

Domestication of rice reshaped associated biodiversity of rice field ecosystem

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Abstract

The domestication of rice (*Oryza sativa* L.) has a rich history with its diversification from wild progenitors based on genetic differences. For human benefit, natural environments have been agriculturally modified. Concurrently, the biodiversity of natural or wild environments is greatly affected. Here, a comparison has been made between the biodiversity associated with wild-type rice and domesticated rice fields. Species were categorized into broad groups, *i.e.* Arthropoda (*Arth*), Other Invertebrate (*OInv*), Vertebrate (*Vert*), Algae (*Alg*), Fungi (*Fng*), Pteridophyta (*Pttd*), and Higher Plant (*HPlan*). Physico-chemical factors including water depth (*WD*), water pH (*pH*), temperature (*T*), total hardness (*TH*), dissolved organic carbon (*DOC*), turbidity (*Turb*), and dissolved oxygen (*DO*) were measured directly in the field. Statistical analysis such as Student's t-test, Kolmogorov-Smirnov test for equal distributions, tests for dominance and multiple indices including Simpson, Shannon, and Evenness were used to assess the biodiversity. Furthermore, Principal Component Analysis (PCA) and Multivariate Analysis of Variance (MANOVA) were used for community comparisons, and SIMPER analysis was used to assess dissimilarity between taxa. The Artificial Neural Network model (ANN) was applied to assess the relative importance of factors governing the system. The present study showed the assemblage of species in the wild along with domestication. The vertebrate species number was well correlated with all the other biotic groups indicating a bottom-up controlling pattern in the rice field ecosystem. The ANN analysis showed that of the environmental factors examined, *WD* played the most important role followed by *pH*, *T*, *DOC*, and *DO* as the next most influential factors in distinguishing wild and domesticated rice field ecosystems. SIMPER analysis demonstrated that arthropods were a major contributor to dissimilarity. Collectively our results showed that the domestication of rice led to a decline in biodiversity.

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Introduction

Rice (*Oryza sativa* L.) is the world's most significant agricultural species, feeding hundreds of millions of people worldwide since its domestication (Londo et al., 2014). It was domesticated from the annual ecotype of *Oryza rufipogon* L. approximately 10,000

years ago (Oka, 1988; Gross and Zhao, 2014) in the floodplains of India and Indochina (Londo et al., 2014). Domestication is a complicated anthropological process in which human usage of plant and animal species results in morphological and physiological diversification of domesticated taxa from their wild progenitors based on genetic differences (Molina et al., 2011).

The domestication process also alters the natural habitat and the ecosystem of wild progenitors during the continuous improvement of agriculture (Chen et al., 2015). Tillage and irrigation are cultivation methods that can change the quantity of standing detritus or open water in a system, affecting the relative abundance of detritivorous aquatic invertebrate species. Wild rice is aquatic, photoperiod sensitive, cross-pollinated in nature, and found in regions with year-round standing water, such as swamps, river edges, and marshes (Oka, 1988). Plant density, annual tillage, phenology, fertilization, and irrigation are the main factors that differ between natural and agro-ecosystem (Macfadyen and Bohan, 2010; Meyer et al., 2012; Chen et al., 2013).

Rice fields harbor a large number of organisms due to their dynamic nature and periodic wet-dry alteration (Fernando, 1993). Different life-history phases and successional changes in flora-faunal diversity are influenced by both allogenic and autogenic factors (Bambaradeniya, 2000). The arthropod biodiversity associated with cultivated rice has been extensively researched (Heong et al., 1991; Roger et al., 1991; Cohen et al., 1994; Schoenly et al., 1996; Cuong et al., 1997; Schoenly et al., 1998; Wilby et al., 2006), but very few studies addressed the total biodiversity (Heckman, 1974; Nashriyah et al., 1998; Bambaradeniya and Amerasinghe, 2004). Cuong et al. (2016) studied arthropod diversity in wild rice fields. Chen and Bernal (2011) and Chen et al. (2013) studied only arthropod communities of wild or domesticated rice fields. So far, there has not been a comparative study on the biodiversity of wild and domesticated rice field ecosystems.

Our study aimed to document total floral and faunal diversity of wild and domesticated rice field ecosystems. We investigated the associated physicochemical factors, the classification of all organisms according to taxonomic group to reveal qualitative and quantitative differences between the two ecosystems, and how habitat quality affects biodiversity, distribution, and community assemblages. Moreover, a brief discussion is provided to understand how domestication reshaped rice field ecosystems through an ecological lens.

Material and Methods

Study region

The study was done throughout the land zones of West Bengal. The state of West Bengal is the largest rice production state in India. It contains 23 districts, including 341 Blocks (administrative divisions of the district) and is situated between 21°30'06" N to 27°10'18" N latitude and 86°02'26" E to 90°34'05" E longitude. West Bengal is on the eastern bottleneck of India, stretching from the Himalayas in the north

to the Bay of Bengal in the south. The total area of this state is 88,752 km²; it is situated south of the Tropic of Cancer and has an average annual temperature of around 28 °C. Average annual precipitation is 1,649 mm. Average humidity is approximately 69% and is more or less uniform throughout the year. Rivers are spread throughout the state, but a dense network is found near the southeastern coastal region (Census of India, 2011). *Oryza rufipogon* could be found in different wet marshland of West Bengal was mapped using ArcMap 10.3 (Fig. 1).

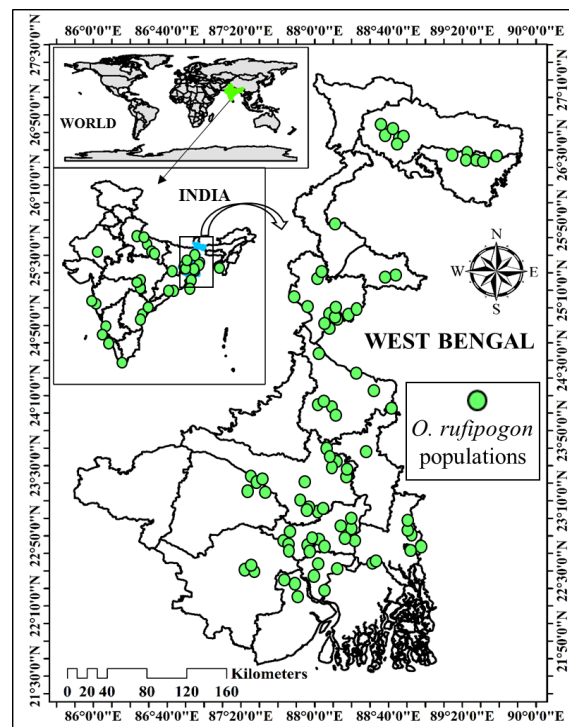


Figure 1: Study site of wild and domesticated rice field ecosystems in West Bengal, India: Circles are the scientific polygons represent the distribution of the *Oryza rufipogon* (wild) populations in the study site.

Sampling methods

Field sampling was carried out in three consecutive years from March 2016 to June 2019. Sampling was carried out at weekly intervals throughout the study period, with morning (7:00–10:00 AM) and evening (15:00–18:00 PM) shifts. Accordingly, there were 170 sampling days during the entire study. There are four sub-habitats in the rice field ecosystem: benthic or littoral, aquatic, transitional, and terrestrial. To record total biodiversity, various forms of sampling were used for various taxa occupying each sub-habitat. Water, soil collection, and sweeping were done through a randomized block design method (Addelman, 1969) to reduce sampling bias. Different sampling methods were performed for different groups.

A qualitative sample of plankton was gathered with a plankton net (45 m) at each rice field and sampling date to later estimate the species richness. According to Eaton et al. (1995), for the quantitative examination of the plankton community, quantitative samples (replicates) of 100 mL were taken by filtering 12 L from random places in the rice field along the gradient of water flow, using a standard dipper (12 cm diameter, 6 cm depth, 400 ml capacity). A 1 mL pipette was used to subsample the quantitative samples, which were then transferred to a Sedgewick Rafter counting chamber. In the field, all samples were stained with erythrosine and preserved with 10% formalin solution. A binocular microscope (Motic SMZ-168), an optical microscope (Olympus CX31), and specialized keys for each of the principal taxa: Cladocera, Copepoda, and Rotifera, were used for taxonomic identification (Koste and Shiel, 1990; Paggi, 1995). Cladocerans and rotifers were classified to the lowest taxonomic level feasible (except for bdelloid rotifers which were identified up to the genus level using Fontaneto and Ricci, 2004). Copepods were classified by order (Cyclopoida, Calanoida, and Harpacticoida) and/or developmental stage (nauplius, copepodite, mature stage) (Reimche et al., 2015). Phytoplankton were identified using a phase contrast light microscope (Olympus IX70, Tokyo, Japan) with bright field and phase contrast illumination at 100 \times –400 \times magnification. Phytoplankton were identified according to Whitford and Schumacher (1973) and Bellinger (1992).

For the sampling of small weed flora (macrophytes and microphytes) in the rice field proper and in the bunds, water samples were collected using a conventional dipper, and then sieved (mesh size 100 mm) to identify aquatic microflora. These were classified into separate categories using a binocular stereo microscope (Olympus SZX16, Tokyo, Japan). Microphytes were identified up to genus level and macrophytic weeds were identified up to species level using the taxonomic key of Kumari (2015).

In order to observe the smaller species, water samples containing aufwuchs, epibenthos, macrophytes, neuston, and sediment were taken. An immediate microscopic examination was performed, following which samples were left to sit for one or two days to allow more elusive species to emerge. To observe aufwuchs growth, thin glass cover slides were inserted in the water. Plexiglass, polyethylene tapes, and glass slides have all been utilized as artificial substrates for this purpose (Sladeczek and Sladeczkova, 1964). Glass appeared to be the most extensively used material and there seemed to be no advantage to using one of the other materials. The glass slide method was proven to be successful for collecting representative samples (Castenholz, 1961).

Taxon abundances were counted using the line transect method for monocot, dicot, and fern diversity, and then converted to number/unit area for

consistency. Taxonomic identifications were made following Craton et al. (2010), Naidu (2012), and with the cooperation of botanical group experts at Crop Research and Seed Multiplication Farm, Burdwan University, West Bengal.

Macrofauna samples were collected using the conventional Tropical Soil Biology and Fertility (TSBF) method (Lavelle 1988; Anderson and Ingram, 1993), which entails excavating monoliths of soil measuring 25 \times 25 \times 30 cm and manually removing organisms in the field. Each monolith represented a physical property measurement sampling site. Later, with the help of trained taxonomists, we identified specimens to the level of morphospecies (as a surrogate for formal species; Oliver and Beattie, 1996), family, and order and recorded the abundance of each morphotype, in order to determine the abundances of taxa (Magurran, 1988; Gotelli and Colwell, 2001). Each colony of earthworms and individual ants were sampled. A 25 \times 25 \times 30 cm monolith was excavated at each quadrant's corner to catch earthworms.

For soil-dwelling or benthic invertebrates a conventional soil corer was used to collect representative soil samples from eight randomly selected sites in the rice field along the gradient of water flow on each sampling day (height: 12 cm, diameter: 6 cm). Using a modified Baermann funnel technique (Walker and Wilson, 1960) and subsequent sieving (mesh size 100 mm), these soil samples were blended independently in the laboratory, and eight sub-samples of approximately 225 cm³ each were separated for extraction of soil-dwelling or benthic invertebrates. Identifications of the soil benthos was preformed following Goodey (1963), Choudhury and Roy (1968), Brinkhurst and Jamieson (1971) and Mukherji and Nandi (2004).

A portable Blower-Vac suction apparatus and a regular sweep net were used to sample the terrestrial arthropod fauna consisting of insects and spiders inhabiting the rice (field proper) and non-rice (bund) habitats, respectively. The arthropods inhabiting the rice plants and weeds were suctioned out using the Blower-Vac device. A plastic enclosure (height: 65 cm, diameter: 45 cm, fitted with a nylon net on top) was installed in 10 random sites in the rice field proper and the bunds, respectively. The arthropods that live in the bund habitat were also sampled with a normal sweep net, which was used to do 20 \times 5 sweeps while walking along the bund, with each sweep spanning 1 m. For the rice pests, predators, and parasitoids, the work of Barrion and Litsinger (1994) was used to identify terrestrial arthropods and Araneae (Mondal et al., 2020). Taxonomic keys by Wilson and Claridge's (1991) and Bal and Biswas (2013) were used to further clarify the Homeoptera. Nishida and Tori (1970), Kehimkar (2008), and Shubhalaxmi (2018) were used to identify the

Lepidopteran visitors, respectively. The works of Subramanian (2009) and Nair (2011) were used to identify the Odonata.

Aquatic insects were sampled by using a normal dipper to gather water from various points in the rice field and then sieving it (mesh size 160 mm). Floating plastic bags on the water's surface were used to catch adult insects that had metamorphosed from aquatic nymph or pupal stages. The same surface area could be covered by each bag by holding the bases of these insect samplers open with big rings. The samples were collected after one day, and the insects were counted and retained for further identification. The field guide by Subramanian and Sivaramakrishnan (2007) was used to identify aquatic insects.

Aquatic molluscs inhabiting the water surface, submerged vegetation, and the mud layer were hand collected from 10 randomly selected rice field sites, using a 0.3 m² quadrat. Aquatic molluscs were identified using the guide by Naggs (1997).

Freshwater fish species were observed in the rice fields, netted with a dip net, or obtained from fishermen who visited the rice fields on a regular basis. Fishermen employ cast (1.5 m diameter and 2.0 × 2.0 mm mesh size) and gill nets widely in the field, catching a variety of large and small fish. Although this method is imprecise, it did capture numerous secretive species and confirm their existence in the rice field. The fish were identified according to Talwar and Jhingran (1991) and Jayaram (1999).

A hand net and a regular minnow trap were used to capture amphibians in rice fields and waterways. The amphibian specimens were identified with the help of various experts and following Daniel (2002). For taxonomic consistency, amphibian nomenclature follows the Amphibian Species of the World database (Frost, 2021 accessed on 21.12.2021).

Reptiles found in the field were physically collected and identified directly in the field. Reptiles were initially identified by following Whitaker et al. (2004) and Das and Das (2018). Some species were photographed to record taxonomic characters and this data was sent to experts in order to further confirm identifications.

Birds in the field were identified using both the naked eye and binoculars (magnification: 7 × 35). The guide to Indian avifauna by Grimmett et al. (2011) was used in species identification, taxonomy, and naming.

Mammalian presence was detected by both direct and indirect observations, such as tracks and excrement. Standard baited traps were left in the field overnight to catch and identify the rodents and shrews present in the fields. The identifications of mammal species followed Ellerman et al. (1961) and Menon (2014).

All sampled populations were categorized under higher taxonomic denominations like phylum, order,

etc. (Appendices 1–4). Further, taxa were grouped into broad categories *i.e.* Arthropoda (*Arth*), Other Invertebrate (*OInv*), Vertebrate (*Vert*), Algae (*Alg*), Fungi (*Fng*), Pteridophyta (*Pttd*), and Higher Plant (*HPlan*). Species that were found exclusively in a particular habitat were considered as unique species.

Physico-chemical factors like water depth (*WD*), water pH (*pH*), temperature (*T*), total hardness (*TH*), dissolve organic carbon (*DOC*), turbidity (*Turb*), and dissolved oxygen (*DO*) were measured *in situ*. A water level gauge, digital thermometer (LUTRON-PTM-816), pH meter (EUTECH-pHTest-10), and dissolved oxygen meter (LUTRON-PDO-520) were used to measure *WD*, *T*, *pH*, and *DO* data, respectively. *TH* was determined using the EDTA method (Ghosh et al., 2020). *DOC* was measured by the combustion method (Fukushima et al., 1996) and *Turb* by the turbidity tube method (Myre and Shaw, 2006).

Statistical analysis

The number of species per categorized taxon was counted in both habitat types to observe how habitat type influenced taxa loss within taxonomic groups. Student's t-tests were performed to check for significant difference between the numbers of species in each categorized taxon with respect to changes in the habitat types. To see the effects of habitat on each categorized taxon, a Bonferroni correction was done following Moran (2003). Total species number and unique species number were also counted and Student's t-tests were performed to see the differences. A Kolmogorov-Smirnov test for equal distributions was done to check the differences between the wild and domesticated field species distribution. Dominance *D*, Simpson 1-D, Shannon *H*, Evenness $e^{-H/S}$ indices were calculated to assess the biodiversity difference between two habitats. Individual rarefaction analysis was done to interpolate estimated taxa number on each habitat. Pearson correlation coefficient was calculated among higher categorized taxa and physico-chemical factors.

Principal Component Analysis (PCA) was done using variance-covariance matrix to visualize the biplot with convex hull that can define the differences between two habitats. Further, Multivariate Analysis of Variance (MANOVA) was used to compare community composition along with the physico-chemical factors between the wild and domesticated rice field ecosystems. A SIMPER analysis was performed using the Bray-Curtis similarities index to identify the dissimilarity between the taxa that showed the differences in the wild and domesticated rice field ecosystems. The analysis also identified each taxon's proportionate contribution to the differences in community assemblages between habitats.

An Artificial Neural Network (ANN) model (Ghosh et al., 2020) was constructed using the physico-chemical factors as input or covariates and the categorized groups of Arthropoda (*Arth*), Other Invertebrate (*OInv*),

Vertebrate (*Vert*), Algae (*Alg*), Fungi (*Fng*), Pteridophyta (*Ptra*), and Higher Plant (*HPlan*) as output or dependent variables for the wild and domesticated rice field ecosystems. Using the aforementioned covariates, a multi-layered perceptron neural network was created. The model was created using the hyperbolic tangent for the hidden layer activation and the identity function for output layer activation. The following equations (Eqs. (1) and (2)) were used to construct the ANN model:

$$Pf \times w = \sum_{n=0}^i Pf_n \times w_n \quad (1)$$

Where Pf = the physico-chemical factors ($Pf_n = Pf_0 \dots, Pf_i$), w is the synaptic weight assigned for each. Pf ($w_n = w_0 \dots, w_i$)

$$E_{SP} = \phi (Pf \times w) \quad (2)$$

Where E_{SP} = number of species in the categorized groups, ϕ = Coefficient of activation function.

Results

In the wild and domesticated rice fields, 31,159 and 52,742 individuals respectively, were collected throughout this investigation. We counted 776 species in 416 families: 299

species in 155 families were arthropods, 170 species in 79 families were other invertebrates, 96 species in 53 families were vertebrates, 62 species in 44 families were algae, 31 species in 19 families were fungi, and 118 species in 66 families were plants (Fig. 2).

There were significant differences ($t = 80.64, p < 0.001$) between total number of species and number of unique species found in the wild and domesticated habitats, compared to 263 ± 34.2 unique species in the wild habitats and 42 ± 6.4 unique species in domesticated rice fields. The wild rice fields harboured 158% greater species number and 6.26 times more unique species than the domesticated rice fields (Fig. 3).

The Evenness index values indicate the wild habitat (0.5964) with more evenly distributed species than the domesticated fields (0.3126). Some species were more dominant in the domesticated fields (0.1329) than the wild fields (0.0688). There were significant differences ($p < 0.0001$) in the Simpson and Shannon indices between the two habitats, which indicated a considerable amount of differences in species diversity between the wild and domesticated rice field ecosystems (Fig. 4).

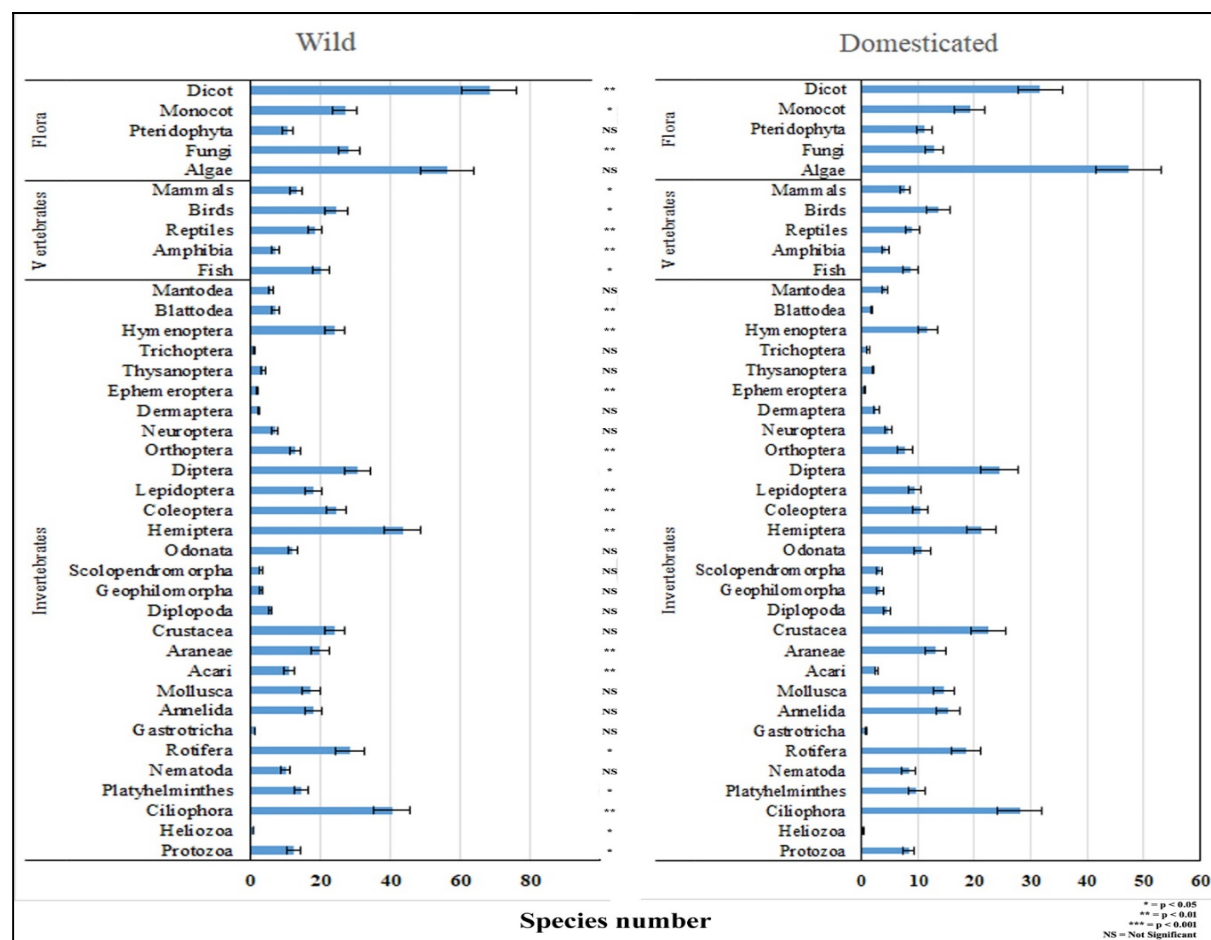


Figure 2: Comparison between the wild and domesticated rice field ecosystems by means of species number of different taxa ($x \pm SE$).

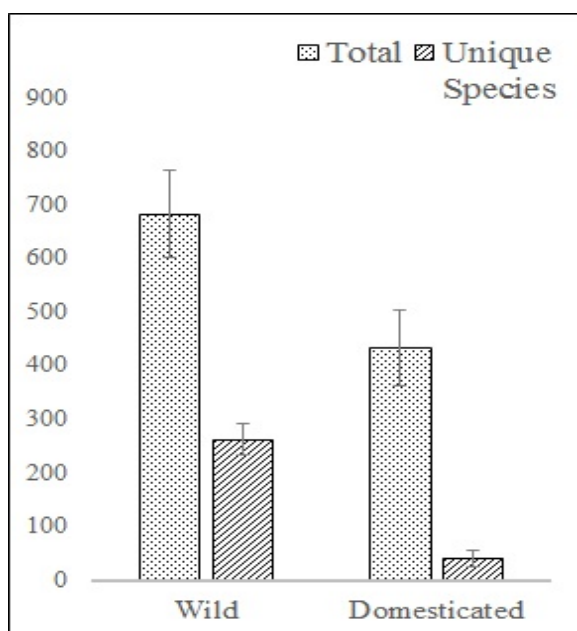


Figure 3: Total and unique number of species in the wild and domesticated rice fields ($x \pm SE$).

The Kolmogorov-Smirnov test for equal distributions showed that there were significant ($p= 0.0007$) distributional differences in community composition between the wild and domesticated rice fields. A Monte Carlo simulation, which generates random permutations, also showed a significant p -value (0.0012).

PCA analysis showed 87.14% variance in principal component 1 (PC1) and 10.09% variance in principal component 2 (PC2). All the loading scores with PC1 for wild rice field showed positive values, whereas domesticated field values showed negative values. So the convex hull for wild and domesticated field made two realms that were very different to each other (Fig. 5).

WD (0.94, -0.33) and *Arth* (0.94, 0.32) comprised a similar correlation with PC1, but inverse values with *TH* (-0.94, -0.24) and quite opposite values with PC2. *Ptrd* (-0.84, 0.36) and *Hplant* (0.84, 0.51) showed inverse correlation values with PC1, but quite similar correlation with PC2. *Fng* (0.89, -0.03) showed a similar correlation value along PC1 with DOC (0.89, 0.18). Except for *pH*, *Turb*, and *T*, all variables showed good correlation with PC1 (Fig. 6).

Pearson correlation values showed strong positive values among *Olnv*, *Vert* (0.84) and *WD* (0.83). *Arth* showed strong negative correlation with *TH* (-0.97), but positive with *HPlant* (0.95), *Vert* (0.92) and *Fng* (0.83). *Vert* exhibits a positive correlation with *WD* (0.93), *HPlant* (0.81), *Fng* (0.89), *Alg* (0.80) and negative relation with *TH* (-0.93), and *Ptrd* (-0.86). *Alg* showed positive correlation with *WD* (0.83) and negative with *Ptrd* (-0.81). *Fng* showed negative correlation with *TH* (-0.82) and positive with *WD* (0.85). *Ptrd* and *Hplant* shows strong negative correlation with *WD* (-0.9) and *TH* (-0.9), respectively. *DOC* exhibited negative correlation with *TH* (-0.9) (Fig. 7).

MANOVA expects the variance of dependent variables within groups and their correlation to be similar. Here, the Wilks' lambda values were 0.0013, $F= 282.1$, which implied that the wild and domesticated rice field ecosystems were not similar in terms of variables ($p < 0.0001$).

The SIMPER analysis determined the proportional contributions of different taxa to variations in community composition between wild and domesticated rice fields. Through Bray-Curtis similarity index calculation, there was 23.6 average dissimilarity between wild and domesticated community composition. *Arth* contributed most (39.94%) dissimilarity between the two habitats, followed by *Vert* (19.51%), *HPlant* (14.25%), *Olnv* (11.86%), *Fng* (6.23%), *Alg* (6.03%) and *Ptrd* (2.16%) (Table 1).

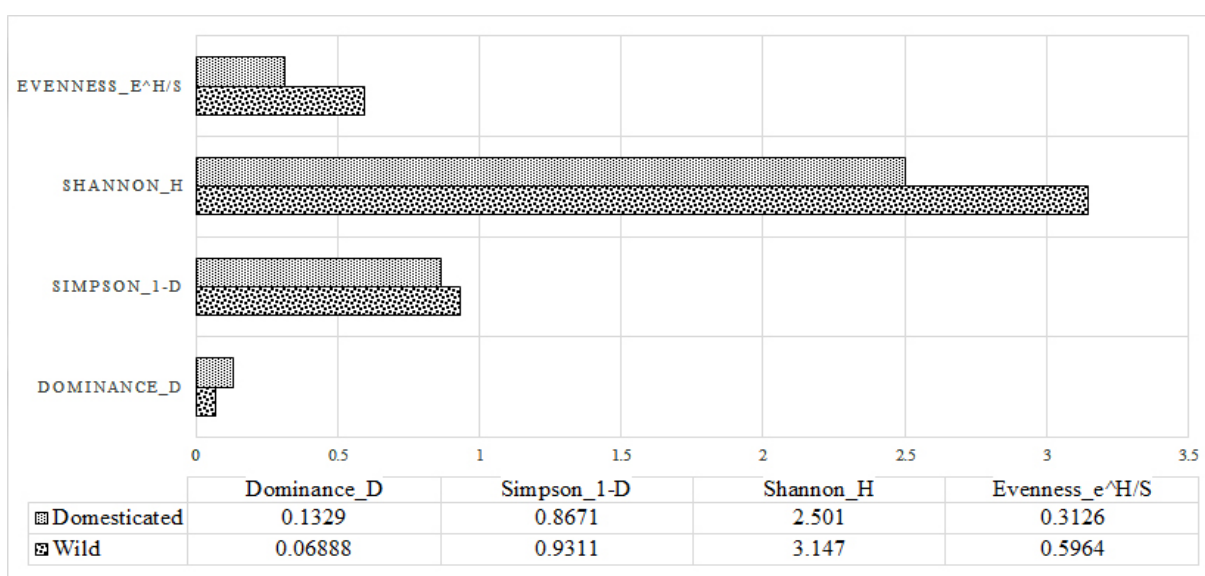


Figure 4: Diversity indices of the wild and domesticated rice field ecosystems. Dominance, Simpson, Shannon and Evenness indices were calculated.

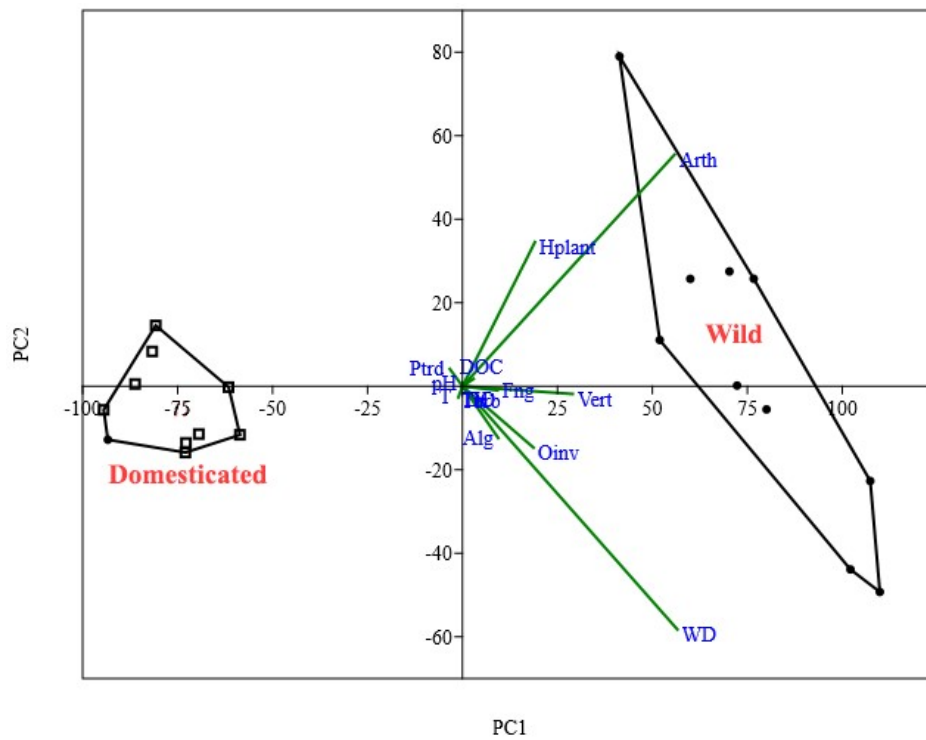


Figure 5: PCA biplot for physicochemical factors and community composition in wild and domesticated rice field ecosystems.

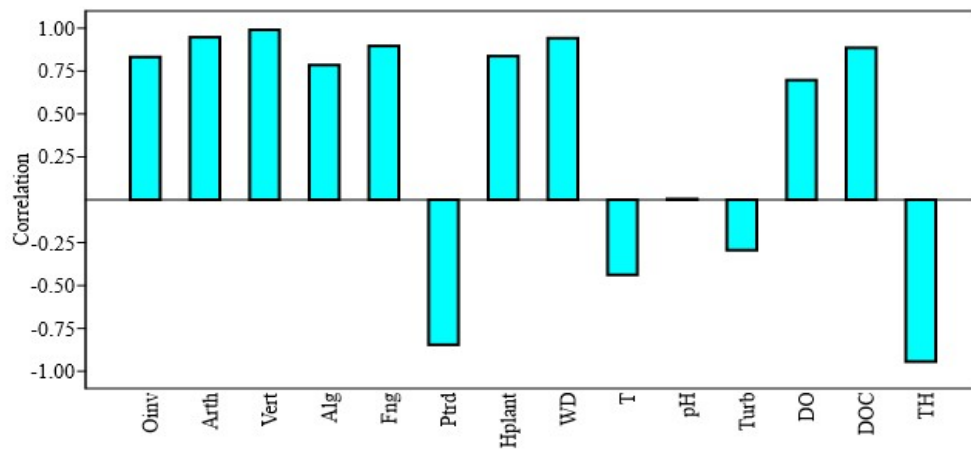


Figure 6: Correlation of major taxon groups and physicochemical parameters with PC1 (+1= significant positive correlation, -1= significant negative correlation).

Table 1: Summarized SIMPER analysis results of groups of taxa in wild and domesticated rice field ecosystems.

Taxon	Av. dissim	Contrib. %	Cumulative %	Mean Wild	Mean Domesticated
<i>Arth</i>	9.425	39.94	39.94	265	163
<i>Vert</i>	4.604	19.51	59.46	86.7	36.9
<i>Hplant</i>	3.363	14.25	73.71	88.9	52.5
<i>Oinv</i>	2.798	11.86	85.57	130	100
<i>Fng</i>	1.471	6.236	91.8	29.8	13.8
<i>Alg</i>	1.424	6.033	97.84	54.8	40
<i>Ptrd</i>	0.5102	2.162	100	7.91	13.3

Note: Examine the taxon wise variations of average dissimilarity, contribution, and cumulative percentage between wild and domesticated rice ecosystems. Mean values of different taxa were estimated between wild and domesticated rice ecosystems.

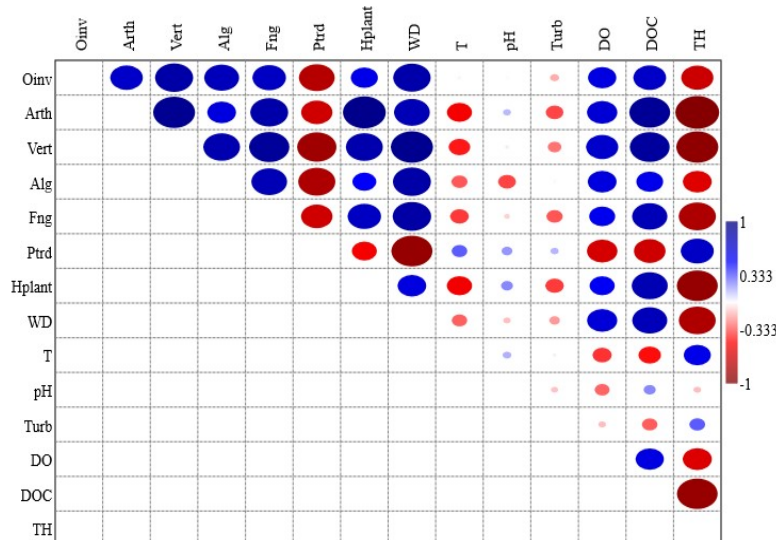


Figure 7: Pearson correlation among major taxon groups and physicochemical parameters. Positive and negative correlations were identified (values between 0 and 1 indicate positive correlation, whereas values between 0 and -1 indicate negative correlation).

The ANN model was used to investigate the impact of different physico-chemical parameters in sediments such as *WD*, *T*, *pH*, *DOC*, *DO*, *Turb*, and *TH* on species number of categorized groups such as *Oinv*, *Arth*, *Vert*, *Alg*, *Fng*, *Ptrd* and *Hplant* in the wild and domesticated rice ecosystem of West Bengal. During the run for the wild rice ecosystem, the model randomly allocated 60% of the input data as training and 40% as testing. Only one hidden layer and three hidden nodes were observed in the network structure. The relative importance analysis result indicated that *WD* was the most important physico-chemical parameter followed by, *pH*, *T*, *TH*, *DOC*, *DO*, and *Turb* for the species number of higher categorized groups in the wild rice ecosystem (Fig. 8).

The model predicted values of *Oinv*, *Arth*, *Vert*, *Alg*, *Fng*, *Ptrd*, and *Hplant* showed good model accuracy in wild ecosystem. linear R^2 values for *Oinv*, *Arth*, *Vert*, *Alg*, *Fng*, *Ptrd*, and *Hplant* were 0.577, 0.691, 0.793, 0.587, 0.773, 0.722 and 0.849 respectively (Fig. 9).

The sum square error (SSE) of training and testing sets for the wild ecosystem were 3.158 and 13.152. During the run for the domesticated rice ecosystem, the model randomly allocated 70% of the input data as training and 30% as testing. Only one hidden layer and four hidden nodes were observed in the network structure. The relative importance analysis result indicated that the *WD* was the most important physico-chemical parameter followed by, *pH*, *T*, *DOC*, *DO*, *Turb*, and *TH* for the species number of higher categorized groups in domesticated rice ecosystem (Fig. 10).

The model predicted values of *Oinv*, *Arth*, *Vert*, *Alg*, *Fng*, *Ptrd*, and *Hplant* showed good model accuracy in the domesticated ecosystem. Linear R^2 values for *Oinv*, *Arth*, *Vert*, *Alg*, *Fng*, *Ptrd*, and *Hplant* were 0.677, 0.850, 0.849, 0.539, 0.801, 0.860, and 0.946, respectively. The sum square error (SSE) of training and testing sets for the wild ecosystem were 0.660 and 7.767 (Fig. 11).

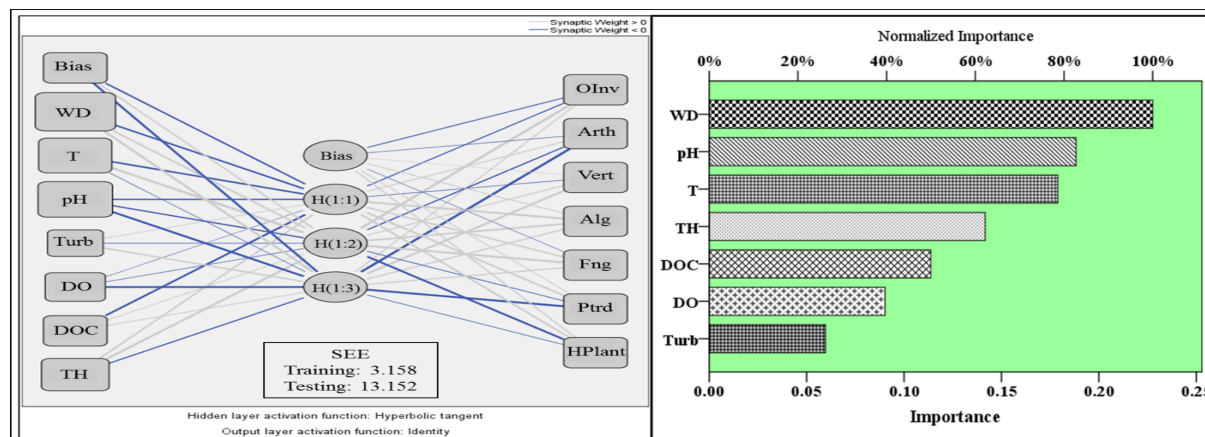


Figure 8: Structural view of ANN model with relative importance analysis for wild rice field ecosystem (SEE= Sum Squire Error). Relative importance 0.20= 100% normalized importance.

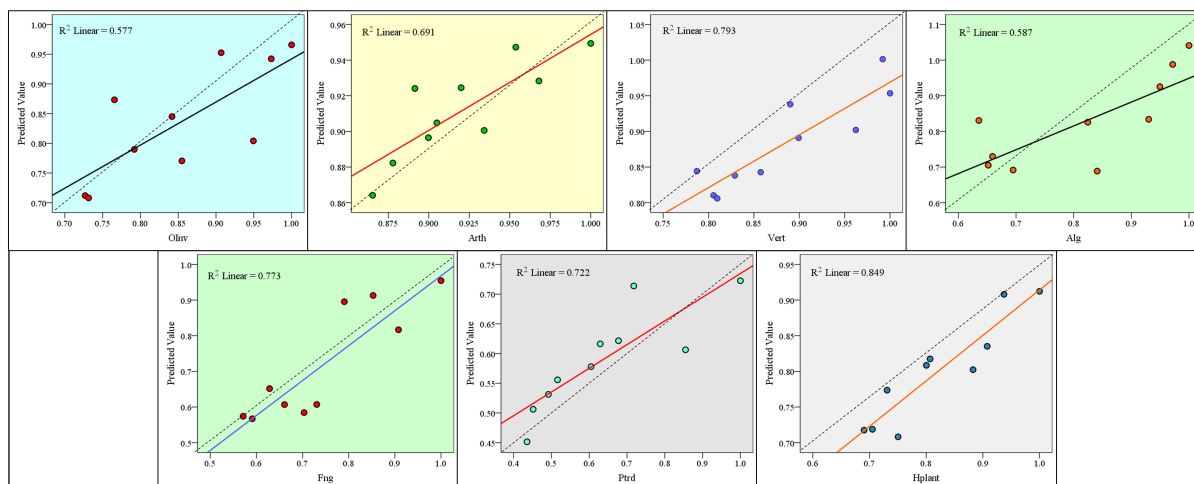


Figure 9: Observed vs predicted values of categorized taxa in wild rice fields. Linear regression R^2 = coefficient of determination ('0' does not determine, '1' completely determines).

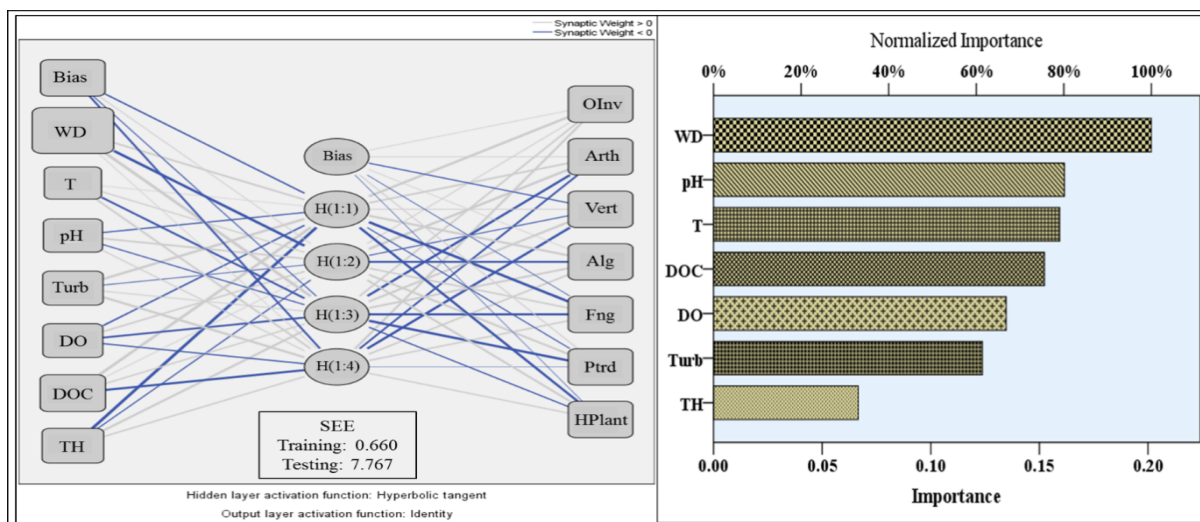


Figure 10: Structural view of ANN model with relative importance analysis for domesticated rice field ecosystem (SEE= Sum Square Error). Relative importance 0.20= 100% normalized importance.

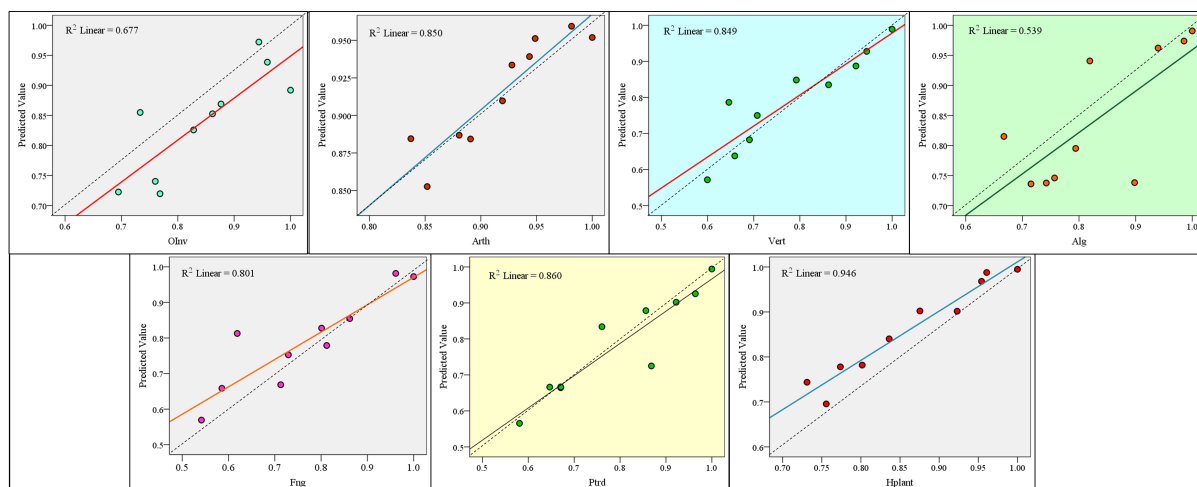


Figure 11: Observed vs predicted values of categorized taxa in the domesticated rice fields. Linear regression R^2 = coefficient of determination ('0' does not determine, '1' completely determines).

Discussion

The current study investigated whether arthropod diversity and community composition changed between wild and domesticated rice fields, given the relevance of biodiversity for ecosystem function. The present study found a 6.26 times higher amount of unique species in the wild rice field compared to the domesticated field ecosystem, which implies that the more diverse habitat in wild rice fields promote endemism in response to changing ecosystem characteristics caused by domestication. This study also showed that there were 191% more vertebrate species, 178% higher plants, 180% arthropods, 218% fungi, 119% algae, 150% other invertebrates in the wild rice field ecosystem. Only in Pteridophyta, the species number is 6% higher in domesticated rice fields. Losses in species number indicate that food webs in domesticated fields are far simpler than in wild ecosystems (Chen et al., 2015). All the diversity indices showed that the domesticated rice field was dominated by some species, which is why evenness values are almost half of the wild fields. Domestication of rice has decreased plant structural complexity by reducing tillering and enhancing plant palatability for some herbivores (Chen and Romena, 2006; Chen et al., 2015).

The species richness was significantly lower in the domesticated fields. Changes in plant diversity through crop domestication may have a great role in explaining why domesticated environments are losing species richness (Pimentel, 1961; Andow, 1991; Chen and Welter, 2002). Monoculture and homogeneity of habitat in the domesticated rice field lowers diversity in comparison to native wild habitats (Pimentel, 1961; Chen et al., 2013).

Multivariate statistical analysis, SIMPER analysis, and PCA results suggested that there were strong differences between the two habitats. Domesticated rice ecosystems involve significant environmental changes such as tillage, pesticide usage, habitat persistence, and water availability (Geiger et al., 2010; Legrand et al., 2011; Chen et al., 2013) that differ between wild and domesticated rice fields, and may have contributed to the substantial reduction in species diversity. The results of the Kolmogorov-Smirnov test suggested that the species distribution in wild and domesticated ecosystems are not equal, however, community composition varied between wild and domesticated rice fields. PCA results also showed a strong link between higher plants abundance and arthropod diversity. On the other hand, algae and other invertebrate diversity was well correlated with water depth. Pteridophyta were sensitive to *pH*, while *DO* was found to be a major controlling factor of vertebrate diversity. Fish, amphibians, and bird diversity was directly or indirectly associated with the water *DO* value. This

result is well supported by the correlation analysis. The vertebrate species number was well correlated with all the other biotic groups indicating a bottom up controlling pattern in the rice field ecosystem. *WD*, *TH*, *DOC*, and *DO* were the main influencing factors to shape wild and domesticated rice field ecosystems. SIMPER analysis demonstrated arthropods were the major contributor to dissimilarity followed by vertebrates and higher plants. Plant domestication may have a significant impact on arthropod, vertebrate, and higher plant diversity and community composition in agroecosystems through human agricultural history, insect-plant coevolutionary patterns, plant chemistry, and the target and extent of plant breeding (Chen and Bernal, 2011; Chen et al., 2015).

ANN analysis showed that *WD* was the most important factor for community composition of both rice field ecosystems. Then, *pH* and *T* showed similar relative importance values in the prediction of the species number of the categorized groups. Wild rice is a perennial in nature and photoperiod sensitive. It is aquatic and found in places with year-round standing water, such as swamps, river banks, and marshes (Kim et al., 2016). In the early Holocene, a warmer and perhaps wetter environment existed, where temperatures were suitable for wild rice development. Climate-driven changes in ancestral wild rice habitat ranges have been occurring since the Pleistocene (Fuller et al., 2010). According to this theory, wild rice populations were restricted to moist tropical regions for example, Indo-China and South East Asia, 20,000 years ago during the Last Glacial Maximum (Dodson et al., 2021). Climate change characterized by rising temperatures and CO₂ levels in the atmosphere and recurrent dry seasons followed by monsoon rains, contributed to the expansion of the wild progenitor distribution range and altered population dynamics (Kim et al., 2016). The changing monsoon environment, with its long, hot, dry summers, would have selected for new, wild, annual forms that gradually became domesticated rice, especially on the Indian subcontinent and across South East Asia. Evolutionary processes at the level of species domestication can affect the ecology of entire communities (Johnson and Stinchcombe, 2007). Integrating the theories about ecological constraints regarding rice domestication, water depth and temperature were identified as the key factors for community composition in wild and domesticated rice fields. Presently, *DOC* and *DO* influenced by agricultural practices, are the next most important factors (Hsu et al., 2011; Mao et al., 2020) in influencing the biodiversity. Artificial selection through the domestication process resulted in changing in biodiversity and community composition between the wild and domesticated rice according to the habitat characters. Reduced biodiversity in agricultural field due to expansion of homogenous habitat through monoculture

can exert substantial negative impacts on global change through global land use, deforestation and climate changes together with broad social-environmental changes.

Conclusions

Biodiversity associated with wild progenitor could play a key role in maintaining biodiversity and genetic diversity of herbivores and their natural enemies, which may be helpful for potential new bio-control methods. Wild and domesticated rice field ecosystems also harbor a large number of unique species. Arthropod diversity contributes most to differences between wild and domesticated fields. The preservation of wild relatives may be particularly essential in order to preserve the vast gene pool. Wild rice is a potential source of interesting alleles or even new mechanisms stress tolerance. These genetic resources, on the other hand, are practically unexplored, with only a few investigations. A rice field is generally a bottom-up controlled system. The present biodiversity of wild and domesticated field defines the evolutionary and ecological history of rice domestication. Domesticated plants and their wild relatives are great models for testing and comparing the short-term impacts of artificial selection and the long-term evolutionary results of natural selection from an evolutionary standpoint.

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Conflict of interest

All the authors declare that there are no conflicting issues related to this research article.

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Appendix 1: List of Plantae families found in the rice fields.

Plantae	Plantae	Plantae	Plantae
Chlorophyta	Charophyta	Angiosperms	Fern
Chlamydomonadaceae	Mestotaeniaceae	Amaranthaceae	Marsileaceae
Polyblepharidaceae	Desmidiaceae	Asteraceae	Salviniaceae
Volvocaceae	Zygnemataceae	Aizoaceae	Adiantaceae
Palmellaceae		Brassicaceae	Selaginellaceae
Macratiniaceae		Commelinaceae	
Characiaceae		Convolvulaceae	
Chlorococcales		Cuscutaceae	
Hydrodictyaceae		Cyperaceae	
Oocystaceae		Euphorbiaceae	
Scenedesmaceae		Fabaceae	
Ulotrichaceae		Lythraceae	
Microsporaceae		Malvaceae	
Chaetophoraceae		Molluginaceae	
Oedogoniaceae		Nyctaginaceae	
Cladophoraceae		Oxalidaceae	
		Poaceae	
		Polygonaceae	
		Portulacaceae	
		Rubiaceae	
		Scrophulariaceae	
		Solanaceae	
		Urticaceae	
		Verbenaceae	

Appendix 2: List of invertebrate families found in the rice fields.

Platyhelminthes	Nematoda	Rotifera	Gastrotricha	Annelida	Mollusca	Mollusca	Arachnida	Arachnida	Crustacea	Diplopoda	Chilopoda	
					Gastropoda	Bivalvia	Acari	Araneae			Geophilomorpha	Scolopendromorpha
Catenulidae	Tripylidae	Brachionidae	Chaetonotidae	Naididae	Viviparidae	Unionidae	Oribatidae	Pisauridae	Argulidae	Paradoxosomatidae	Mecistocephalidae	Scolopendridae
Stenostomidae	Monochidae	Colurellidae		Glossiphonidae	Bithyniidae		Arrenuridae	Lycosidae	Centropagidae	Pachybolidae		
Typhloplanidae	Actinolaimidae	Euchlanidae		Hirudidae	Ampullariidae		Eylidae	Oxyopidae	Cyclopidae			
Dalyelliidae		Dicranophoridae		Moniligastridae	Thiaridae		Unionicolidae	Salticidae	Cypridae			
Echinostomatidae		Filiniidae		Potamodrilidae	Lymnaeidae			Tetragnathidae	Cyclestheriidae			
Plagiorchiidae		Gastropidae		Megascolecidae	Planorbidae			Araneidae	Chydoridae			
Aspidogasteridae		Notommatidae			Bulinidae			Miturgidae	Daphniidae			
		Synchaetidae			Ancylidae			Thomisidae	Macrothricidae			
		Testudinellidae						Corinnidae	Moinidae			
		Trichocercidae						Gnaphosidae	Sididae			
		Trichotridae						Clubionidae	Corallanidae			
		Lecanidae							Talitridae			
		Collotheceidae							Palaemonidae			
		Flosculariidae							Ilyocyprididae			
		Philodinidae							Parathelphusidae			
									Portunidae			

Appendix 2. (Continued)

Odonata	Hemiptera	Coleoptera	Lepidoptera	Diptera	Orthoptera	Neuroptera	Dermaptera	Ephemeroptera	Thysanoptera	Trichoptera	Hymenoptera	Blattodea	Mantodea
Coenagrionidae	Belostomatidae	Gyrinidae	Satyridae	Chironomidae	Gryllidae	Crysopidae	Forficulidae	Ephemeridae	Thripidae	Hydropsychidae	Formicidae	Blaberidae	Empusidae
Libellulidae	Nepidae	Dytiscidae	Hesperidae	Chloropidae	Gryllotalpidae	Ascalaphidae					Eulophidae	Epilampridae	Eremiaphilidae
Gomphidae	Ranatridae	Hydraenidae	Pyralidae	Culicidae	Acrididae	Myrmeleontidae					Mymaridae	Termitidae	Hymenopodidae
Aeshnidae	Pleidae	Hydrophilidae	Pieridae	Dolichopodidae	Tettigoniidae						Eucharitidae	Blattellidae	Mantidae
	Mesovellidae	Hydroscaphidae	Lycaenidae	Empididae							Figitidae		
	Gerridae	Curculionidae	Arctiidae	Ephydriidae							Chalcididae		
	Hydrometridae	Carabidae	Crambidae	Ceratopogonidae							Platygastridae		
	Notonectidae	Elateridae	Geometridae	Muscidae							Vespidae		
	Corixidae	Staphylinidae	Noctuidae	Phoridae							Ichneumonidae		
	Hebridae	Coccinellidae	Nymphalidae	Sphaeroceridae							Scelionidae		
	Pentatomidae	Chrysomelidae		Stratiomyidae							Trichogrammatidae		
	Lygidae	Scarabaeidae		Tabanidae							Apidae		
	Pyrhocoridae	Cantharidae		Tachinidae							Halictidae		
	Delphacidae	Lampyridae		Bombyliidae							Specidae		
	Cicadellidae	Byrrhidae		Sarcophagidae									
	Cercopidae	Tenebrionidae		Faniidae									
	Alydidae	Meloidae		Bibionidae									
	Reduvidae	Cerambycidae		Drosophilidae									
	Miridae			Tipulidae									
	Coreidae			Syrphidae									
	Aphididae			Ascididae									
	Nabidae			Cecidomyidae									
	Membracidae			Calliphoridae									
	Rhyparochromidae												
	Pseudococcidae												
	Derbidae												
	Dictyopharidae												
	Aphrophoridae												
	Flatidae												
	Lophopidae												
	Ricaniidae												
	Cicadidae												

Appendix 3: List of vertebrates families found in the rice fields.

Fish	Amphibia	Reptiles	Birds	Mammals
Mastocembelidae	Dicroglossidae	Agamidae	Sturnidae	Herpestidae
Cyprinidae	Bufonidae	Scincidae	Ardeidae	Muridae
Clariidae	Microhylidae	Gekkonidae	Psittacidae	Soricidae
Channidae		Colubridae	Cisticolidae	Sciuridae
Anabantidae		Elapidae	Alcedinidae	Felidae
Gobiidae		Viperidae	Corvidae	Viverridae
Heteropneustidae		Homalopsidae	Passeridae	Vespertilionidae
Cobitidae		Typhlopidae	Ciconiidae	Canidae
		Varanidae	Threskionithidae	
			Estrildidae	
			Tytonidae	
			Strigidae	
			Jacaniidae	
			Rallidae	
			Anatidae	

Appendix 4: List of other families found in the rice fields.

Protozoa	Protozoa	Chromista	Chromista	Chromista	Chromista	Chromista
Euglenozoa	Amoebozoa	Heliozoa	Ciliophora	Ochrophyta	Cryptophyta	Miozoa
Euglenaceae	Mastigamoebidae	Actinophryidae	Holophryidae	Synuraceae	Cryptomonadaceae	Gymnodiniaceae
	Amoebidae		Colepidae	Euchromulinaceae		
	Arcellidae		Spathidiidae	Mallomonadaceae		
	Diffugiidae		Didiniidae	Ochromonadaceae		
	Euglyphidae		Actinobolinidae	Chrysocapsaceae		
			Amphileptidae	Characiopsidaceae		
			Tracheliidae	Xanthophyceae		
			Loxodidae	Bacillariophyceae		
			Chlamyodontidae	Coscinodiscaceae		
			Nassulidae	Flagellariaceae		
			Colpodidae	Eunotiaceae		
			Microthoracidae	Naviculaceae		
			Tetrahymenidae	Gomphonemaceae		
			Parameciidae	Cymbelaceae		
			Cohnilembidae	Surellaceae		
			Frontoniidae			
			Pleuronematidae			
			Metopidae			
			Spirostomidae			
			Stentoridae			
			Condyllostomatidae			
			Halteriidae			
			Strobilidiidae			
			Oxytrichidae			
			Euplotidae			
			Aspidiscidae			
			Expalkellidae			
			Vorticellidae			
			Epistylidae			
			Astylozoonidae			
			Urceolariidae			
			Dendrosomatidae			