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## Invasion of the cosmopolitan species *Echinochloa colona* into herbaceous vegetation of a tropical wetland system

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**Abstract** The negative effects of alien plant species on ecosystem structure and functions are increasingly recognised, and efforts to control these species are vital to restore degraded ecosystems and preserve biodiversity. However, we lack a full understanding of factors that determine alien species invasions along spatial gradients in herbaceous vegetation of tropical systems. We therefore examined the effects of community properties, environmental variables and human-related disturbance factors on the invasion of the alien grass *Echinochloa colona* (L.) Link at small- and large scales in the Kilombero Valley wetland, Tanzania. Generalized additive mixed models showed that *E. colona* abundance on a small scale was negatively related to above-ground biomass and evenness of resident species, whereas *E. colona* abundance was positively related to grazing intensity. On a large scale, biomass (negatively related to *E. colona* abundance) and distance to river (positive) were important in explaining *E. colona* abundance. These findings support the assertion that different factors may contribute to the invasion of alien plant species at different spatial scales, as also reported in many temperate systems. Overall, our results show that successful invasion of alien species is a function of plant community properties, human-related disturbance and favourable environmental conditions. Effective management strategies should consider mitigations that can increase the biomass and evenness of native species and a reduction of grazing pressure to restore the wetland and conserve biodiversity.

**Keywords** Biomass · Diversity · Evenness · Alien species · Spatial scales · Human-related disturbance

### Introduction

Alien plants are increasingly acknowledged to alter habitats and ecosystems and thereby threaten global biodiversity (Millenium Ecosystem Assessment 2005; Vilà et al. 2011). Thus, control of their spread and monitoring their ecological effects is important to reverse biodiversity loss. However, this requires understanding of factors determining community vulnerability to invasion along spatial gradients, especially for ecosystems with most high biological invasions such as wetlands (Zedler and Kercher 2004; Ehrenfeld 2008). In explaining invasibility of plant communities, Elton (1958) proposed that more diverse communities are less susceptible to alien species invasions. Subsequently, Elton's hypothesis has been tested by a number of empirical studies, but with inconsistent results (Davis 2009; Fridley 2011) whereby both positive (Meiners et al. 2004) and negative (Symstad 2000) relationship between diversity and invasion has been reported. However, development in community ecology theories (e.g. Shea and Chesson 2002; Blackburn et al. 2011) and more evidence from observational, theoretical and experimental studies (reviewed by Herben et al. 2004; Fridley et al. 2007) suggest that inconsistencies in observed patterns of diversity–invasibility relationship is partly due to differences in spatial scales and context of studies. In this respect, studies looking at small scales ( $\leq 10 \text{ m}^2$ ) often find negative relationship between diversity and invasibility while those carried out at broad-scales (usually  $\geq 1 \text{ km}^2$ ) in most cases find the opposite relationship (Fridley et al. 2007; Richardson 2011). At small scales, biotic factors such as species interactions are thought to be responsible for negative diversity–invasibility relationships (Levine and D'Antonio 1999; Levine et al. 2004), as there are few available niches (niche complementarity effect) for the

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invaders to establish and higher chances to include invasion-resistant species (sampling effect) in diverse communities (Fargione and Tilman 2005). Extrinsic factors (which usually co-vary with diversity), such as environmental heterogeneity and disturbances, are suggested to structure plant communities at broad spatial scales. Indeed, research shows that changes in environmental conditions created by flooding events alter plant species composition (Andrew et al. 2012) and community structure (Keddy 2010) in wetland ecosystems. Flooding deposits litter, changes soil characteristics (e.g. moisture, organic content and chemistry), alters nutrient availability and reduces competitive exclusion (Pollock et al. 1998). Moreover, it has also been demonstrated that flooding may interact with grazing to shape species composition, richness and diversity (Chaneton and Facelli 1991; Moran et al. 2008) through for example formation and maintenance of gaps in grasslands (Cornaglia et al. 2009). Thus, extrinsic factors override competition and native species as well as alien species are both favoured by environmental conditions which in turn lead to a broad-scale diversity–invasibility positive relationship (Davies et al. 2005; Davis 2009).

Recent developments in invasion biology propose that community vulnerability to invasions does not depend only on community properties such as species composition, richness and diversity but also on other attributes such as plant biomass and species evenness (e.g. Hillebrand et al. 2008; Hillebrand and Matthiessen 2009). For example, using an experimental study it was demonstrated that biomass of native species was the most important factor which promoted invasion resistance in native grasslands (Lulow 2006). In the same experiment, species richness that is commonly used in invasion biology studies (Levine and D’Antonio 1999; Fridley et al. 2007) was not as important as biomass in promoting resistance against plant invasion (Lulow 2006). Moreover, evenness or relative abundances of species increased invasion resistance in native grassland communities at Manhattan Kansas USA, through decreasing dominance (Smith et al. 2004).

In the Kilombero wetland in Tanzania, the focus area of this study, the alien annual grass *Echinochloa colona* (L.) Link is frequent in herbaceous plant communities (Andrew et al. 2012). *Echinochloa colona* is reported to invade agricultural landscapes, pastures and seasonally flooded habitats and can change native species composition and other community properties (McIntyre et al. 2005). It is unclear from previous studies, however, why species like *E. colona* are such successful invaders in many areas. Moreover, although the relationships between plant species invasions and spatial scales have attracted considerable interest at global level, there is generally a dearth of information on biological invasions of alien plant species in tropical systems (Nunez and Pauchard 2010). In particular, factors that influence invasibility of native communities along spatial gradients remain little studied in tropical systems (emphasized by Fridley et al. 2007). Knowledge of scale dependent

ecological relationships is important to effectively develop mitigation for strategies of plant invasions, and restore invaded sites. The objective of this study was therefore to identify factors associated with the invasion success of *E. colona*, and explore if these factors differ between two spatial scales within a tropical wetland system. Specifically we ask: (1) Is invasion of *E. colona* related to community richness, evenness, diversity and above-ground biomass (henceforth termed biomass) of resident species, and human-related disturbance and environmental conditions? (2) Do the relationships between *E. colona* invasion and community properties, human-related disturbance and environmental conditions differ between small (i.e. variation among quadrats within plots) and large scale (i.e. variation among plots)? (3) What are the management implications of these relationships for the Kilombero Valley Ramsar site? We predict that community properties especially species richness would be important in explaining invasion of *E. colona* at small spatial scale consistent with the premise of Elton (1958). Since the area is used extensively for human activities (Ntongani and Andrew 2013; Andrew 2014) and flooding takes place annually, together these factors potentially create resource heterogeneity and we therefore predict that grazing disturbance and distance to river would be important for large scale invasion (Levine and D’Antonio 1999; Shea and Chesson 2002).

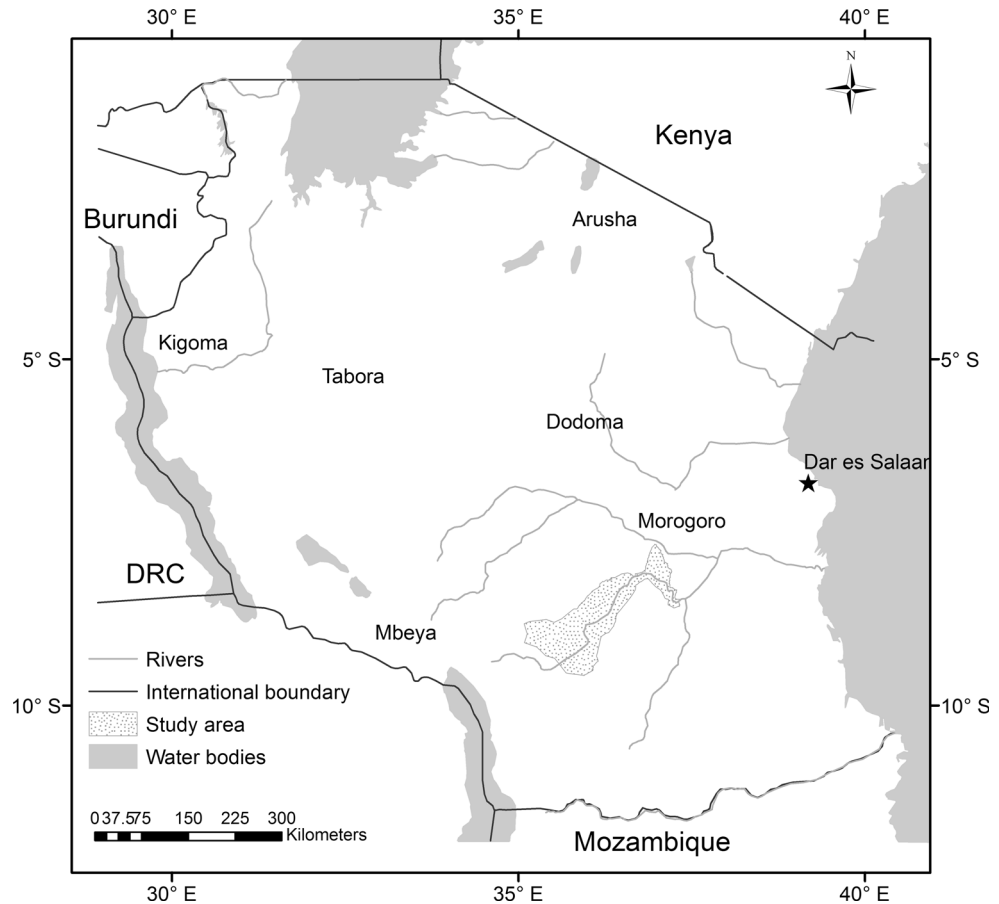
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## Methods

### Study site

The study was carried out in the Kilombero Valley Floodplain wetland in Morogoro region, southern-central Tanzania (8°32’0’’S, 36°29’0’’E, Fig. 1). The Kilombero wetland is a high biodiversity Ramsar site that covers 7,967 km<sup>2</sup> at 210–400 m.a.s.l. elevation (Ramsar 2013). The wetland falls under the floodplain wetland type and is the largest low altitude inland freshwater wetland in East Africa. The area is sub-humid with a mean annual temperature of 26 °C and a mean annual total rainfall of 1,600 mm (Bakengesa et al. 2011). It has a bimodal rainfall with short rains (light and sporadic) from December to February and long rains (heavy and regular downpour) from March to May or June (Bakengesa et al. 2011). The river flows in the SW–NE direction and floods annually during the long rains, and the valley remains flooded for at least 3 months (Andrew et al. 2012; Andrew 2014). The Kilombero wetland is formed in the depression of late Archaean metamorphic rocks with Pliocene and Pleistocene deposits (Beck 1964). Kilombero wetland has fertile clay soils, which are inundated during long rains and crack open during dry season (July–October). Fire occurs in the valley during the dry season, particularly between August and October (Andrew 2014).

**Fig. 1** The location of Kilombero wetland in Morogoro region, southern-central Tanzania



The Kilombero wetland hosts around 350 plant species, including indigenous species like *Crotalaria polygaloides* (Fabaceae), *Dalbergia melanoxylon* (Fabaceae) and *Aframomum alpinum* (Zingiberaceae). Eight plant communities are recorded in the valley; low lying valley grasslands, tall grasslands, papyrus swamps, marginal grasslands, marginal woodlands, combretaceous wooded grasslands and miombo woodland (Starkey et al. 2002). The Ramsar Convention of 1971 allows sustainable use of natural resources within the designated Ramsar sites, but today unregulated livestock husbandry and agriculture (crop production including shifting cultivation) is commonly practiced in the valley (Starkey et al. 2002). In this study we focused on the marginal grasslands where human activities are pronounced and inundation takes place annually (Andrew et al. 2012). This community is located near the edge of the valley, close to human settlements, and between tall and wooded grasslands along the river-mountain vegetation continuum. Next to *E. colona*, the native species *Paspalum scrobiculatum*, *Digitaria velutina*, *Hygrophila auriculata* and *Chamaecrista mimosoides* are common in this community. The marginal grasslands have a relatively large area and contain a large proportion (33 %, 115 species) of the plant species found in the wetland, allowing investigation of community properties, human-related disturbance and environmental factors that could potentially influence invasion of resident vegeta-

tion by alien species. Before the expansion of agriculture, the grasslands were important for wildlife, particularly during the wet season. Wildlife used the valley for grazing while indigenous people historically depended mainly on fishing for their livelihoods (Bakengesa et al. 2011). The wetland accommodates 75 % of the world's remaining puku antelopes (*Kobus vardonii*); a near threatened species (Ramsar 2013). Furthermore, the wetland is internationally recognized as an important bird area, supporting more than 300 bird species (Ramsar 2013). The Kilombero Game Controlled Area (KGCA), with high density of large mammals, such as elephants (*Loxodonta africana*), hippopotamus (*Hippopotamus amphibious*), buffalos (*Syncerus caffer*), common zebra (*Equus quagga*) and lions (*Panthera leo*), is located in the interior part of the valley (Starkey et al. 2002).

#### Focal species

*Echinochloa colona* (Junglerice, Poaceae) is a cosmopolitan invading annual grass species native to India, but widely distributed in the tropics and subtropics where it is thought to be introduced with rice seeds. It is often abundant on fertile soils, stream sides, rangelands and pastures, and on seasonally flooded landscapes, and prefers low altitudes (Phillips et al. 2003; McIntyre et al.

2005; CABI 2013). Experimental studies suggest that light is an important factor for seed germination and the species responds positively to nutrient addition (Chauhan and Johnson 2009). It produces abundant small seeds with a short dormancy period and long viability (up to 3 years). *Echinochloa colona* can reproduce vegetatively and in some areas it flowers throughout the year. All these traits make it a successful competitor and colonizer of disturbed habitats in agricultural systems and semi-natural environments (CABI 2013). Andrew et al. (2012) estimated that *E. colona* covered about 20 % of the Kilombero marginal grasslands. It is identified in literature as a noxious weed and an invasive species (Palmer and Maurer 1997; Dantsey-Barry 2002).

### Vegetation sampling

In total, sixty 20 × 50 m plots were randomly selected and surveyed between February and March 2010, to investigate the potential influence of community properties (biomass, richness, evenness and diversity), human-related disturbance and environmental conditions on the invasion of resident vegetation by *E. colona*. These plots were positioned on the north-eastern side of the Ramsar site where the valley forms mostly a peneplain. In this area, there are patches of rice farms that were avoided during the vegetation survey. Consequently, plots were laid on areas with only grassland dominance. In each plot, twenty 50 × 50 cm quadrats were randomly located and species identities recorded and cover estimated using the point intercept method (PIM) (Goodall 1952). A point intercept table (50 cm long, 50 cm wide and 50 cm high) was placed above each quadrat and a pin (3 mm diameter and 80 cm long) was inserted vertically through 25 points spread uniformly on the grid. Thus, the sample comprised a total of 500 (25 points × 20 quadrats) points per plot. The cover of each species was estimated by recording the number of contacts each species made with the pin. All contacts with the pin were recorded even if the same individual was in contact with the pin more than once (Frank and McNaughton 1990). Instead of counting individuals we used cover estimates for the *E. colona* abundance (i.e. from the PIM data), because the grasslands had dense cover and at the local scale *E. colona* form ramets and thus it is difficult to separate individual plants in the field. Most plant species were identified in the field and those that could not be identified therein were identified at the Arusha National Herbarium of Tanzania. Plant identification follows Haines and Lye (1983), Polhill (1988) and Beentje and Ghazanfar (2010).

### Environmental and human-related disturbance variables

To obtain an estimate of vegetation height, a modified glass disc (weight of 150 g, volume of  $8.6 \times 10^{-4} \text{ m}^3$ ) was dropped at the centre of each vegetation quadrat

from an upright position and when it stopped falling, the height of the vegetation above the ground was measured (Schaich et al. 2010). To estimate cow dung density in the 20 × 50 m plots, we counted dung within a subplot of 4 × 4 m around each of the 20 vegetation surveyed quadrats within each plot. To estimate grazing intensity we counted all grazed leaves that made contact with the pin during the vegetation survey in a quadrat. We measured elevation of plots (at the centre) using a hand held calibrated Global Positioning System (GPS). We used Landsat scene and GPS (Garmin 76 Cx) to determine distance between centre of plot and the Kilombero River. Points taken by GPS were overlaid onto the geo-referenced Landsat scene and using ArcView GIS 3.3 Software (Environmental Systems Research Institute 2002) distance was finally computed. Twenty soil cores (20 cm deep, 5 cm diameter) from the vegetation survey quadrats were bulked and mixed thoroughly to form a composite soil sample from each plot. Soil samples were analysed for soil moisture content and total organic carbon. To obtain soil moisture, a weight of fresh soil sample was measured and the sample was oven dried at 105 °C to a constant weight and then reweighed. Moisture content of the soil was calculated as a percentage of the dried soil weight. Prior to total organic carbon analysis, the soil samples were air-dried, ground in a mortar and sieved to <0.2 mm diameter after removing plant material (e.g. roots and debris). The soil was finally analysed for total C using wet digestion method (Walkley and Black 1934). The soil moisture, total organic carbon, distance to river, elevation, dung density, vegetation height and grazing intensity, together with Shannon-Wiener diversity, richness, evenness and biomass (Table 1) were finally used to explain variation in abundance of *E. colona* in the Kilombero wetland.

### Statistical analyses

Prior to data analyses we constructed two data sets to examine which of the community properties, human-related disturbance and environmental conditions that can influence the invasion of *E. colona* at different spatial scales. The first data set included the response (abundance of *E. colona*) and standardized explanatory variables collected at the small scale (quadrat). We computed species richness ( $S$ ), Shannon-Wiener diversity ( $H'$ ), evenness ( $E$ ) and biomass ( $B$ ) for all quadrats. To determine species richness in a quadrat, we added the number of species present in that quadrat. The Shannon diversity index was computed with *BiodiversityR* package following Kindt and Coe (2005) and evenness as  $E = H' / \ln S$  where  $S$  is the number of species in the quadrat (Magurran and McGill 2011). To estimate the biomass we used the sum of number of pin hits of resident species in a quadrat (Bråthen and Hagberg 2004). Prior to the analysis we checked for multicollinearity of



**Table 1** Plant community properties, environmental conditions and human-related disturbance variables recorded in 20 × 50 m plots (n = 60) in the Kilombero wetland Morogoro, Tanzania

Variables and units	Mean (± SD)	95 % confidence interval	Minimum	Maximum
Soil moisture (%)	10.1 ± 2.9	9.4–10.8	1.1	15.7
Total organic carbon (%)	2.1 ± 0.8	1.9–2.3	0.7	3.9
Elevation (m)	254.7 ± 8.3	252.6–256.8	245	280
Distance to river (m)	5219 ± 3873	4239–6199	430	14358
Cow dung density (no. 1000 m <sup>-2</sup> )	20 ± 33	11.6–28.3	1	223
Vegetation height (m)	0.17 ± 0.08	0.15–0.19	0.05	0.36
Grazing intensity <sup>a</sup> (no.)	50 ± 68	33.3–67.7	1	369
Diversity (no.)	1.53 ± 0.44	1.42–1.64	0.51	2.36
Richness (no.)	11 ± 3.56	10.1–11.8	4	19
Evenness (no.)	0.65 ± 0.14	0.61–0.68	0.25	0.89
Biomass (no.)	705.8 ± 258.81	640.3–771.3	88	1288

<sup>a</sup> Estimated from number of grazed leaves that made contact with the pin during cover estimation. “no.” shows dimensionless variables

**Table 2** Spearman correlation coefficients between community properties and environmental and human-related disturbance factors at Kilombero wetland, Morogoro, Tanzania

	Richness	Shannon evenness	Biomass	Soil moisture	Total organic carbon	Elevation	Grazing intensity
Richness							
Shannon evenness	0.19						
Biomass	<b>0.41 (0.33)</b>	–0.10					
Soil moisture	–0.04	–0.11	0.003				
Total organic carbon	–0.20	–0.13	<b>–0.27</b>	0.10			
Elevation	–0.10	–0.18	–0.002	0.17	<b>0.34</b>		
Grazing intensity	<b>–0.45 (–0.25)</b>	<b>–0.39</b>	–0.16	0.14	0.13	<b>0.31</b>	
Distance to river	<b>–0.41</b>	–0.13	–0.21	0.12	0.14	0.18	<b>0.44</b>

Values in parentheses are significant coefficients at small scale whereas other values are coefficients at large scale

Statistical significant correlations ( $P < 0.05$ ) are indicated with bold numbers. Units for predictor variables are as indicated on Table 1

all predictor variables, and diversity was highly correlated with richness and evenness (Spearman's correlation, all  $r_s \geq 0.63$ ,  $P < 0.05$ ) at small scale. We retained only richness and evenness since together they comprises the components of diversity (Magurran and McGill 2011). There were relatively low correlations among the grazing intensity, cow dung density and vegetation height (all  $r_s \leq 0.42$ ,  $P < 0.05$ ) at small scale and both dung density and grazing intensity were both used in the analyses as these human-related disturbances are known to facilitate invasions (Hobbs and Huenneke 1992). Initial analysis indicated that there was a non-linear relationship between *E. colona* abundance and standardized predictors in our small scale data set. Therefore, we employed generalized additive mixed models (GAMMs) to evaluate the relationships between the abundance of *E. colona* and predictor variables at small scale. Plots were used as random terms for GAMM analyses (Wood 2006). We used standard model-fitting and adequacy checking procedures to obtain an optimal model. Because the response is count data, log link function and Poisson error distribution were considered during modeling. We developed four candidate models describing the relationship between *E. colona* abundance and the predictors for small scale (Appendix 1). Each candidate model was fitted to the data using *mgcv*

package in R (R Development Core Team 2011), and model with the lowest Akaike information criterion (AIC) was chosen as the optimal one (Crawley 2007).

The second data set (for the large spatial scale analysis) included the same explanatory and response variables as above but these variables were computed per plot. We computed *S*, *H'*, *E* and *B* using total number of contacts per species over all quadrats per plot. All dung and number of grazed leaves were summed in plots and we used mean plot vegetation height in the analysis. Because there were high correlations among grazing intensity, cow dung density and vegetation height (all  $r_s \geq 0.67$ ,  $P < 0.05$ ) at large scale, only the grazing intensity was used in the large scale analysis. There were generally low correlations ( $r_s < 0.5$ ; Table 2) among the independent variables that we used to explain the abundance of *E. colona* in Kilombero wetland as recommended by Fox (2000). We used generalized additive models (GAMs) to examine the relationships between the abundance of *E. colona* and predictor variables for large scale analysis. Overdispersion was corrected using quasi-GAM modeling (Zuur et al. 2009) and we used generalized cross-validation (GCV) scores to obtain the best model (Appendix 2). We used cross-validation to estimate the amount of smoothing and during fitting, the degrees of freedom was also estimated (Wood 2006). We

**Table 3** The relationship between *Echinochloa colona* abundance and environmental factors, human-related disturbance and community properties at small scale in Kilombero wetland, Morogoro, Tanzania

Variables	Estimate	Std. error	<i>t</i> -value	<i>P</i> value
Parametric terms				
Intercept	0.785	0.157	4.997	< 0.001
Biomass	−1.171	0.059	−19.968	< 0.001
Smooth parameters				
Grazing intensity			16.604	< 0.001
Evenness			4.082	0.044

Results presented are from the most optimal model. For smoothing parameters, *t*-values are *F*-values showing significance of the smoothed effect. Only statistical significant relationships ( $P < 0.1$ ) are shown. Units for predictor variables are shown in Table 1

further confirmed the appropriateness of the selected optimal models to our data sets using standard diagnostic plots (Crawley 2007; Zuur et al. 2009). All statistical analyses were performed using R statistical software version 2.13.1 (R Development Core Team 2011).

## Results

### Variation of *Echinochloa colona* at small scale

*Echinochloa colona* abundance was negatively related to biomass of resident species at small scale (Table 3; Fig. 2a). The abundance of *E. colona* was not significantly related to species richness, cow dung density, elevation, soil moisture, total organic carbon and distance to river (Table 3). Abundance of *E. colona* appears to increase with grazing intensity (Fig. 2b). However, the cross validation estimated the degrees of freedom for the function to be 1.22 suggesting that there are some evidence of non linearity in that relationship (Fig. 2b). The abundance of *E. colona* decreased with the increase in species evenness at small scale (Fig. 2c). There was no interaction between environmental factors, human-related disturbance and community properties in explaining the abundance of *E. colona* at small scale (Table 3). Overall, grazing intensity and evenness and biomass of resident species explained almost 40 % of the variation (adjusted  $R^2 = 39.9$  %) in the abundance of *E. colona*.

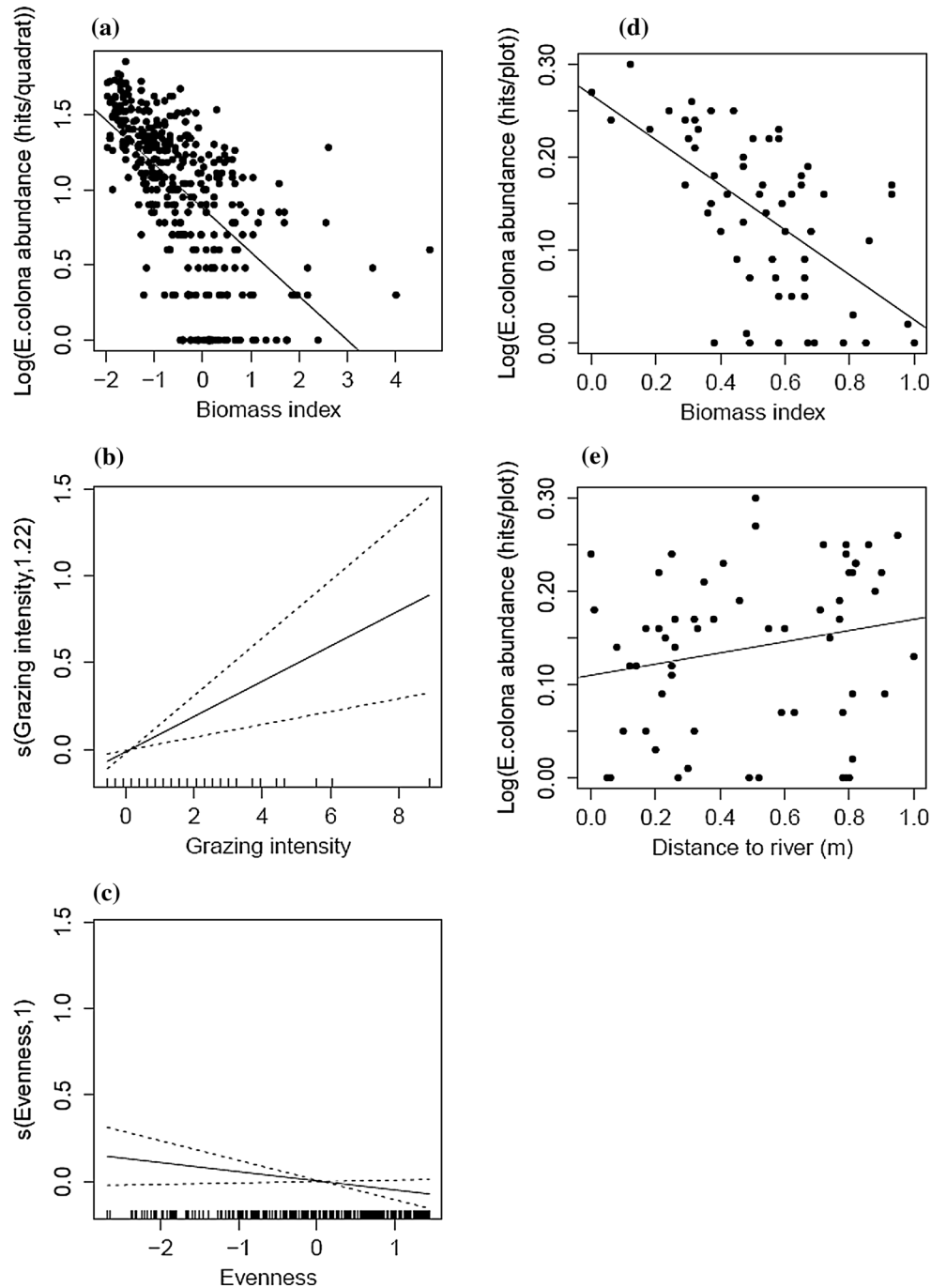
### Variation of *Echinochloa colona* at large scale

The abundance of *E. colona* was negatively related to the biomass of resident species (Table 4; Fig. 2d) while it was positively related to the distance to river at large scale (Table 4; Fig. 2e). Variation in abundance of *E. colona* at the large scale was not significantly related to soil moisture, total organic carbon, elevation, grazing intensity and richness and evenness of resident species (Table 4). There was no significant interaction between community properties, environmental variables and human-related disturbance in explaining the abundance of *E. colona* at the large scale (Table 4). The distance to

river and biomass of resident species accounted for over 55 % ( $R^2 = 55.4$  %) of the variation in the abundance of *E. colona*.

## Discussion

Our results showed a negative relationship between the abundance of *E. colona* and evenness of resident species on a small scale (Table 3; Fig. 2c). This agrees well with other empirical research from grassland systems as well as studies from other vegetation types, which suggest that communities with high evenness are less invulnerable (Hillebrand et al. 2008) due to either competition (Tilman et al. 1997; Huston 1999) or complementary resource use (Loreau and Hector 2001) or both effects (Fargione and Tilman 2005; Richardson 2011) among resident species. Moreover, using an experimental study it was demonstrated that increased dominance caused stronger invasibility of dicot invaders but had no effect on monocot invaders (Wilsey and Polley 2002), suggesting that increased evenness decreased invasibility of grasslands especially if local niches are filled by representatives from available functional groups (Mwangi et al. 2007). Additionally, in another study looking at how community properties (i.e. species richness and dominance) determined invasibility, it was shown that decreased dominance moderated invasibility of native grasslands while richness was not important for invasion resistance (Smith et al. 2004). Conceptually, this implies that increased evenness lead to higher invasion resistance (Hillebrand et al. 2008) possibly by more complete resource utilisation which increases competitive resistance (Huston 1999; Davis et al. 2001). Correlation analysis revealed that evenness was positively related to diversity ( $r_s \geq 0.63$ ,  $P < 0.05$ ) at the small scale. Therefore, a plausible explanation for the negative relationship between evenness and *E. colona* abundance could be that, areas of Kilombero wetland with relatively high native species evenness (and possibly diversity) may be less susceptible to species invasions because some of the native species (e.g. *Melinis minutiflora* and *Digitaria velutina*) may have traits and resource use patterns similar to the invader. Therefore these resident species confer ecosystem resistance to invasion by *E.*



**Fig. 2** Relationship between the abundance of *Echinochloa colona* and human-related disturbance and community properties at Kilombero wetland, Morogoro, Tanzania. Figures for grazing intensity ( $df = 1.22$ ) and species evenness ( $df = 1.00$ ) show estimated smoothing curves. *Solid lines* are the smoothers whereas

the *dotted lines* represent the 95 % confidence bands. The degrees of freedom show curviness (or bendiness) of the smoothers. **a–c** show important variables for small scale analysis while **d** and **e** indicates significant variables for large scale analysis, respectively

*colona* through complete niche occupation and intense competition (Fargione and Tilman 2005; Mwangi et al. 2007). Consequently, our first prediction that species richness would be important for explaining invasion of *E. colona* at the small spatial scale is not supported.

Biomass of resident species predicted the invasion of *E. colona* at both small and large spatial scales (Tables 3,

4; Fig. 2a, d). This is in line with other studies, which have also found that species or functional groups with particularly high biomass substantially increase community resistance to invasions (Borman et al. 1991; Symstad 2000). Moreover, these findings have also later been supported by Lulow (2006), who found that the biomass of native species reduced the invasibility of

**Table 4** The relationship between *Echinochloa colona* abundance and environmental factors, human-related disturbance and community properties at large scale in Kilombero wetland, Morogoro, Tanzania

Variables	Estimate	Std. error	<i>t</i> -value	<i>P</i> -value
Parametric terms				
Intercept	6.194	0.272	22.862	< 0.001
Biomass	−2.973	0.453	−6.569	< 0.001
Distance to river	0.617	0.328	1.881	0.065

Results presented are from the most optimal model. Only statistical significant relationships ( $P < 0.1$ ) are shown. Units for predictor variables are shown in Table 1

remnant grass species in the Central Valley, CA, USA. In the same experiment it was demonstrated that plots with higher native grass species richness did not reduce invasion but biomass reduced the susceptibility to community invasion (Lulow 2006). Experimental studies (e.g. Chauhan and Johnson 2009) suggest that light is important for germination of *E. colona* species. Thus in Kilombero, intensive competition for light and possibly space may have caused the negative relationship between *E. colona* abundance and resident species biomass (Tilman et al. 1997). It has been suggested that species interactions tend to be higher as species produce high biomass and thus at Kilombero greater resistance to plant invasion may be a result of complementary resource use, competition and high biomass among resident species (Borman et al. 1991; Huston 1999; Orwin et al. 2013).

At the small scale, abundance of *E. colona* was positively related to grazing intensity (Table 3; Fig. 2b). Grazing is important for plant community structure and dynamics in areas frequently grazed, such as pastures and rangelands (Milchunas et al. 1988). It has been suggested that many invasive species are either opportunists or generalists (Zedler and Kercher 2004), and take advantage of the enhanced niche opportunities created by grazing disturbance (Shea and Chesson 2002; Richardson 2011). In general, grazing creates gaps, compact soils and reduces the vigour of resident species (Hobbs and Huenneke 1992; Teuber et al. 2013). All these ecological processes may directly or indirectly favour the invasion of plant invaders, such as *E. colona*. We predicted that grazing intensity would be important for large scale invasion of *E. colona* but since the grazing intensity is important for invasion at small scale, our prediction is thus only partially supported. This may suggest that in relatively highly disturbed areas such as ours, human-related disturbances such as grazing may still contribute to the successful invasion of alien species at small spatial scales as also noted by other authors (e.g. Hobbs and Huenneke 1992; Altman and Whitlatch 2007).

Distance to river was positively related to the abundance of *E. colona* at the large scale, suggesting that as you move away from the river, *E. colona* abundance increases. Both the flooding and grazing disturbance may explain this relationship. Flooding, which increases with proximity to the river, is important for maintaining

native vegetation in wetland systems (Moran et al., 2008; Keddy 2010; Andrew et al. 2012; Andrew 2014). Since *E. colona* cannot tolerate prolonged inundation (CABI 2013) it is less abundant in flood prone areas near the river. Human-related disturbances, particularly livestock grazing, tend to increase as you move away from the river (Starkey et al. 2002; Table 2). *Echinochloa colona* is known to be abundant on highly disturbed soils and fertilized sites in grassy woodlands of Australia (McIntyre et al. 2005). Since *E. colona* prefers mesic, nutrient rich and disturbed areas, grasslands sites away from the river favour the establishment of this invasive species in the Kilombero valley (Phillips et al. 2003; CABI 2013). Thus, our prediction that distance to river would be important for large scale invasion of *E. colona* is supported.

We predicted that different factors would influence the invasion of *E. colona* at different spatial scales. Indeed, our results suggest that grazing intensity, biomass and evenness of resident species are all explaining variation in *E. colona* abundance at the small scale, whereas biomass and distance to river was important at a large spatial scale. These results support the assertion that different factors contribute to alien species invasions at different spatial scales (Fridley et al. 2007; Davis 2009) but, biomass is important at both spatial scales. In this study we have demonstrated that although evenness is rarely considered in diversity–invasibility studies (Mattingly et al. 2007; Hillebrand et al. 2008) it may be generally important (Hillebrand and Matthiessen 2009). Species evenness can potentially buffer native communities against invasion better than richness which is more commonly used in invasion studies (e.g. Symstad 2000; Meiners et al. 2004; Fridley et al. 2007), because the relative abundances (of species) can account for more variance than the absolute numbers of species in community diversity (Wilsey et al. 2005). It is therefore important to consider species evenness in community ecology studies such as diversity–invasibility relationships to better our understanding of biological invasions (Mattingly et al. 2007) and general functioning of native plant communities (Hillebrand and Matthiessen 2009; Orwin et al. 2013). Although we did indeed find that the abundance of *E. colona* decreased with evenness and biomass of resident species and increased with distance to river and grazing intensity, our results should be treated with caution since our study is observational. We



cannot make a strict conclusion about causal relationships. To conclude firmly on causal relationships one would have to conduct experiments.

### Conclusions and management considerations

Wetlands provide numerous vital ecosystem goods and services and their importance is increasingly appreciated in the face of global climate change. However, wetlands are landscape sinks where a combination of multiple disturbance factors (e.g. debris depositions and livestock grazing), high moisture and nutrient levels, make them vulnerable to alien species invasions (Zedler and Kercher 2004; Ehrenfeld 2008). Upon successful invasions, wetland invaders often form monotypic stands of vegetation with altered habitat structure, plant community diversity; food webs and reduced overall biodiversity (see review by Vilà et al. 2011). Generally, these effects following successful plant invasions tend to accumulate over time and eventually wetland functions, including provision of ecosystem goods and services (e.g. purification of water and biodiversity support), dwindle (Millenium Ecosystem Assessment 2005). *Echinochloa colona* is widespread in Kilombero and its effects are likely to be associated with its dominance (Pyšek and Pyšek 1995) and consequences of further dispersal may be deleterious in the long run, if not counterchecked by management interventions in this system. Identification of factors that influence the success of invaders is a key step towards effective management of alien species invasions in wetland systems (Blackburn et al. 2011). Overall, this study suggests that community properties, particularly biomass and evenness of resident species and human-related disturbance (through grazing) may influence the abundance of *E. colona* in the Kilombero wetland. Therefore, effective management strategy should consider mitigations that can increase the biomass and evenness of native species and reduction of grazing pressure to restore the wetland. Such mitigations would typically reduce dominance of invasive species and restore ecosystem services, which are of great importance to biodiversity conservation and livelihoods (Millenium Ecosystem Assessment 2005). Thus, to increase biomass and evenness of native species, active

restoration through planting of herbaceous native species (e.g. grasses) could be considered. However, this would require a careful and systematic selection of native species with competitive-dominant traits that will be able to compete with non-native species and resist invasions by alien species. These efforts together with the decrease in grazing pressure would ultimately support the recovery of Kilombero Ramsar site. Recent studies show that cattle grazing in Kilombero is high and increasing (Ntongani and Andrew 2013; Andrew 2014). Therefore new management strategies should be evaluated. One strategy that has had success in Australian rangelands is the so-called cell grazing where animals are moved between cells (commonly fenced areas) over short time durations (Richards and Lawrence 2009). Cell grazing involves intensive pasture monitoring that may be difficult in Kilombero. On the other hand, the traditional practice of herding in Kilombero may facilitate the introduction of a similar management regime. Since cell grazing has been shown to improve rangeland quality by reducing undesirable plant species (e.g. weedy and unpalatable species), and increase palatable and native plant species as well as vegetation cover (McCosker 2000; Richards and Lawrence 2009), it could be employed at Kilombero. Further studies are needed to better understand the impact of *E. colona* and long term plant community-invader-human disturbance dynamics in the wetland system.

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### Appendix 1

See Table 5.

**Table 5** Assessment of the four candidate models whereby model 1 with the lowest Akaike information criterion (AIC) is considered the most optimal model explaining the relationship between the abundance of *Echinochloa colona* and community properties, human-related disturbance and environmental conditions at small scale in Kilombero wetland, Morogoro, Tanzania

Model number	Candidate model	AIC	R <sup>2</sup> (%)
1	<i>E. colona</i> abundance = Biomass + smoother function (evenness) + smoother function (Grazing intensity), family = quasipoisson	3948.986	39.90
2	<i>E. colona</i> abundance = Biomass + Grazing intensity + smoother function (evenness), family = quasipoisson	3950.968	39.90
3	<i>E. colona</i> abundance = Richness + evenness + smoother function (Grazing intensity), family = quasipoisson	3985.226	4.61
4	<i>E. colona</i> abundance = Richness + smoother function (evenness) + smoother function (Grazing intensity), family = quasipoisson	3995.073	4.82

Explained variation (adjusted R<sup>2</sup>) is also given for every model

## Appendix 2

See Table 6.

**Table 6** Assessment of the four candidate models whereby model 2 with the lowest generalized cross-validation (GCV) scores and explains relatively more variation is considered the most optimal model explaining the relationship between the abundance of *Echinochloa colona* and community properties, human-related disturbance and environmental conditions at large scale in Kilombero wetland, Morogoro, Tanzania

Model number	Candidate model	GCV score	$R^2$ (%)
1	<i>E. colona</i> abundance = Distance to river + smoother function (Biomass), family = quasipoisson	96.24	54.10
2	<i>E. colona</i> abundance = Biomass + Distance to river, family = quasipoisson	96.24	55.40
3	<i>E. colona</i> abundance = Distance to river + smoother function (Biomass) + smoother function (Distance to river x species richness), family = quasipoisson	99.02	54.01
4	<i>E. colona</i> abundance = smoother function (Biomass x Distance to river), family = quasipoisson	96.24	54.01

Explained variation (adjusted  $R^2$ ) is also given for every model

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