some cases direct artificial selection. Consistent with this, regions with larger current human influence are also the most important sources of exotic species, as are regions with larger areas recently allocated to crops and grazing. Among human-modified landscapes, agricultural systems constitute major examples of human niche construction where both plant adaptations to human land use and human adaptation to use some species are expected (Laland and Boogert 2010).

Table 1. Specific hypotheses and predictor variables used to disentangle the relative importance of main filtering processes (Filtering) that modulate their inter-continental flows of species through three general questions. We also indicated whether the results validate or not the hypothesis with the predictors tested (yes/no/mixed). MPD (mean pairwise phylogenetic distance) gives the average phylogenetic distance to the native assemblage species in each native region; MNTD (mean nearest taxa distance) gives the phylogenetic distance to their nearest native species in each native region; GDP is the per capita gross domestic product at purchasing power parity; SLA is the specific leaf area.

| Question | Filtering | Specific hypothesis | Predictor variable | Support for the hypothesis |
|----------|-----------|---------------------|-------------------|---------------------------|
| Which grass species are likely to leave their native range? | biotic, biotic | Fast lifespans | Lifespan (annual/perennial) | yes |
| | | Fast return on investments, acquisitive strategy | SLA | yes |
| | dispersive, biotic | Small, widely dispersing seeds | Seed mass | yes |
| | | Highly competitive | Maximum culm height | yes |
| | dispersive, biotic | Greater connectivity to other regions increases export of colonizing species | GDP | no |
| | dispersive | Longer coexistence with humans increases export | Era of human settlement | yes |
| | abiotic | Climate selects for traits that promote invasiveness | Mean annual temperature, mean annual precipitation | mixed |
| | | Long-term climate stability increases export | Late Quaternary climate stability | no |
| | biotic | More export from large populations and diverse communities | Species richness | yes |
| | | More export from communities with traits associated with invasibility | Traits (SLA, maximum culm height, seed mass, lifespan, C3/C4) | mixed |
| | biotic | High rates of human disturbance increases export | Human influence index, land use | yes |
| | | More export from regions with longer history of grazing and cropland | Past % of land allocated to grazing and crop | yes |
| Which regions are sources of exotic grass species? | biotic | Phylogenetic distance to native community increases colonization | MPD, MNTD | no |
| | biotic | Phylogenetic distance to native community decreases colonization | MPD, MNTD | yes (but depend of the model used, see results) |
| | biotic | High fire frequency promotes colonization | Fire frequency | no |
| | biotic | High rates of human disturbance promote colonization | Human influence index | no |
| | abiotic | Greater similarity to climate in native range increases colonization probability | Climate distances to native range | yes |
| | dispersive | Long-term climate instability promotes colonization | Late Quaternary climate stability | mixed |
| | dispersive | Greater connectivity to other regions increases export of colonizing species | Geographic distance, GDP | no |

and diversification worldwide (Linder et al. 2017) and display a high level of recent establishment outside their native range.
In contrast, areas with more recent human arrivals today host the most exotic species. This may be because these areas have grass floras that are evolutionarily naïve and susceptible to rapid declines when faced by the dual pressures of anthropogenic landscape modification and species introductions. A similar mechanism has been proposed to explain the higher rate of large mammal extinctions in areas with more recent human arrival (Martin 1984, Sandom et al. 2014).

We found higher richness of exotic species in regions with higher native richness. This result is expected at broad spatial scale according to the ‘rich get richer’ hypothesis, which predicts that regions that offer more resource opportunities for native species also do so for invasive species (Gallien and Carboni 2017). Beyond the taxonomic richness of native assemblages, their functional diversity can be informative to infer community resistance. Recently, Visser et al. (2016) demonstrated that the low numbers of invasive grasses in South Africa can be explained by the specific trait states that make South African grasses successful competitors in environments characterized by fire, grazing and disturbance i.e. large leaves, tall culms and C4 photosynthetic pathway. At a global scale, we found that the highest richness of exotic species occurred in grass floras with low SLA, low seed mass and low proportions of C4 species. Also, the differences in the composition of symbiotic communities between native and exotic ranges, not considered here, might also be an important determinant of introduction success, but especially in

**Figure 2.** Predictors of (a) the number of native grass species that have left each region, or (b) the number of grass species exotic in each region. Standardized coefficient estimates (± SD) were obtained from linear models. The higher the absolute values of the coefficients, the stronger the effects in the model. Predictor variables include native grass richness, current climate, past climate change velocity, average functional traits of the native grass flora, and current and past human influence on environment. The latter includes the length of co-occurrence with humans (ranging from the regions of origin for the genus Homo [reference level] to regions first colonized by anatomically modern humans, see the Methods section for details) and the mean area covered by grazing at different time points (0 and 2017 CE).
case of specialized associations for which the prevalence is not well known (Richardson et al. 2000).

Our study examined the relationship between the number of grass species that have left a region to naturalize elsewhere with species traits and biotic and abiotic factors of the source regions. As predicted, we found that the regions with larger numbers of native grass species had on average larger numbers of leaving species. The highest richness in leaving species came from warmer regions with higher temperature seasonality and lower precipitation seasonality, which can be expected given the strong correlation between grass richness and temperature at the global scale (Visser et al. 2014). We found mixed evidence for the idea that regions with native assemblages with trait states that are associated with colonization success elsewhere tend to have many species that have left a region to colonize elsewhere. For example, we found that tall species and annual species are most likely to leave their native range, while regions that have short-statured
and annual species are the most important sources of exotic species. Species traits influence both the propensity to naturalize beyond the native range and which regions a species can naturalize into. We found that species with higher SLA, taller stature and annual life-history strategy were more likely to naturalize outside their native range, consistently with what Visser et al. (2016) found for naturalized and invasive grass species in a selection of regions and with another result focused on height (Canavan et al. 2019). These species displayed on average highly competitive trait states. C4 photosynthesis was associated with higher probabilities of naturalizing beyond the native range. While this photosynthetic pathway is expected to provide a competitive advantage in high temperature and low CO2 atmospheric conditions (Ehleringer et al. 1997), C4 photosynthesis increased the colonization probability most in cooler regions.

As expected at a global scale, species traits interacted with characteristics of regions in the native range to determine the probability of naturalizing elsewhere and with characteristics of regions outside the native range to determine the naturalization probability. The photosynthetic pathway appeared particularly important. For example, C4 species are more likely than the C3 grasses to leave their native range, but especially so in cool regions. And, relative to C3 grasses, C4 grasses exhibited weaker climate matching between
precipitation in their native and exotic ranges, but stronger matching for temperature. C4 grasses responded less negatively to fire frequency than C3 species, and more negatively to climate change velocity.

Together, our results on the characteristics of exotic grasses are largely consistent with previous studies performed at other extents for grasses and other plants (Grotkopp and Rejmanek 2007, Pyšek and Richardson 2008, Sandel and Dangremond 2012). For our study, we have gathered the most complete data on grass traits to our knowledge. While three of the traits used here have very good coverage, two others do not (SLA and seed mass). The consistence of the results with and without trait imputation, which represented a good alternative to analysis with missing data (Penone et al. 2014), suggests that these results are probably reliable. Nevertheless, additional trait data would greatly strengthen this analysis. Moving beyond functional traits, it would be informative to have more information on introduction history and effort. Such data are not yet available for grasses at a global scale, but some proxies can be used. For example, introduction effort might be related to usefulness of species. Among bamboos, species with more cultivars or species with traits conferring useful construction properties (e.g., woodiness) were more likely to have been introduced (Canavan et al. 2016). Thus, a next step to better understand which grasses have naturalized elsewhere would be to document more exhaustively the past and current use of grass species. At the same time, detailed analyses of temporal patterns in herbarium records also have the potential to reveal temporal patterns of introductions (Sandel and Dangremond 2012). Recent efforts have been made in gathering the year of introduction for many plant species and showed the direct or indirect effects of history of introduction on naturalization (Feng et al. 2016, Maurel et al. 2016). The datasets used to document human-driven species movements are still growing and are constantly being updated and crosschecked. They can still be biased to the countries with a longer history of introduction monitoring (Pyšek et al. 2008). The most problematic areas are islands where it is difficult to assess the species status, whether they lie within the distribution range or on the fringes, and particularly small islands like the Mascarenes or the Micronesia. Especially for grasses, in many countries, botanists and checklist writers might have been not aware of (past) grass introductions, meaning that exotic species may be listed as native. Finally, our distribution data was coarse resolution, and many regions contain substantial climate heterogeneity. Thus, our measures of the mean conditions within a region may not reflect the actual conditions experienced by a particular species in that region. This is an important limitation, but its resolution must await higher-resolution distribution information.

Conclusion
The global pattern of exotic grass transfers is complex and shaped by a combination of species traits and regional characteristics. Most exotic grasses come from regions with high native richness, short-statured, annual grasses and long-term occupation with hominins. Species with high SLA, tall stature, small seeds, C4 photosynthesis and annual life cycles are most likely to establish outside their native range. When they do, they tend to become naturalized in warm, seasonal climates, where hominins have arrived recently and where native grass assemblages are characterized by low SLA, low seed mass and C3 photosynthesis.

Data availability statement
Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.bvq83bk63> (Monnet et al. 2020).

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Supplementary material (available online as Appendix ecog-04609 at <www.ecography.org/appendix/ecog-04609>). Appendix 1–2.