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Vascular plant diversity in Southeast Asian rice ecosystems is determined by climate and soil conditions as well as the proximity of non-paddy habitats

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Abstract

Rice ecosystems vary greatly in climate, edaphic conditions, landscape heterogeneity, agricultural management and biodiversity. However, ongoing land use intensification and conversion to large-scale monoculture are threatening this diversity. We analyzed how rice-growing regions in Southeast Asia differ in diversity and composition of vascular plants in paddy rice ecosystems, and how the local and regional biodiversity of these plants is determined by variations in abiotic conditions, habitat type (paddy vs. bunds) and the proximity of non-paddy habitats. The vegetation of paddies and their bunds was surveyed in seven important rice production regions located in highlands and lowlands of Vietnam and the Philippines. Within the regions we sampled 67 pairs of study sites comprising a total of 122 paddies and 134 bunds. We identified major drivers of field-level weed diversity (alpha diversity) separately for bunds and paddies. Species turnovers (beta diversity) across sampling sites, between paddies and their bunds, and between regions were visualized using the Bray-Curtis coefficient of dissimilarity and DCA ordinations. Species richness on bunds was mainly influenced by the proximity of non-paddy habitats, mean annual temperature and soil acidity. Soil moisture was the decisive factor for the variation in paddy weed richness. In both habitat types, Shannon diversity and the number of insect-pollinated plants showed patterns similar to species richness. Regional differences in plot species richness were stronger on bunds than in paddies. Species turnover was high among habitat types and between upland and lowland regions. Future ecological engineering approaches can build on our findings to promote pollination services more efficiently in Southeast Asian rice landscapes.

Keywords

Agro-ecosystems; alpha diversity; insect-pollinated plant species; irrigated rice production; Philippines; rice weeds; species turnover; Vietnam

Abbreviations

AIC = Akaike Information Criterion, DCA = detrended correspondence analysis, GLMM = generalized linear mixed-effects model, H = Shannon diversity, LME = linear mixed-effects, PH = Philippines, SD = standard deviation, S_{ipo} = number of entomophilous (i.e. insect-pollinated) plants, S = species richness, VIF = variance inflation factor, VN = Vietnam

Main text

1. Introduction

The world's population is predicted to reach 9.8 billion in 2050 (United Nations, 2017). Population growth, changes in consumption habits and augmented bioenergy use are likely to increase the global demand for agricultural products during the coming decades (Alexandratos and Bruinsma, 2012; Foley et al., 2011; Martin and Sauerborn, 2013). In Southeast Asia, about 32% of the terrestrial surface is already covered by agricultural land, ca. 28% is used to produce crops (FAO, 2020). Rice is the most important food crop and main source of income in rural areas (GRiSP, 2013). In 2018, 50 million ha were cultivated with rice in Southeast Asia (FAO, 2020). Further agricultural expansion is at the expense of valuable natural and semi-natural habitats and associated organisms, and conventional land-use intensification dramatically threatens farmland biodiversity (Cunningham et al., 2013; Foley et al., 2011; Kehoe et al., 2017; Newbold et al., 2015; Tilman et al., 2017). Agrobiodiversity plays a crucial role in maintaining essential ecosystem functions and services in agro-ecosystems like pest control, crop pollination, maintenance of soil fertility and water quality, erosion control, aesthetic and cultural values, provision of food, fodder, biofuels and fibers etc. (Altieri, 1999; Martin and Sauerborn, 2013). In general, higher plant species richness augments the spectrum of resources like nectar, pollen and habitats, and probably leads to a higher resilience against disturbances in agro-ecosystems. But if intensification continues over the next few decades as predicted, the global biodiversity value of agricultural lands will be substantially reduced (Egli et al., 2018).

Wild rice domestication began probably about 9000 years ago and rice is now grown in irrigated paddies, or in rainfed lowland, rainfed upland and flood-prone ecosystems (Khush, 1997). Paddy rice production systems consist of three main habitat types (Bambaradeniya and Amerasinghe, 2003): the paddy (or field proper), the bund (levee) and the ditch (water supply canal). Together these habitat types form a mosaic of potentially high ecological, economical and socio-cultural value (GRiSP, 2013). Paddies have mostly small local plant species pools (Miyawaki, 1960), often reduced by weed control, whereas the vegetation on bunds is usually more abundant and speciose (Fried et al., 2018). Both habitat types host a variety of globally rare species (Fried et al., 2017, 2018; IUCN, 2015; Nowak et al., 2015). In total, more than 1,800 plant species associated with rice cultivation were listed for South and Southeast Asia alone (Moody 1989). How this enormous plant diversity varies along environmental and spatial gradients and which drivers cause species loss is not well understood. The drivers of the Southeast Asian rice weed diversity are scale-dependent due to complex, multi-levelled agro-ecological patterns and processes. Despite recent research on the species composition in South and Southeast Asian rice weed communities (Fried et al., 2017, 2018; Kumalasari, 2014; Nowak et al., 2015, 2016), the factors underlying species diversity across habitats and regions remain to be determined. Besides climate, altitude, edaphic conditions and agricultural management, the surrounding landscape (e.g. the proximity of non-paddy habitats) may turn out to be a decisive factor for alpha, beta and gamma plant diversity in rice production systems. Lately, several studies examined the effects of the surrounding landscape on the plant diversity of agricultural areas, mainly in the Mediterranean (e.g. Armengot et al., 2011; Bassa et al., 2011; José-María et al., 2010) or temperate regions (e.g. Gabriel et al., 2005; Poggio et al., 2013; Roschewitz et al., 2005). Similar studies from tropical or subtropical rice fields are scarce and are inconclusive with respect to the effects of the proximity of non-crop habitats on weed diversity (Kumalasari, 2014; Zhou et al., 2018). In this study, we analyze how local and regional-scale factors determine vascular plant diversity in tropical paddy rice agro-ecosystems. We sampled plant species in seven regions of Southeast Asia and covered three spatial levels: plots, landscapes and regions (in order of increasing area). We addressed the following questions: (a) What are the abiotic conditions and surrounding landscapes in the local paddy rice agro-ecosystems and what is their relative importance for vascular plants? (b) How and to which extent do plant diversity and composition differ within a region, between the paddies and their bunds, and across regions?

2. Methods

2.1 Study regions and experimental design

Our study regions, scattered over extensive areas in Southeast Asia, encompass considerable variation in climate, landscape heterogeneity, edaphic conditions, agricultural management and biodiversity. We surveyed four study regions in Vietnam (VN) and three in the Philippines (PH), each covering 15 × 15 km (Fig. 1, Table 1).

The Vietnamese regions were located in the Mekong Delta in the southern province Tien Giang (VN4), and along the Red River in the northern provinces of Hai Duong (VN1), Vinh Phuc (VN2) and Lao Cai (VN3), between sea level and 1,390 m. The tropical to subtropical monsoon climate has a wet season from May to September dominated by southeasterly winds and a dry season caused by northeasterly winds between October and April. The southern Mekong Delta is characterized by warm-humid conditions all year round whereas temperatures in the subtropical north are cooler during the dry season. Less warm summers and cool winters are typical in the northwestern mountains, although the local climate varies considerably. Mean annual temperatures range from 16 °C (Lao Cai) to 28 °C (Tien Giang), where mean annual precipitation differs between 2,500 mm and 1,500 mm, respectively (Rivas-Martinez and Rivas-Saenz, 1996-2009; Sterling et al., 2008; Vân, 2016).

The three Philippine study regions range from sea level to 1,095 m and are located on Luzon Island in the provinces of Laguna (PH1), Nueva Ecija (PH2) and Ifugao (PH3). The tropical climate is characterized by the southwest monsoon causing a wet season from May to October, and the northeast monsoon bringing the dry season between November and April. Local climates have relatively constant temperatures throughout the year, but vary in rainfall seasonality. Mean annual temperatures range from 19 °C in the mountains of Ifugao to 28 °C in the lowlands. Mean annual precipitation varies between 1,800 mm (Nueva Ecija) and 3,700 mm (Ifugao). Tropical cyclones occur frequently between July and November (Coronas, 1920; CRU, 2008; GRiSP, 2013).

Rice weed management and cultivation practices differ most strongly between lowland and upland regions rather than between countries (De Datta 1981; GRiSP 2013; Fried et al. 2017, 2018): rice is usually harvested twice a year in lowland regions, whereas the mountain climate allows for only one crop cycle per year. Intensive manual labor, the use of traditional upland rice cultivars and reduced or zero input of synthetic herbicides and fertilizers are further characteristics of the traditional upland rice farming systems in Ifugao (PH3) and Lao Cai (VN3). Besides, weeds and the uppermost soil layer are typically removed from the upland bunds prior to the transplanting of rice seedlings, and the use of water buffalos for puddling and harrowing of paddies is still common. In contrast, lowland farmers mostly use machinery and apply synthetic products for pest control and fertilization. Particularly Tien Gang (VN4) is characterized by high chemical input, vast monoculture areas and three crop cycles per year. In Laguna (PH1), bund weeds are subject to frequent cutting, but herbicides are used less than in other lowland regions. For further details on land-use, structural heterogeneity and soil characteristics of the study regions, see Klotzbücher et al. (2015).

We employed a paired study design to detect scale-dependent effects of abiotic conditions and surrounding landscape on the vegetation. In the following, the term “rice field” refers to the entity of a paddy and its bunds, whereas each “site” comprised a rice field irrespective of whether only the vegetation of its bunds or also of its paddy was surveyed during the study. The study sites were selected preferentially according to their accessibility and approachability of farmers during the sampling period. In total, we selected five to eighteen pairs (landscape level) of study sites (plot level) in each region (regional level), resulting in 134 sites, 67 pairs and 7 regions (Table 1). Each pair of sites comprised one monoculture site that was entirely surrounded by rice fields, and one structurally more diverse site that shared at least one border with one or more non-paddy habitats (such as agroforests, gardens or grasslands) resulting in "diverse" surroundings (and representing an enhanced habitat diversity). Distance between sites ranged from 40 m to 590 m (mean ± SD: 244 ± 120 m).

2.2 Vegetation survey

The vegetation survey was conducted within the framework of an interdisciplinary research project on sustainable rice production (LEGATO; Settele et al., 2018). We established a total of 256 vegetation plots (122 in paddies, 134 on bunds), comprising 16 to 70 plots in each of the seven study regions (Table 1). Twelve paddies were abandoned or the crop had changed during the sampling period although the corresponding bunds had already been sampled. Every plot was sampled once between 2012 and 2015, either during wet or during dry season. Vascular plant species were recorded with their cover/abundance values using the nine-class Braun-Blanquet scale (Reichelt and Wilmanns, 1973). In each paddy, all vascular plant species were recorded in a representative rectangular plot of 20 m^2. Five 2 m^2 subplots were randomly selected on the bunds, stratified as to sample the vegetation at least once on each side of the paddy, because of their variation in width, shape and stability. Cover-abundance values were transformed into percentages (r = 0.1, + = 0.5, 1 = 2.5, 2m = 2.5, 2a = 10, 2b = 20.5, 3 = 37.5, 4 = 62.5, 5 = 87.5) (Dierschke, 1994). The species inventory of the five subplots was pooled and percentages were averaged to represent plots of 10 m^2 size per bund. Altitude and geographical coordinates were determined by GPS device (Garmin eTrex Vista® HCx) in the center of each study site.

The following works were used for plant identification: Cook, 1996; eFloras, 2008; Harada et al., 1987, 1993; Ho, 1999, 2000, 2003; Le, 2007; Nguyen, 2002; Nguyen and Nguyen, 2007; Pancho and Obien, 1995; Soerjani et al., 1987. Voucher specimens of each plant species were collected and stored in GOET (Herbarium of the University of Göttingen). The taxonomy follows The Plant List (2013).

2.3 Environmental variables

Mixed soil samples were collected (10-20 cm depth) from five randomly selected spots per plot and analyzed in laboratories of Göttingen University and the Helmholtz Centre for Environmental Research – UFZ. A conductivity gauge of the type pH538 (WTW GmbH) was used to measure the electrical conductivity (*EC*) in the supernatant suspension of a 1:2.5 soil:H_2O mixture, before assessing the soil pH with a pH meter of the type pH358 (Krannich GmbH & Co.KG). Contents of C_{org} and N_{total} were measured with the Dumas combustion method using a VARIO MAX (elementar), afterwards humus content was estimated ($C_{org} \times 1{,}725$). Texture was determined on a moist sample of fine earth and through visible characteristics (FAO, 2006). Soil moisture was categorized into four levels by visual inspection: 1 - moist but solid soil; 2 - wet and soft soil; 3 - very wet and muddy soil with interspersed puddles; 4 - flooded soil completely covered by water. Fanny Langerwisch from the Potsdam Institute for Climate Impact Research supplied monthly mean temperatures from the years 2001-2006 based on a time-series dataset (CRU TS 3.0) provided by CRU et al. (2008). The local landscape surrounding each site (variable *LandSur*) was assessed categorically according to the presence (at diverse sites) or absence (at monoculture sites) of non-paddy habitats in their direct proximity. Regional land use intensity and structural diversity classes were taken from Settele et al. (2013).

2.4 Data analyses

All statistical analyses were done in R (version 3.5.2; R Core Team, 2018). Cultivated species were disregarded. Data of bunds and paddies were treated separately. We used linear mixed-effects models (LME, 'lme4' package version 1.1-19; Bates et al., 2015) with a Gaussian error distribution or generalized linear mixed-effects models (GLMM) with a Poisson error distribution during an explorative model selection process to identify predictor variables with highest explanatory value and significant effect (p < 0.05) on our response variables species richness (S), Shannon diversity (H), and the number of entomophilous plants (insect-pollinated species, i.e. all vascular plants except *Equisetaceae*, *Urticaceae*, graminoids, ferns and submerged hydrophytes; S_{ipo}). Corresponding to the final model residual diagnostics, we decided to use the Poisson GLMM for responses S and S_{ipo} in paddies (count data), and Gaussian LME for S and S_{ipo} on bunds and H in both habitat types. The used predictors were *LandSur*, *MeanTemp*, *pH*, *EC*, *C/N*, *Humus*, *Moisture* (only for paddies) and *Texture* (only for bunds). Correlation among response variables was tested using Kendall's correlation coefficient τ. We did not incorporate altitude in our models due to a correlation with mean annual temperature ($\tau = -0.18$, $p < 0.001$). The variables *Region* and *Landscape* were treated as nested random effects to account for the non-independence of sites within landscapes (or pairs, respectively) and regions. Continuous predictor variables were standardized (mean = 0, SD = 1). All variables are listed in detail in Table 2, correlation matrices are given in Appendices B.7 and B.8 of the Supplementary material. Model selection was based on Akaike's Information Criterion (AIC) and residual diagnostics according to Zuur et al. (2010). We used forward selection as former global tests with models including all predictors performed significantly better than their corresponding null models (cf. Blanchet et al., 2008). Predictors that led to the strongest decrease in AIC were included first into our models. We checked for interactions with already included fixed effects before including remaining predictors or their interactions into existing models. Heteroscedasticity and distribution of residuals were checked visually in diagnostic plots for each model. Collinearity among predictors was detected using variance inflation factors (VIFs, 'car' package version 3.0-6; Fox and Weisberg, 2019), with all VIFs < 2 accepted in the final model (Zuur et al., 2010). Fitted Poisson-GLMMs were not overdispersed. We assessed conditional R^2 ('performance' package version 0.4.4; Lüdecke et al. 2020) and marginal R^2 ('r2glmm' package version 0.1.2; Jaeger 2017) for each model before assessing partial R^2 ('r2glmm' package) of corresponding predictors. Explained variances of random terms were calculated manually as the proportion of the total variance of the random effects models. Means of the predictors depending on *LandSur*-levels, habitat types or regions were compared using Two Sample t-Tests if the data was normally distributed, or Wilcoxon-Mann-Whitney tests if non-normally distributed. Pairwise Wilcoxon Rank Sum tests were used for pairwise comparisons of species richness between regions or moisture levels with corrections for multiple testing (Holm).

Analyses of species turnover and composition were performed with the 'vegan' package (version 2.5-4; Oksanen et al., 2019). Singletons and doubletons were eliminated from the dataset before excluding plots without weeds. The terms alpha and beta diversity refer to a wide variety of phenomena with various spatial scales (Tuomisto, 2010a). We use these terms as follows: alpha diversity equals the species diversity (S, S_{ipo} or H) on the plot level, beta diversity quantifies the variation in species composition of plots within a region, between bunds and paddies (across all regions) or between the seven regions. To quantify the compositional dissimilarity between different plots we used the Bray-Curtis coefficient (Bray and Curtis, 1957), which ranges between 0 (species composition and abundances between two plots are identical) and 1 (two plots do not share any species). Species turnover within regions (β_{intra}) was calculated with Bray-Curtis dissimilarities between plots based on original species cover-abundances. Regional means were calculated by averaging all β_{intra} values of the corresponding region (mean of all site pairs). Species turnover between regions (β_{inter}) was calculated with Bray-Curtis dissimilarities based on the mean cover-abundance of each species in a region. We also performed detrended correspondence analysis (DCA) on the square root-transformed species data to use the length of axis 1 as a direct measure of species turnover (c.f. Tuomisto 2010b) and to visualize differences in species composition between regions and habitat types.

Kendall's correlation coefficient τ was used to test for correlations of alpha diversity (S, S_{ipo} and H) between bunds and paddies of the same study site, and between regional means of plot-level species richness and beta diversity (Bray-Curtis dissimilarities between plots) in both habitat types.

3. Results

3.1 Floristic diversity

A total of 315 plant taxa (117 in paddies, 305 on bunds) were recorded in the studied rice landscapes, belonging to 98 genera and 63 families. We recorded 198 species (or 63% of the total species) exclusively on bunds, ten species (3%) occurred only in paddies and 108 species (34%) in both habitats (Appendix A.1 Supplementary material). Ten species were cultivated (mostly intercropped on bunds), 193 species are insect-pollinated and 97 species are red-listed as of “Least Concern” (IUCN, 2015). About 40% of all taxa were recorded less than three times. The mean number of species recorded per plot averaged 27.8 ± 11.7 species on bunds (range: 0-53) and significantly less ($p < 0.001$) in paddies ($S = 6.5 \pm 5.8$, range: 0-29). Species richness was highly correlated with H ($\tau = 0.60$, $p < 0.001$) and S_{ipo} ($\tau = 0.85$, $p < 0.001$) on bunds, and likewise with H ($\tau = 0.80$, $p < 0.001$) and S_{ipo} ($\tau = 0.86$, $p < 0.001$) in paddies. Species richness was also correlated between bunds and paddies of the same study site ($\tau = 0.34$, $p < 0.001$), as were H ($\tau = 0.21$, $p = 0.002$) and S_{ipo} ($\tau = 0.39$, $p < 0.001$).

3.2 Effects of local surroundings and abiotic conditions on the plant diversity of bunds

Surrounding landscape (monoculture vs. diverse; *LandSur*), mean annual temperature and soil pH showed the strongest effects on the plant species richness of bunds (Fig. 2, Table 3, Appendices A.2, A.3 and B.1 Supplementary material). Bunds that were in proximity of non-paddy habitats showed higher species richness (32 ± 10.5, range 0-53) than those that were not (24.9 ± 11.8, range 0-46, $p = 0.001$). Mean annual temperature had the second most prominent effect and an additional negative effect in interaction with rice monoculture around sites. Below a threshold of about 21 °C, rising temperatures clearly reduced species richness, almost independently of the surrounding landscape, whereas above this point, the decrease in species richness was mitigated in diverse sites (Appendix B.2 Supplementary material). Decreasing soil pH generally enhanced species richness on bunds, although this predictor showed the weakest significant effect in our model (Appendix B.3 Supplementary material).

Regional differences in species richness were strong, ranging from a mean of 38.7 ± 7.1 species on bunds in VN2 to 7.5 ± 10.5 species on bunds in VN4 (Fig. 3a, Table 4, Appendix A.3

Supplementary material). The patterns found for species richness depending on surrounding landscape, mean annual temperature and soil pH were clearly bound to region-specific effects. For example, regions with cooler mean annual temperatures (i.e. VN3 and PH3) supported fields with higher and less variable species richness, almost irrespective of the surrounding landscape (Appendix B.2 Supplementary material), whereas variation in species richness in relation to soil pH was higher at monoculture sites of these regions, but remained relatively stable between monoculture and diverse sites in all other regions (Appendix B.3 Supplementary material).

Models with H and S_{ipo} as response variables showed weaker but mostly similar patterns, although the effects of variable soil pH were not significant (Fig. 2, Table 3, Appendices B.4 and B.5 Supplementary material). Bunds in proximity of non-paddy habitats had in average a higher Shannon diversity (mean: 2.4 ± 0.5) compared to monoculture sites (mean: 2.1 ± 0.8), and also higher richness of entomophilous plants ($\text{mean}_{\text{diverse}}$: 18.0 ± 6.8 and $\text{mean}_{\text{monoculture}}$: 13.4 ± 7.0, respectively). Again, H and S_{ipo} were reduced with rising mean annual temperatures, especially at monoculture sites, and varied among the study regions.

3.3 Effects of local surroundings and abiotic conditions on plant diversity in paddies

The only significant effects on the plant diversity in the paddies were related to soil moisture content (Fig. 4, Table 5, Appendices A.2 and A.3 Supplementary material). We observed differences in species richness among all four moisture levels, but not all levels differed significantly from each other ($p < 0.05$). We recognized comparable patterns in the models with H or S_{ipo} as response variables, though effects on H were weaker (Table 5, Appendix A.3 Supplementary material). Plant species richness ranged from 1.8 ± 1.3 in VN4 paddies to 11.4 ± 4.9 in PH1 paddies, and was more balanced between regions compared to the bunds, though some significant regional differences were found (Table 4, Fig. 3b). In paddies, regional differences of H and S_{ipo} are again comparable to those of species richness (Appendices B.4 and B.5 Supplementary material).

3.4 Species turnover

The regional means of the Bray-Curtis dissimilarities among plots (mean β_{intra}) were on average lower between bunds (mean: 0.70 ± 0.06) than between paddies (mean: 0.82 ± 0.07). The highest species turnover was observed between bunds of PH1, and the lowest in VN3. In the paddies, VN2 showed the highest mean β_{intra} and VN4 the lowest (Table 4). Mean species richness showed no significant correlation with mean β_{intra}, neither on bunds ($\tau = -0.61$, $p = 0.069$) nor in paddies ($\tau = 0.24$, $p = 0.56$).

Bray-Curtis dissimilarities among regions (β_{inter}) were also generally lower on bunds (mean: 0.74 ± 0.09) than in the paddies (mean: 0.85 ± 0.08). Highest dissimilarities were found between upland and lowland regions: on bunds between PH1 and VN3, and in paddies between VN3 and VN4 (Table 6). Regions VN1 and VN2 showed the most similar species composition on bunds as well as in paddies.

The DCA showed a clear distinction in the species composition of the two habitat types (Appendix B.6 Supplementary material): site scores of the bunds are located on the mid to lower left side whereas the paddy scores are spread on the mid to upper right side. Perpendicular to this separation line (from the upper left to the lower right corner of the graph), site scores are aligned in more or less vertical stripes according to their regional affiliation, and thus, highlight the regional differentiation in species composition. An axis length of 5.07 (DCA1) also indicates a complete species turnover along the first axis, and hence between the two habitat types and among the seven regions.

4. Discussion

We showed that the local plant diversity can be linked to different abiotic conditions and the presence or absence of non-paddy habitats in proximity of the study sites. Further on, regions and habitat types differ in diversity and composition of rice weeds.

4.1 Drivers of rice weed diversity on bunds

The species richness on bunds was mainly influenced by the surrounding landscape, mean annual temperature and soil acidity. The close proximity of other habitat types was the key driver of the plot-level plant diversity (alpha diversity) on rice field bunds probably due to propagule influx from adjacent habitats (mass effect; Shmida and Wilson, 1985). Species pools on bunds might profit from the immigration of plants through dispersal from adjacent areas. Such neighborhood effects on plant diversity were described from temperate wheat fields (Gabriel et al., 2005) and subtropical areas dominated by rice and other crops (Zhou et al., 2018). In Indonesia, species richness on bunds with other crops or trees and in multiple-crop landscapes was higher than on ordinary bunds and in monoculture landscapes (Kumalasari and Bergmeier, 2014). In our study regions, species richness is reduced by on average almost 20% in monoculture landscapes, whereas effects on Shannon diversity and the number of entomophilous plants were slightly weaker. In homogenous landscapes, plant diversity levels might also be more prone to indirect negative effects of other variables: monoculture sites showed generally stronger decreases in species richness with rising mean annual temperatures. In mountain sites, soil-acidity dependent species richness variation was higher in monoculture compared to diverse sites. We conclude that plant diversity in structurally complex rice landscapes is more resilient against the effects of agricultural intensification. Neighboring effects might again be enhanced in landscapes of complex composition because of an increased availability of suitable habitats that can serve as refuges and corridors for rice weeds, such as wetlands, grasslands, home gardens, other crop fields or fallows. Besides, plant diversity was influenced by the surrounding landscape in agricultural areas in the tropics (Martínez et al., 2015), the subtropics (Zhou et al., 2018), the Mediterranean (José-María et al., 2010) and temperate regions (Gaba et al., 2010; Gabriel et al., 2005; Maskell et al., 2019; Poggio et al., 2013; Roschewitz et al., 2005).

Regarding climatic conditions, we showed that mean annual temperature had a significant negative effect on plant diversity, especially at higher altitudes and at monoculture sites, perhaps due to higher topographical variation and reduced land-use intensity in the uplands. Higher species richness in upland areas was also observed in Indonesian paddies and bunds (Kumalasari, 2014), and altitude was identified as an important discriminating factor of plant communities in rice fields of Indonesia (Kumalasari, 2014), Nepal (Nowak et al., 2016) and Tajikistan (Nowak et al., 2013). A favorable climate as well as topographic and soil heterogeneity provide suitable conditions for plant life in mountainous regions of North Vietnam and the Philippines. The local farmland flora may also be enriched due to overlapping altitudinal distribution ranges of temperate/subtropical and tropical plant species in mid-elevations, as reported in studies on the diversity of introduced plants from other tropical mountain areas (Jakobs et al., 2010; Tassin and Rivière, 2003). Fried et al. (2017, 2018) found several genera in the species pools of PH3 and VN3 that are common to temperate regions. At some sites, the negative effects of high temperatures may be weakened by advantageous macro- and microclimatic conditions. However, the question why plant diversity independent of regional affiliation decreased with higher temperatures remained yet unresolved. This effect may well result from higher land-use intensity in the hot lowlands, but biogeographical reasons may also exist (higher species pools outside lowlands). We tried to create meaningful land-use indices and incorporate them (as well as information about local weed management strategies) into our models, but weed management was too heterogeneous among study regions to allow for a proper statistical analysis of our data. However, land-use intensity in a particular region (e.g. in the mountain region Lao Cai, VN3) was not generally lower in fields at high altitudes (with cooler temperatures) than in fields at low altitudes (with higher temperatures) in the same region, whereas in regional comparison, highland regions generally use less input of synthetic fertilizers and pesticides than lowland regions. Most probably, land-use intensity is the best explanation for differences of plant diversity between regions (see Fig. 3), but not within each region. In our analyses, we included “Region” (and with it also region-specific differences, e.g. the strong differences of land-use intensity) in the random term of our models to reveal region-independent variables with effects within regions. Mean annual temperature, in contrast to any land-use index or weed control method, thus had a region-independent effect on plant diversity. We also used partial datasets (e.g. by excluding VN4 or by restriction to only lowland/highland regions) during model selection to ensure that we do not have statistical artefacts due to the distinctiveness of the study regions (e.g. because of their distinct weed management or climate) but the variables with significant effects remained the same among the models of the partial datasets. Future studies might focus on a particular region (with more local data) or provide more intersecting data to enable a sound statistical solution of the effect of land-use intensity (or weed management) on plant diversity.

Plant growth and development depends on the availability of soil nutrients which leads to competition between rice plants and weeds, and thus influences species distributions. The availability of nutrients to plants is bound to the soil acidity making it an important chemical property of rice soils (Fageria et al., 2011). Soil pH can influence the germination and composition of rice weeds (Singh and Singh 2009). Our previous studies in the study area have already identified soil acidity as a major determinant of the arable species composition (Fried et al., 2017, 2018). Our new findings also indicate a significant, region-independent increase of vascular plant diversity with decreasing soil acidity. Soil measurements are desirable in further rice vegetation analyses to explain interactions between soil, management, crop and weeds in more detail.

4.2 Drivers of rice weed diversity in paddies

Species diversity in paddies was much lower than on bunds, which corresponds to findings from China (Nemoto and Otsuka, 2014), Indonesia (Kumalasari, 2014), Japan (Fukamachi et al., 2005), and Sri Lanka (Bambaradeniya et al., 1998). Impacts of agricultural management, i.e. flooding, weed control and seeding, are generally more severe in paddies and lead to a comparatively depauperate and uniform flora. Particularly soil moisture was significantly negatively correlated with plant diversity in paddies. These findings are consistent with other studies on effects of water depth and availability on weed diversity and/or composition in tropical and subtropical paddies (Bambaradeniya et al., 1998; Juraimi et al., 2011; Kumalasari, 2014; Nowak et al., 2015, 2016; Tomita et al., 2003). Proper water management has been the traditional method of weed control long before synthetic herbicides became available. Standing water suppresses weed growth directly by reducing plant germination and establishment, and indirectly through the inherent size advantage of the crop (Tuong et al., 2005). Different strategies concerning level, duration and timing of flooding have been proposed, though most agree that flooding in the early stages of crop establishment reduces weed growth most effectively (e.g. Bhagat et al., 1996; Chauhan, 2013; De Datta, 1981; Hill and Mortimer, 2001; Williams et al., 1990), but distribution, growth and reproduction vary between species and soil moisture levels (e.g. Arai et al., 1955; Bhagat et al., 1996; De Datta, 1981; Juraimi et al., 2011; Kamoshita et al., 2010; Morita and Kabaki, 2002). C3 plants might outcompete C4 plants under water-saturated conditions (Tanaka, 1976), and flooding speed and intermittent draining might affect particularly algae and aquatic weeds (Hill et al., 1994). Sound knowledge on local species composition and community variation is essential to detect specific plant functional groups with beneficial effects for the local rice ecosystems and may help in adapting management strategies to make rice production more sustainable. Seasonal changes in rainfall and humidity should be less important in irrigated landscapes of permanent water availability, especially with respect to paddy vegetation. Temperature seasonality is pronounced particularly in the mountains (VN3 and PH3) where rice cultivation, and accordingly the sampling of the vegetation, was restricted to the wet season. Only some rice fields in the lowland regions were sampled in the dry season where temperature seasonality effects should be negligible.

The proximity of non-paddy habitats showed no significant effect on species richness. This corresponds to findings from Indonesia, where nearby semi-natural vegetation did not enhance species richness in paddy fields, but on bunds (Kumalasari and Bergmeier, 2014). In Mediterranean cereal fields, landscape heterogeneity influenced plant diversity on boundaries and field edges, but not in field centers (José-María et al., 2010). Paddies are highly disturbed and unsuitable habitats for other plants than rice and its most closely associated weeds, so weed control effects might displace those related to the surrounding landscape. Additionally, rice plant communities are often fragmentary and characterized by comparatively low species richness (Miyawaki, 1960), making drivers of paddy plant diversity even harder to detect. This could as well be a reason why regional differences in plot level (alpha) diversity in paddies were weaker than on bunds. Nevertheless, effects of environmental conditions on the composition of the local plant communities of paddies were recently revealed (Fried et al., 2017).

4.3 Region-specific effects on the weed diversity

Apart from drivers of plant diversity acting in all regions, we found regional differences of alpha diversity that can only be explained by region-specific factors. We documented severely decreased plant diversity at the study sites in the Mekong Delta (VN4), and to a lesser degree in Nueva Ecija (PH2), probably resulting from the highly intensive agricultural production methods and the consequently rather monotonous local landscape. In contrast, relatively high levels of plant diversity were observed in the heterogeneous rice terrace landscapes of Ifugao (PH3) and Lao Cai (VN3), where the climate allows for only one rice crop per year and the reduced usage of fertilizers, herbicides and machinery. Rice agro-ecosystems in mountains are often characterized by traditional upland rice cultivars, reduced application of synthetic fertilizers and herbicides, and by selective manual weed control (De Datta, 1981; Doanh and Tuan, 2004; Galinato et al., 1999; GRiSP, 2013; Husson et al., 2001; Paudel, 2011; Roder et al., 1997; Roder, 1997). Regional rice weed diversity surely profits from specific traditional cultivation methods and high local landscape heterogeneity. Recently, Fried et al. (2017, 2018) documented the distinct weed control and cultivation methods of each study region. Land use practices and intensity vary so greatly among regions that no region-independent variable with general effects on the plant diversity was detected.

4.4 Species turnover across sampling plots, between the paddies and their bunds, and between regions (beta diversity)

On bunds, Bray-Curtis dissimilarities between the plots revealed moderate species turnover within regions. There was a tendency of beta diversity to decrease with increasing alpha diversity, land use intensity and declining regional landscape heterogeneity, but we did not detect any significant correlation. Interestingly, species turnover across bunds of the rice terraces in the mountain regions Ifugao and Lao Cai was rather low despite high species numbers (in relation to the number of recorded plots) and alpha diversity, low land use intensity, and overall high regional landscape heterogeneity. In the hilly lowland of Vinh Phuc the pattern was similar. A reason for this might be a higher chance of recording shared species when the number of species per site increases. In contrast, species turnover was high across bunds in PH2 and VN4, where alpha diversity is low due to very intensive monoculture rice production, up to three crop cycles per year, and frequent application of herbicides (also on bunds) (Fried et al., 2018). Low species richness as in regions VN4 and PH2 with even the more common plant species occurring only sparsely cause high species turnover rates on bunds. Such effects might be compensated by larger sampling effort. The highest beta diversity on bunds was documented from Laguna on Luzon Island, where we had moderate species richness but an ample list of species that occurred sparsely and irregularly (cf. Fried et al., 2018). In paddies, lowest species turnover rates were found in the two contrasting regions VN3 and VN4, but no general pattern of beta diversity and its drivers could be revealed. Similar studies are not known to us, so we recommend future research in this field.

We also found high levels of species turnover between regions. The Bray-Curtis dissimilarities shown in Table 4 underlined the strong differences in the species composition between regions that we presented in the DCA results. These findings are reflected by previous overall floristic inventories of rice fields in Vietnam and the Philippines (Moody, 1989). Geographical variability in climate and soil (least in close regions like VN1 and VN2), and differences in agricultural management (especially between uplands and lowlands) are the main factors characterizing the local rice weed communities (Fried et al., 2017, 2018). Regional differentiation might further be driven by historical events like isolation, migration and speciation.

Our results of DCA and Bray-Curtis dissimilarities might be influenced by excluding rare species (40% of the recorded taxa) although this is a common practice to avoid noise in multivariate analyses (c.f. Poos and Jackson 2012). Nonetheless, we found many more species on bunds than in paddies, while previous studies have already shown that almost half of the recorded taxa in paddies occurred in less than 2% of the plots (Fried et al., 2017). We assume that a high rate of propagule influx from bunds (and perhaps irrigation channels) may enrich the local paddies' species inventory with casual plants, depending entirely on the reproductive success in adjacent habitats. The correlations of plot-level plant diversity (S, S_{ipo} and H) between bunds and paddies of the same study site support this assumption. Similar neighborhood effects are known from subtropical rice production sites in South China (Zhou et al., 2018) as well as from temperate wheat fields (Gabriel et al., 2005). The predominant life form in paddies, annual amphibious plants (Bolòs and Masclans, 1955; Fried et al., 2017; Miyawaki, 1960), is particularly capable of supporting sink populations in hostile environments through high seed production, dispersal and regeneration rates (cf. Kunin, 1998; Santamaría, 2002). Bunds host the majority of rice weeds, in numbers and cover, and serve as an important source, refuge and corridor of plants in rice agro-ecosystems (Fried et al., 2018). They are an important and integral part of the rice agro-ecosystem with a distinct flora and vegetation and play a key role in the Southeast Asian agrobiodiversity.

5. Conclusion

We found great regional variability in the plant species composition of local rice production landscapes. Neighboring habitats play an important role as source habitats for propagules of plant species in rice fields. Especially bunds represent important habitats for plant species that are not necessarily harmful to rice cultivation. Bunds and direct neighborhoods of rice fields could contribute to sustain and promote biodiversity of plants and associated animals, such as pollinators and parasitoids of pests or other pest antagonists, in rice production landscapes. In the study area, closer proximity to structurally more complex habitats led to higher numbers of entomophilous plants on bunds, while pollinator diversity, their functional diversity and plant-pollinator network complexity increased in rice fields and home gardens (Hass et al., 2018; Schrader et al., 2017) compared to those in monoculture. Diversification of rice agro-ecosystems through the protection and promotion of plant biodiversity may also lead to higher resilience against disturbances, but species composition and preservation of native species should have greater priority than conservation of species richness per se (Tylianakis et al., 2010). High plant species diversity can be conserved or promoted by reduced management intensity, conservation and restoration of extensively managed habitats, such as agroforests, and irrigation schemes that help to reduce pesticide inputs. Sustainable rice production systems should take care of biodiversity and the proper management of the bunds. Targeted managements of plant species on the bunds could prove as a potential measure for ecological engineering (Settele et al., 2018) and promote multiple ecosystem services, including pest control and pollination (Westphal et al., 2015), in rice landscapes that often comprise a mosaic of home gardens, orchards and rice paddies.

Author contributions

E.B., I.K. and O.F. planned the research, J.Se., N.V.S. and C.W. led parts of the project and logistics planning, O.F. conducted the field sampling, analyzed the taxonomy, landscape heterogeneity and soil conditions, and led the writing, O.F. and J.Sc. performed the statistical analysis, V.G. mapped land cover types, while all authors critically revised the manuscript.

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Appendix A. Supplementary material

Appendix A.1: List of taxa found in Southeast Asian rice landscapes during the years 2012 to 2015 with their status in The IUCN Red List of Threatened Species (IUCN 2015). Species counted in our index "S_{ipo}" (marked as entomophilous) have showy flowers or are known from scientific literature (e.g. eFloras 2008) for being insect-pollinated.

Appendix A.2: Type III Analysis of Variance Table with Satterthwaite's method of variables with significant effects on plant species richness (*S*), Shannon index (*H*) and the number of entomophilous plants (S_{ipo}) on Southeast Asian rice field bunds (n = 123) and paddies (n = 110). *P*-values are based on *F*-statistics.

Appendix A.3: Effect sizes (% explained variances and R^2) of the models and corresponding predictor variables. R^2 is given for the entire model and for the fixed terms, respectively. Explained variance of random terms is corresponding to random variance of final model.

Appendix B. Supplementary material

Appendix B.1: Generalized model predictions of the effects of surrounding landscape, mean annual temperature and soil acidity on the species richness of studied rice field bunds, based on linear mixed-effects models.

Appendix B.2: Generalized model predictions (based on linear mixed-effects models with dotted lines showing 95% confidence intervals) of the effects of mean annual temperature and surrounding landscape on species richness of Southeast Asian rice field bunds. Species richness decreases with mean annual temperature, in particular if bunds belong to monoculture sites. Points represent original data points.

Appendix B.3: Generalized model predictions (based on linear mixed-effects models with dotted lines showing 95% confidence intervals) of the effects of soil pH and surrounding landscape on regional species richness on bunds. Overall, decreasing soil acidity enhanced species richness, but regional differences and the effect of surrounding landscape were more conspicuous. Points represent original data points.

Appendix B.4: The study regions (for full names see Fig. 1) were characterized by distinct levels of plot-level plant diversity (a) on bunds and (b) in paddies. Significant differences ($p <$

0.05) of Shannon diversity (*H*) between regions are indicated with letters (n_{bunds} = 123 and $n_{paddies}$ = 110).

Appendix B.5: The study regions (for full names see Fig. 1) were characterized by distinct levels of plot-level plant diversity (a) on bunds and (b) in paddies. Significant differences ($p <$ 0.05) of the number of entomophilous plants (S_{ipo}) between regions are indicated with letters (n_{bunds} = 123 and $n_{paddies}$ = 110).

Appendix B.6: DCA ordination depicting plant community composition in paddies and their bunds. Site scores of the DCA ordination are shown along axes 1 (eigenvalue 0.50) and 2 (eigenvalue 0.37). Symbol sizes indicate the species richness at sites. The total inertia was 9.72.

Appendix B.7: Correlation matrix of variables recorded on bunds. Numbers represent Pearson's correlation coefficient.

Appendix B.8: Correlation matrix of variables recorded in paddies. Numbers represent Pearson's correlation coefficient.

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