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Research

Floodplain succession pattern along Budhi-Rapti River bank, Chitwan, Nepal

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Abstract

Riverine floodplain is one of the most productive lowland ecosystems in Nepal. However, floodplain ecology is less understood due to its fluctuation. Budhi-Rapti River in Chitwan, central Nepal formed a floodplain along the Khorsor zone of Barandabhar corridor. This study was carried out to understand the floodplain ecosystem development after plant succession. The space for time substitution method of vegetation sampling was adopted in order to sample the floodplain created at different chronosequence. The floodplain that lies perpendicular to and 200 m away from the Budhi-Rapti river was sampled. Systematic sampling was done along two parallel transects, almost 200 m apart from each other. Sampling along the transect started right after 200 m away from the Budhi-River bank. Initial position of these transects towards Budhi-Rapti river was believed to be the youngest floodplain, which slowly getting older after passing away from the river. Abundance of vascular plant species was recorded in sample plots of 20 × 20 m each subdivided equally into 4 subplots (each of 100 m^2). Along each transect, vegetation data was recorded from a series of 20 plots, placed 50 m apart from each other. Successional scores were calculated and utilized as environmental variables after applying non-metric multi-dimensional scaling (NMDS) through metaMDS. Total and life form (herbs, shrubs and trees) richness patterns were calculated. Altogether, 158 species of vascular plants under 60 families and 136 genera were recorded. Gramineae was the richest family followed by Leguminosae, Asteraceae and Cyperaceae. Total species richness showed significant negative correlation with the NMDS1 and NMDS2, which justified a convergent pattern of succession. Herb, orchid and shrub species richness also showed significant declining pattern with NMDS1. *Persicaria barbata, Parthenium hysterophorus, Ageratum conyzoides* and *Typha angustifolia* were early succession indicator species; whereas *Albizia lucidior, Miliusa velutina, Ficus hispida, Bauhinia purpurea* and *Brassaiopsis glomerulata* were the late succession tree species. This study agreed with the convergent model of succession.

Key-words: chronosequence, convergence, NMDS, primary succession, RDA, spatio-temporal, species richness.

Introduction

Ecological succession – the science of ecosystem development after colonization by different plant species, their life forms and their gradual changes in degrees of dominance, diversity and abundance over time – remains paradox in the biological science (Pielou 1966; Sousa 1979). Ecological succession has its root in the early 19th century. Myriads of scientific researches have been conducted to answer the question related to successional changes (Pidgeon 1940; Connell and Slatyer 1977; Chapin *et al*. 1994; Caccianiga *et al*. 2006). Barren land succession pattern after volcano (Vitousek *et al.* 1993; Nara *et al.* 2003; Walker and del Moral 2003), glacier moraine succession pattern after deglaciation (Chapin *et al.* 1994; Fastie 1995; Dolezal *et al.* 2008), river basin succession pattern after floods (Bryant 1987; Salo *et al.* 1986; Johansson *et al.* 1996; Schimel *et al.* 1996) are some of the important studies to understand science of primary succession.

Various biological colonization models have been proposed to unravel the mechanism of succession by plants and their life forms (Kitayama *et al.* 1995; Wardle *et al.* 2004). Facilitation, inhibition and tolerance are three common mechanisms to explain biological colonization patterns in succession (Connell and Slatyer 1977; Sigler *et al.* 2002; Bruno *et al.* 2003). Earlier studies unveiled the importance of colonizing species' life-form composition (Dolezal *et al.* 2008), habitat conditions (Tilman 1985), soil chemistry and soil nutrients (Carson and Barrett 1988), and below ground microbial activities (Ohtonen *et al*. 1999) in the succession pattern. Likewise, properties of succession such as species richness patterns along temporal gradient was studied by Álvarez-Molina *et al.* (2012).

Development of complex communities through simple plant life forms such as lichen crusts to stands of trees are the characteristic features of the primary succession (Grime 1977) where herbs, sub-shrubs and shrubs are their intermediate stages (Wiegleb and Felinks 2001; Zhang 2005). It is obvious that there is a variation in the species composition (Dzwonko and Loster 1992; Dolezal *et al.* 2008) and richness (Grubb 1977; Álvarez-Molina *et al.* 2012) of each plant life form through temporal gradient during succession. Particularly,

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the number of species are changing through time. Succession pattern can either be converging when number of species decreases with time (Rydin and Borgegård 1988; Lichter 1998; Fukami *et al.* 2005) or diverging when number of species increases with time (Wood and del Moral 1987; Sarmiento *et al.* 2003; Nicol *et al.* 2005; Baniya *et al.* 2009). Convergence pattern exemplifies the condition where there is decrease in the total species richness through time (Tilman 1987; Martínez *et al.* 2001). In contrast, the divergence pattern represents the increase in total species richness through time (Glenn-Lewin and van der Maarel 1992).

During succession, patterns of species richness might also be different according to life forms (Wardle *et al.* 1995). For instance, herbaceous species showed decreasing richness pattern with temporal gradient (Walker and del Moral 2003), but tree species showed both increasing (Nemergut *et al.* 2007) as well as unimodal (Guo 2003) richness patterns with temporal gradient. According to the life-history strategies during colonization, species are ruderals (*r*) and competitors (*k*) during succession. All early colonizing species are called ruderals or '*r'* selected species whereas the late colonizing species are competitors or '*k'* selected species.

Above and below ground habitat conditions undergo a series of modifications during successional events (McLendon and Redente 1992; Olff *et al.* 1993; Lichter 1998). Canopy cover fluctuates with time (Pena Claros 2003; Pugnaire *et al.* 1996) that varies amount of light fallen on the ground. These properties ultimately bring changes primarily on the higher life forms, like trees and climbers, but limits abundance and richness of understory herbs and shrubs (Grubb 1977). Meanwhile, there are changes in below ground properties, such as physiochemical properties of soil and its fertility (Crews *et al.* 1995) as well as changes in soil microbial activities (Ohtonen *et al.* 1999) during succession.

River basin is an ecosystem where colonization pattern can be clearly visualized from early to late stages of succession. Lowland in Nepal is almost flat, formed after deposition of sediments carried by upstream rivers. River basin succession study is one of the unique sectors where soil texture changes from sandy (nutrient poor, high moisture, high minerals, and low humus content) to alluvial soil (nutrient rich, low moisture, low minerals and high humus content) (McLendon and Redente 1992; Vetaas 1994; Lichter 1998; Ohtonen *et al.* 1999; Jones and Henry 2003). These respective changes facilitate the plants of different strategies, i.e. *r*- and *k*-selected species (Grime 1977). At the same time, disturbance (such as fire and grazing) may play a pivotal role in seed dispersal in the river basin succession (Salo *et al.* 1986; Ward and Stanford 1995; Turner *et al*. 1998).

Chitwan National Park and its Buffer Zone in south-central Nepal encompasses a unique ecosystem for distinct fauna such as Bengal Tiger and One horned Rhino, and flora such as *Shorea robusta*. Rapti and Budhi-Rapti rivers passing through this national park and buffer zone shifted frequently in different directions at different periods that fragmented the landscape each year. Habitats thus created after shifting of river is a good site to study plant colonization.

Succession study is always constrained by measurement of temporal gradient since it was built. Shorter temporal gradient can be measured after direct measurement. However, direct measurement of longer temporal gradient is not feasible. Thus, indirect measurement of succession by means spatio-temporal ordination method is a good choice (Matthews 1978; Vetaas, 1994; Aikio *et al*. 2000; Mesquita *et al.* 2001; Caccianiga *et al.* 2006). In this method, space is substituted by time which is a highly adopted method of measuring succession. This study of primary succession along the Budhi-Rapti floodplain has been initiated with the general objective of deciphering the succession pattern of colonizing plant species. The specific objectives were to find the life form species richness and species composition pattern along Budhi-Rapti river bank, Chitwan National Park, Central Nepal.

Materials and Methods

STUDY AREA

Budhi-Rapti river bank lies at the Khorsor zone of Barandabhar corridor in Chitwan National Park (CNP), south-central Nepal (Figure 1). CNP is the first national park in Nepal, established in 1973, covering an area of 932 km^2 (DNPWC 2010). CNP comprises diverse ecosystems from lowland tropical forests to floodplains and Churia hills draining by Rapti, Reu and Narayani rivers. Altitude of CNP ranges from 100 to 815 m above sea level (asl). Almost 70% of the park area is dominated by Tarai hardwood sal (*Shorea robusta*) forest, followed by deciduous riverine forest (7%), and *Pinus roxburghii* forest (3%) (DNPWC 2010). Budhi-Rapti floodplain acts as a wildlife corridor between CNP and Mahabharat foothills (Panwar 1986; Litvaitis *et al.* 1996; Aryal *et al.* 2012). The east-west national highway passes through the Barandabhar forest. This is a highly disturbed forest under severe human pressure.

The study area lies in the tropical monsoon climatic zone with three seasons: summer, winter and monsoon. During winter (October to February) northerly dry winds enter here from the Himalayas and the Tibetan plateau so that the temperature is reduced up to 8°C. Rainfall is scanty during winter. Temperature reaches up to 37°C (DNPWC 2015) during summer (February to mid-June). The hottest months are May to early June. Monsoon starts from mid-June and lasts in late September during which 80% of the annual rainfall occurs. July and August receive maximum rains. Mean daily temperature ranges from 25^{0}C to 34^{0}C (DNPWC 2015) during this season. Monsoon rain causes dramatic floods and changes in the character and courses of rivers.

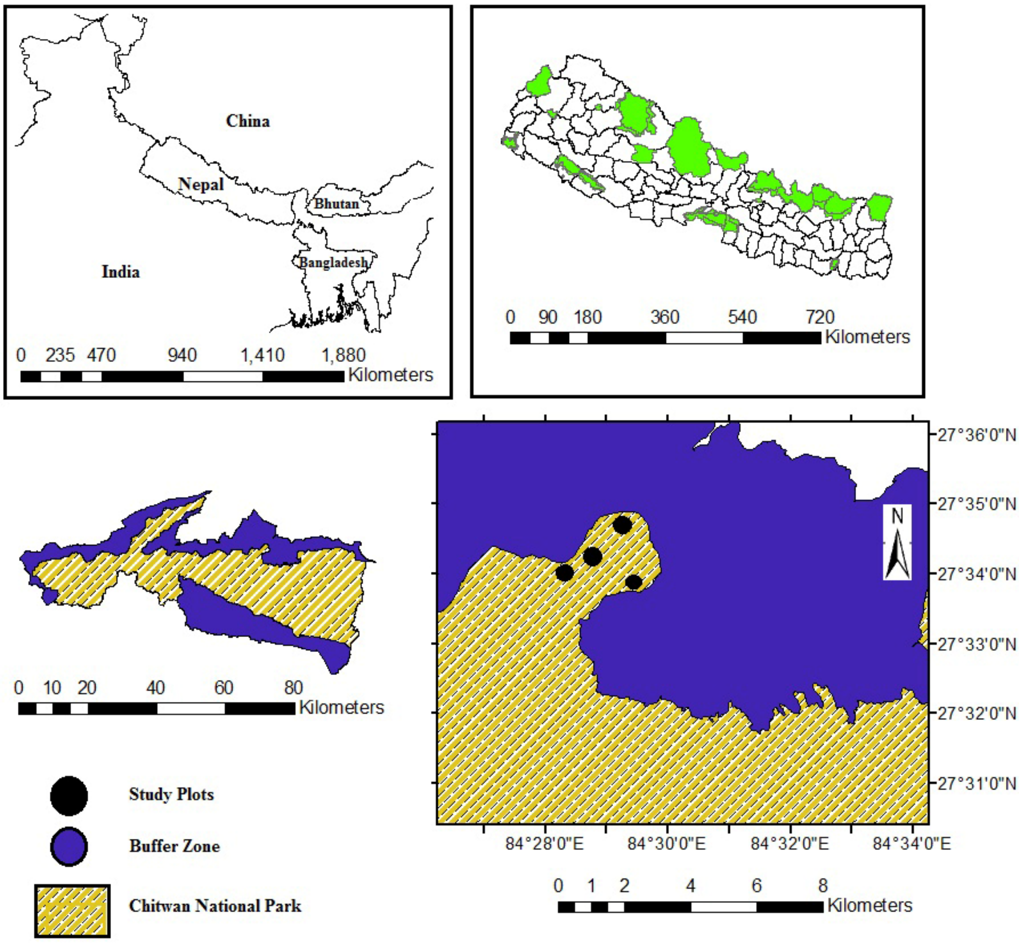

Figure 1. Map of the study area

LOCATION OF THE SAMPLING PLOT AND MEASUREMENT

The field work for this study was conducted during June and October of 2014. First, a reconnaissance survey was made for the preliminary idea about the floodplain formation, orientation and location. In addition, information about the formation of the Budhi-Rapti floodplain was also obtained through review of relevant literature and interview with CNP authorities and local elderly people. The floodplain was believed to be the youngest and slowly getting matured with increasing distance from the river. Thus, sampling was done on the floodplain after relaying on the principle of space-with-time substitution method as developed by Matthews (1978).

Data on the plant species colonization pattern was obtained after sampling the vegetated floodplain that lied perpendicular to the Budhi-Rapti river but almost 200 m away from the river bank. Systematic sampling was applied along two parallel transects (T1 and T2) separated almost 200 m apart from each other (Figure 2). Sampling along the transect started right after 200 m away from the Budhi-Rapti river bank. Initial position of these transects towards Budhi-Rapti river was believed to be the youngest floodplain, which slowly getting

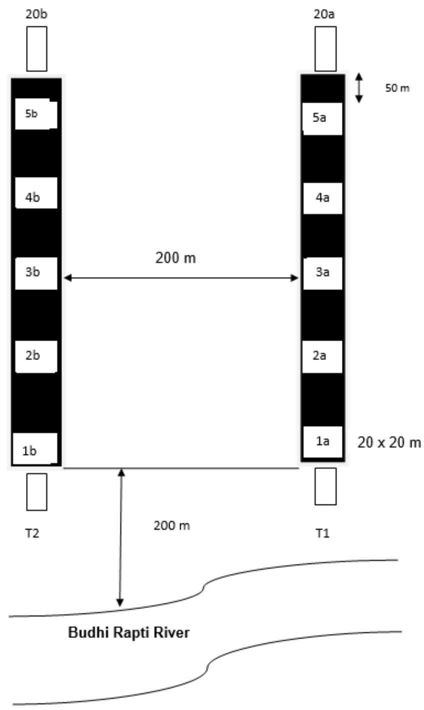

Figure 2. Sampling design.

older after passing away from the river. Abundance of vascular plant species was recorded in sample plots of 20 × 20 m each subdivided equally into 4 subplots (each of 100 m^2). In each transect, 20 such plots were placed consecutively and 50 m apart from each other (Figure 2). Consecutive plots, along the parallel transects (T1 and T2), were believed to have similar temporal scale, thus assigned same number but different alphabets i.e., 1a and 1b; 2a and 2b, and so on. Subplots were marked as 1, 2, 3 and 4 in the clockwise direction. Presence and absence of all vascular plant species within each subplot was recorded in the scale of 1 or 0 respectively. Thus, presence of a species in a plot means an abundance score of 1 to 4. In total, 40 plots were sampled in two transects with a total sampling area of 1.6 ha.

PLANT COLLECTION, HERBARIUM PREPARATION AND IDENTIFICATION

Voucher specimens of all species encountered in sample plots were collected and dried properly. Preliminary identification of plant species was done with the help of field guides (e.g., Polunin and Stainton 1984; Stainton 1988) and through expert consultation in Biodiversity Conservation Center (BCC), Chitwan, Nepal. Species identity was later confirmed by comparing with the specimens deposited at the national herbaria (TUCH and KATH). However, some species, mainly belonging to the genera *Vanda*, *Oberonia*, *Bulbophyllum* and *Carex* remained unidentified. They were definitely separate species but were ranked here by generic name only. Plant species were categorized into six life-forms: herb, shrub, climber, tree, orchid and fern (Baniya *et al.* 2009). Press *et al.* (2000) was followed for the nomenclature of flowering plants and Gurung (1991) was followed for the nomenclature of pteridophytes.

MEASUREMENT OF TEMPORAL GRADIENT

Spatio-temporal gradient was the main predictor variable in this study, which was indirectly obtained as the first axis sample score value after non-metric multidimensional scaling (NMDS) analysis of samples by species dataset (Matthews 1978). We believed NMDS orders samples based upon species abundance as sample scores value after simple indirect ordination method. Position of each sample plot indicated temporal score. No priori or transformation was considered during NMDS. Previous studies (e.g., Whittaker 1987; Zhang *et al*. 2016) applied NMDS sample scores to measure succession in their studies. Lower NMDS first axis sample score represents early succession and higher NMDS first axis sample score represents late succession. Likewise, zero NMDS first axis score represents the mid succession. We acknowledge the value of detrended correspondence analysis (DCA) for the analysis of similar dataset. However, we understood DCA applies transformation by segments and thus we did not use it in our case.

NUMERICAL ANALYSIS

Sample by species data matrix was prepared prior to the quantitative analysis. Sample plots 1a and 1b entered first were believed to be the youngest gradient representing plots, likewise plots 20a and 20b represented the oldest gradient in this study. Since two-two plots represented the same temporal gradient, thus these were made one-one after total averaging. This averaging was done with abundance score from 0 to 8. Thus, total plots became 20 with area of 800 m^2 (2 × 20 × 20 m) after averaging. Reason for this total averaging was just to avoid spatial autocorrelation. All analyses were based on 800 m^2 (2 × 20 × 20 m) plots.

Pearson's correlation coefficients were calculated between response variables [total species richness and its derivatives (climber richness, fern richness, herb richness, orchid richness, shrub richness and tree richness)] and predictors variables, such as NMDS1, NMDS2 and elevation. Correlation coefficient matrix was prepared with probability value (p) (Oksanen *et al.* 2015).

Normality among the response variables were checked by using *Shapiro Wilcox* test. The generalized linear model (GLM; MacCullagh and Nelder 1989) was used for the simple linear regression analysis between response and predictor variables. The GLM up to the second order models were tested. The F-statistics was used to select the statistically best significant model ($p \leq 0.05$). The graphics was prepared from the best selected model.

Non-metric multidimensional scaling (NMDS) is an indirect ordination method in which samples and species are ordered in an ordination space based on various types of distances (Euclidean distance in this case). Its axes are representative of underlying gradients. This gradient has been used to map samples in simplified, two-dimensional ordination space (Schmidtlein *et al*. 2007). Thus, sample score values presented by NMDS1 and NMDS2 were utilized as environmental variables as suggested by previous researchers (Matthews 1978; Aikio *et al.* 2000; Mesquita *et al.* 2001; Caccianiga *et al.* 2006; Sahu *et al.* 2008).

In this study NMDS1 sample score was found highly correlated with the total species richness than was with NMDS2 (see Table 1). Thus, the total species richness change with NMDS1 must likely represents a temporal gradient.

Zero inflation in the data set was detected after the changing trend in the axis length value during the detrended correspondence analysis (DCA). The axis length value found higher in some of the higher axis. This error in the dataset caused multi-collinearity. Thus, this error was corrected after removing single or double times occurring species throughout the whole dataset prior to the multivariate analysis. Thus, performed DCA resulted the first axis length value less than 2.5 SD units. This allowed us to apply redundancy analysis (RDA) for the direct gradient analysis to see the pattern of species composition along the floodplain. During RDA, the best fitted statistically significant environment variables were chosen after internal regression, forward selection and 999 times permutations (Oksanen *et al.* 2015). Statistically significant results obtained after RDA were shown thrown graphics.

All operating systems were performed through Ubuntu and libreoffice as office package. All statistical analyses were done in R program (R Core Team 2016). Ordination was done by using *vegan* package (Oksanen *et al.* 2015).

Results

PLANT SPECIES DIVERSITY

A total of 158 plant species under 60 families and 136 genera were recorded. Gramineae was the richest family followed by Fabaceae, Asteraceae, Cyperaceae, Lamiaceae, Euphorbiaceae and Verbenaceae (Appendix 1). Herb was the most dominant life form with 66 species, followed by tree (48 species), shrub (23), climber (12), fern (6) and orchid (3) (Figure 3).

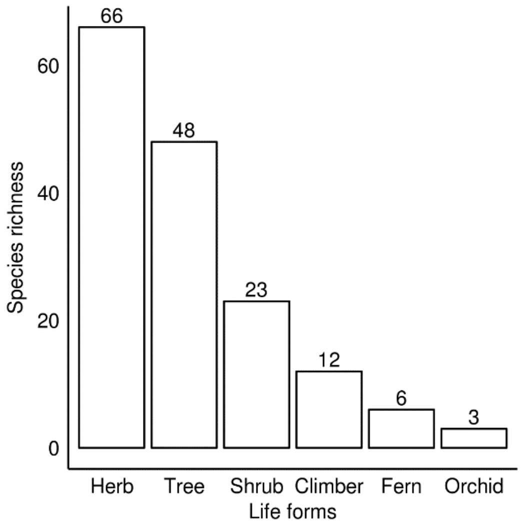

Figure 3. Species richness pattern with different life forms.

PEARSON CORRELATION COEFFICIENTS AMONG VARIABLES

The total species richness showed statistically significant ($p \leq 0.05$) positive correlation with herb richness (r = 0.94, Table 1). Likewise, total species richness showed significant positive correlation with orchid richness (r = 0.62) and shrub richness (r = 0.56). Negative correlations were found between NMDS1 and total species richness (r = –0.69), herb richness (r = –0.58), orchid richness (r = –0.78) and shrub richness (r = –0.72) (Table 1). Similarly, orchid richness showed statistically significant positive relationships with herb richness (r = 0.50) and shrub richness (r = 0.58).

REGRESSION ANALYSIS

Total species richness showed significant negative linear relationships (R^2 = 1.0) with NMDS1 and NMDS2 (Figures 4a, 4b; Appendix 2). No significant relationship obtained between climber species richness and NMDS1 and NMDS2 (Appendix 2). Fern species richness also showed insignificant relationship with both NMDS1 and NMDS2 (Appendix 2). Herb species richness showed significant negative linear relationship (R^2 = 0.3 and 0.4 respectively) with NMDS1 and NMDS2 (Figure 5a, 5b; Appendix 2). Orchid species richness also showed significant negative linear relationship (R^2 = 0.5) with NMDS1 (Figure 6), but the relationship with NMDS2 was insignificant (Appendix 2). Similarly, shrub species richness

Table 1. Pearson correlation coefficient matrix showing relationships among variables. The significant correlation coefficients ($p \leq 0.05$) are marked in bold.

Variables*	NMDS1	NMDS2	Alt	Sppn	Clim_rich	Fern_rich	Herb_rich	Orchid_rich	Shrub_rich	Tree_rich
NMDS1	1	0	-0.03	**-0.69**	0.06	0.38	**-0.58**	**-0.78**	**-0.72**	0.08
NMDS2		1	0.17	**-0.47**	0.02	-0.27	**-0.59**	0.03	0.28	-0.19
Alt			1	-0.13	0.03	0.3	-0.22	0.13	-0.13	0.22
Sppn				1	-0.12	0.03	**0.94**	**0.62**	**0.56**	0.21
Clim_rich					1	-0.11	-0.24	0	-0.04	-0.22
Fern_rich						1	0	-0.35	-0.32	0.38
Herb_rich							1	**0.5**	0.37	0.08
Orchid_rich								1	**0.58**	-0.04
Shrub_rich									1	-0.16
Tree_rich										1

* Alt – altitude; Clim-rich – climber species richness; Fern-rich – fern species richness; Herb_rich – herbaceous species richness; NMDS1 - non-metric multidimensional scaling axis 1; NMDS2 - non-metric multidimensional scaling axis 2; Orchid_rich – orchid species richness; Shrub_rich – shrub species richness; Sppn – total species richness; Tree_rich – tree species richness.

showed significant negative linear relationship ($R^2 = 0.5$) with NMDS1 (Figure 7) and insignificant relationship with NMDS2 (Appendix 2). Relationships of tree species richness with NMDS1 and NMDS2 were also insignificant (Appendix 2). There was no significant pattern between altitude and both axis values of NMDS (Appendix 2).

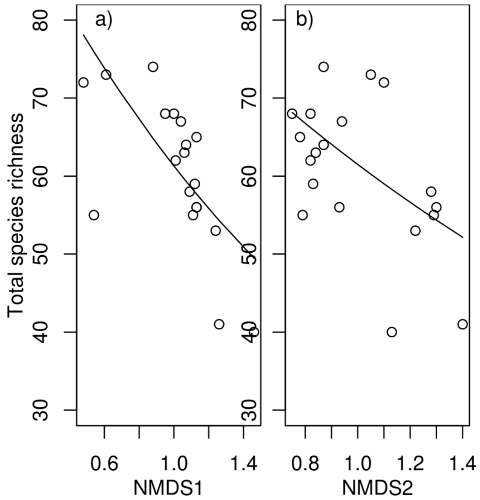

Figure 4. Relationship between total species richness and NMDS1 (a) and NMDS2 (b) based on simple linear regression analysis using generalized linear model.

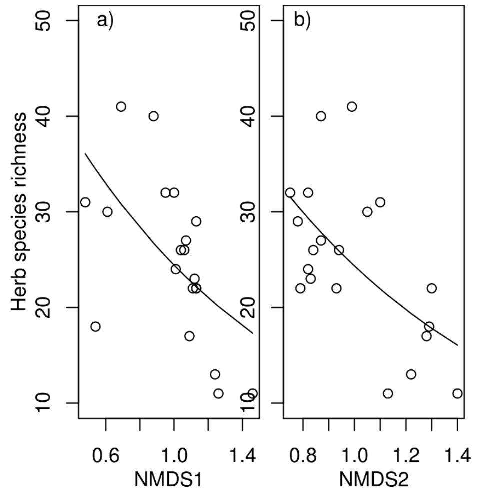

Figure 5. Relationship between herb species richness and NMDS1 (a) and NMDS2 (b) based on simple linear regression analysis using generalized linear model.

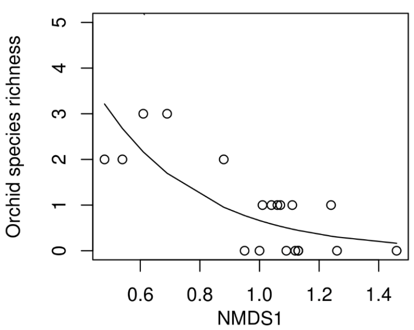

Figure 6. Relationship between orchid species richness and NMDS1 based on simple linear regression analysis using generalized linear model.

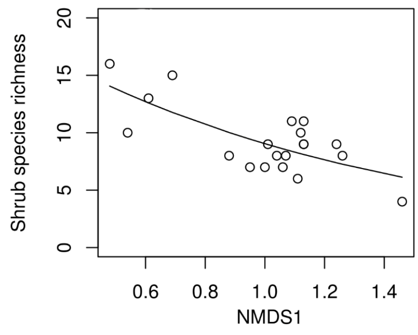

Figure 7. Relationship between shrub species richness and NMDS1 based on simple linear regression analysis using generalized linear model.

ORDINATION

DCA summary – The sample by species data matrix showed shorter lengths of gradient, 1.7 standard deviation unit (SD unit) by the first axis of DCA (Table 2). The length of gradient was found decreasing gradually with increasing axis. The variance explained by other axes was also found gradually decreasing with increasing axis. These results confirmed the linear pattern among species along the main succession gradient studied and allowed to choose linear direct ordination method, which is redundancy analysis (RDA).

Table 2. DCA summary.

	DCA1	DCA2	DCA3	DCA4
Eigenvalues	0.2	0.14	0.07	0.06
Decorana values	0.23	0.12	0.07	0.04
Axis lengths	1.65	1.41	1.33	1.26

RDA analysis – Two statistically significant environmental axes, *viz*. NMDS1 and NMDS2 were obtained after 999 times permutations with species score. These number of permutations normalized the correlation value. The NMDS1 represented significantly the first axis of RDA that corresponded to the main gradient of this study which was the temporal gradient. The negative end of NMDS1 represented indicators to younger succession whereas the positive end represented indicators to the oldest gradient. All species as well as samples nearer around these respective ends of the gradient were indicators of that particular type of temporal gradient.

Abundance of *Albizia lucidior* (abbreviated as Albi. Luci in the ordination diagram), *Lygodium japonicum* (Lygo. japo), and *Fimbristylis dichotoma* (Fimb.dich) were highly significant towards plots with the highest value of NMDS1 (Figure 8; Appendix 1). The highest abundance of *Parthenium hysterophorus* (Part.hyst), *Persicaria barbata* (Pers.barb) and *Ficus religiosa* (Ficu.reli) towards the negative end of RDA first axis supported the plots with the least value of NMDS1, which were early colonizers. The abundance of *Albizia lucidior* and *Lygodium japonicum* towards the positive end of RDA first axis may indicate that these were the late succession indicator species. NMDS2 represented by the second axis of RDA (Table 1, Figure 8). The abundance of *Commelina benghalensis* (Comm.beng), *Hypoxis aurea* (Hypo.aure), *Cyperus niveus* (Cype.nive) and *Alternanthera philoxeroides* (Alte.phil) supported by the least value of NMDS2 indicated high disturbance and less moisture towards negative end of RDA second axis (Figure 8; Appendix 1). The highest abundance of *Persicaria pubescens* (Pers.pune), *Flemingia macrophylla* (Flem.macr) and *Ageratum conyzoides* (Ager.cony) towards positive end of RDA second axis may support more moisture loving and less disturb indicators.

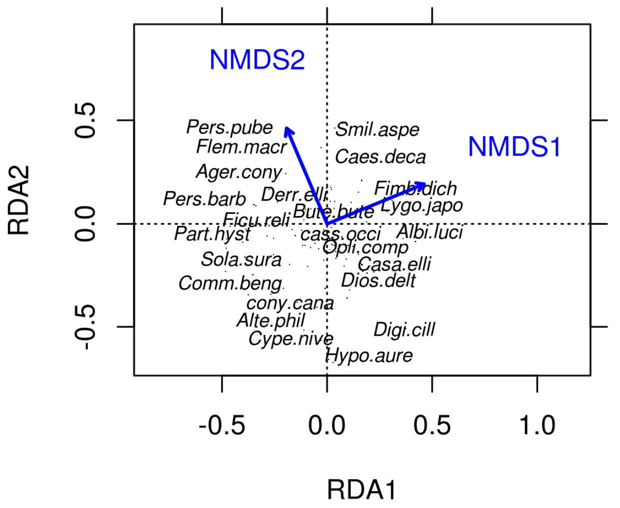

Figure 8. Species and environment biplot after redundancy analysis (RDA). Species abbreviation as in Appendix 1.

Discussion

Succession is a universal and ubiquitous phenomenon which varies with space and properties. Budhi-Rapti river that passes through Chitwan National Park and its buffer zone shifted frequently in different directions at different periods thus creating unique floodplain area. The floodplain has been colonized by different plant species. Plant species of different life forms have found colonized in a definite pattern which characterized the habitat as well as environment created either by themselves or externally imposed. Hence, our findings stated that the area has been experiencing a deterministic and convergent type of succession. This culminates into matured sal (*Shorea robusta*) forest at the end of the successional gradient.

The floodplain showed herb species richness comparatively higher than other life forms. The probable explanation of this result could be that the studied temporal gradient is still younger. The environment created by soil of the study sites, *i.e.* the sand dunes formed nearby the river bank is relatively younger. Younger sand dunes would have lesser humus but high amount of mineral content which primarily favors the growth and establishment of short growing plants. Generally, these characters are good match for herbs which exhibit a short life span and are generally opportunistic (i.e., *r*-selected) species (Jones and Henry 2003). Likewise, trees and shrubs are found colonized at matured sand dunes.

Measurement of succession gradient is almost impossible at short duration of observation. However, gradient is universal and succession is no exception (Huston 1994). Measurement of succession is a matter of big challenge. Introduction of ordination in community ecology (Matthews 1978; Vetaas 1994; Aikio *et al.* 2000; Mesquita *et al.* 2001; Caccianiga *et al.* 2006; Baniya *et al*. 2009) and implementation of non-metric multidimensional scaling (NMDS) (Matthews 1978; Aikio *et al.* 2000; Mesquita *et al.* 2001; Caccianiga *et al.* 2006) greatly helped to overcome this shortcoming. The NMDS utilizes, via *vegan*, a free community ecology analysis package (Oksanen *et al.* 2015). During NMDS, samples and their species are presented on the basis of their abundance without bias. Sample score values of the NMDS first axis is always highly correlated with main gradient of study, which is succession in this case. Adoption of NMDS1 as succession gradient has been justified by this study.

As the value of NMDS1 increases, abundance of climax-stage-loving species also increases. The second axis may represent the soil moisture gradient as having higher abundance of moisture-loving species and alluvial-soil-loving species towards this NMDS2 gradient. These two axes were taken as major environmental variables to explain species richness, its derivatives and their composition during succession. High occurrence of those indicator species around successional and moisture gradients also matched with similar earlier results such as Olff *et al.* (1993).

The total species richness stood as the strongest response variable in this study that showed statistically significant ($p \leq 0.05$) but negative linear relationship with both NMDS1 and NMDS2. Tree, herb, shrub, orchid, climber and fern richness indicated their major share to the total species richness. Herb and shrub species richness were found decreasing with increasing NMDS1 scores. However, tree species richness was found insignificantly related with both NMDS axes. High richness of tree species at late stage of succession may facilitate higher canopy cover (Turner *et al.* 1998), high carbon biomass, high water table but low soil moisture (Olff *et al.* 1993). Conversely, more diversity and species richness were found towards the beginning of NMDS1 or plots nearby river bank (early succession).

During this floodland succession, herbs and shrubs species may indicate the early-stage species with their higher richness at lower range of NMDS1. Similarly, at the later stages, tree species are also increasing. Due to higher canopy cover at climax stage there would be less herb and shrub species (Turner *et al.* 1998). Due to high soil moisture at the beginning of this study, or at the early succession stages, there were higher number of invasive species (direct observation from the field). Thus, the decreasing pattern of total species richness with NMDS1 is justified. This is matched with justification given by Aikio *et al.* (2000), Mesquita *et al.* (2001), and Caccianiga *et al*. (2006) in their study.

The observed successional changes in the species composition may also be associated with the seed dispersal pattern of respective species which may be facilitated by wild herbivores (Duncan and Chapman 1999). Plant species of short life cycle or ruderals may increase richness after germination if seeds got chance to drop off from their fur while visiting water sources. That may result high diversity at early stage habitats due to less competition for light and moisture resources compared to late successional habitats.

Total species richness is significantly correlated with herb species richness, i.e. the total species richness is largely governed by the number of herb species in the study site. Junk and Piedade (1997) found similar finding of higher number of terrestrial herbaceous species nearby Amazon floodplain. The result of convergent pattern of total species richness is in agreement with a number of previous studies (Lichter 1998; Fukami *et al.* 2005; Sluis 2002) though the driving factor in this study may be different than the previous studies. Decrease in total species richness can also be explained by various factors that may change during successional stage (represented by NMDS1). Soil biophysical properties – soil characteristics (organic matter content, nutrient cycling; Carson and Barrett 1988), microbial activity (Ohtonen *et al.* 1999), pH and moisture (Olff *et al.* 1993); aboveground vegetation – litter fall, canopy cover and disturbance (Turner *et al.* 1998) may have resulted this model. However, the pattern of species richness for each life from differs on increasing gradient. For instance, in case of herbaceous species, there is significant decrease in richness with increasing NMDS1. Changes in soil characteristics from sandy to clay or alluvial and decrease in soil nutrients (Vitousek and Reiners 1975; Tilman 1985; Mitsch *et al.* 2005) on one hand, and increased canopy cover of tree species on the other represent the changes in the habitat condition during succession (Prach and Pyšek 2001; Wiegleb and Felinks 2001).

Various factors, like seed dispersal, animal movement and grazing may contribute high herb species richness nearby the river bank. Similar condition prevails in case of shrubs. In contrast, fern richness and tree richness increased with increasing distance from the river bank not significantly. Shady and moist condition of forest floor provide suitable site for ferns to flourish (Yarranton *et al.* 1974; Chapin *et al.* 1994). Furthermore, disturbance, like fire has little influence on the regeneration of pteridophytes **(**Turner *et al.* 1998; Walker *et al.* 2010**)**. Likewise, the increased tree species richness may have facilitated by high nutrient input, high microbial activity and efficient intake of nutrient by trees. Frequent outbreak of fire, high canopy cover and litter fall also limit the growth and development of shrubs and herbs underneath the forest (Olff *et al.* 1993; Fukami *et al.* 2005). Consequently, habitat of increased tree species richness assisted the higher number of climbers in the respective habitat, resulting an increasing pattern of climber species richness with NMDS1. Herb species such as *Persicaria barbata, Parthenium hysterophorus,* and *Ageratum conyzoides* having high abundance towards the positive end of NMDS2 but negative end of NMDS1 represented the early successional species. Likewise, high abundance of tree species such as *Albizia lucidior, Ficus religios, Shorea robusta* (not seen in figure axes) towards positive end of NMDS1 axis represent the late successional species. This study clearly supported the earlier findings of convergence pattern of floodplain succession.

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Appendix 1. Plant species recorded in the sample plots, their abbreviated form (used in ordination), lifeform, frequency and NMDS1 score value.

S.N.	Scientific name	Short form	Family	Life form	Frequency %	NMDS1
1	*Achyranthes aspera* L.	Achy aspe	Amaranthaceae	Herb	5	-0.800
2	*Adiantum capillus-veneris* L.	Adia capi	Pteridaceae	Fern	39	0.156
3	*Aegle marmelos* (L.) Corr.	Aegl marm	Rutaceae	Tree	1	-0.963
4	*Ageratina adenophora* (Spreng.) R.M. King & H. Rob.	Ager aden	Asteraceae	Herb	5	-0.406
5	*Ageratum conyzoides* (L.) L.	Ager cony	Asteraceae	Herb	44	-0.116
6	*Albizia lucidior* (Steud.) I.C. Nielsen	Albi luci	Fabaceae	Tree	28	0.290
7	*Albizia procera* (Roxb.) Benth.	Albi proc	Fabaceae	Tree	6	0.153
8	*Alstonia scholaris* (L.) R. Br.	Alst scho	Apocynaceae	Tree	78	0.138
9	*Alternanthera philoxeroides* (Mart.) Griseb	Alte phil	Amaranthaceae	Herb	27	-0.209
10	*Alternanthera sessilis* (L.) R. Br. ex DC.	Alte ses	Amaranthaceae	Herb	31	0.125
11	*Amaranthus viridis* L.	Amar viri	Amaranthaceae	Herb	2	-0.041
12	*Anisomeles indica* (L.) Kuntze	Anis indi	Lamiaceae	Herb	3	-0.931
13	*Anogeissus latifolius* (Roxb. ex DC.) Bedd.	Anog lati	Combretaceae	Tree	1	0.124
14	*Anthocephalus chinensis* (Lam.) Walp	Anth chin	Rubiaceae	Tree	1	0.302
15	*Antidesma bunius* (L.) Spreng.	Anti buni	Euphorbiaceae	Tree	2	0.234
16	*Apluda mutica* L.	Aplu muti	Poaceae	Shrub	11	-0.290
17	*Ariopsis peltata* Nimmo	Ario pelt	Araceae	Herb	8	-0.039
18	*Artemisia indica* Willd.	Arte indi	Asteraceae	Shrub	4	-0.451
19	*Artocarpus lakoocha* Roxb.	Arto lako	Moraceae	Tree	1	-0.071
20	*Asparagus officinalis* L.	Aspa offi	Liliaceae	Shrub	2	0.306
21	*Bauhinia purpurea* L.	Bauh purp	Fabaceae	Tree	2	0.606
22	*Bombax ceiba* L.	Bomb ceib	Bombacaceae	Tree	1	0.131
23	*Brachiaria kurzii* (Hook. f.) A. Camus	Bras kurz	Fabaceae	Herb	19	-0.115
24	*Brassaiopsis glomerulata* (Blume) Regel	Bras glom	Araliaceae	Tree	2	1.022
25	*Breynia retusa* (Dennst.) Alston	Brey retu	Euphorbiaceae	Shrub	12	0.370
26	*Bulbophyllum* sp.	Bulb spp	Orchidaceae	Orchid	11	-0.657
27	*Butea buteiformis* (Voigt) Mabb.	Bute bute	Fabaceae	Shrub	2	0.193
28	*Caesalpinia decapetala* (Roth) Alston	Caes deca	Fabaceae	Climber	14	0.381
29	*Calamus acanthospathus* Griff.	Cala acan	Arecaeae	Shrub	5	-0.053
30	*Callicarpa macrophylla* Vahl	Call macr	Verbenaceae	Shrub	48	-0.035
31	*Carex filicina* Nees.	Care fili	Cyperaceae	Herb	17	0.341
32	*Carex inanis* Kunth	Care inan	Cyperaceae	Herb	3	-0.433
33	*Carex nivalis* Boot	Care niva	Cyperaceae	Herb	7	0.135
34	*Carex* sp.	Care spp	Cyperaceae	Herb	9	0.137
35	*Careya arborea* Roxb.	Care arbo	Lecythidaceace	Tree	7	0.041
36	*Casearia elliptica* Willd.	Casa elli	Flacourtiaceae	Shrub	27	0.135
37	*Cassia occidentalis* L.	Cass occi	Fabaceae	Shrub	1	0.282
38	*Cassia tora* L.	Cass tora	Fabaceae	Herb	25	-0.453
39	*Centella asiatica* (L.) Urban	Cent asia	Apiaceae	Herb	9	-0.187
40	*Cestrum nocturnum* L.	Cest noct	Solanaceae	Shrub	6	-0.365
41	*Chromolaena odorata* (L.) R.M. King & H. Rob.	Chro odor	Asteraceae	Shrub	79	-0.021
42	*Chrysopogon aciculatus* (Retz.) Trin	Chry acic	Poaceae	Herb	8	-0.393
43	*Cissus repens* Lam.	Ciss repe	Vitaceae	Climber	29	0.125
44	*Citrullus colocynthis* Schrad.	Citr colo	Cucurbitaceae	Climber	33	0.116
45	*Cleistocalyx operculatus* (Roxb.) Merr. & L.M. Perry	Clei oper	Myrtaceae	Tree	77	0.011

S.N.	Scientific name	Short form	Family	Life form	Frequency %	NMDS1
46	*Clerodendrum viscosum* Vent.	Cler visc	Verbenaceae	Shrub	134	0.031
47	*Colebrookea oppositifolia* Sm.	Cole oppo	Lamiaceae	Shrub	16	0.001
48	*Colocasia esculenta* (L.) Schott.	Colo escu	Araceae	Herb	44	-0.099
49	*Commelina benghalensis* L.	Comm beng	Commelinaceae	Herb	19	-0.420
50	*Conyza canadensis* (L.) Crong.	Cony cana	Asteraceae	Herb	23	-0.232
51	*Conyza leucantha* (D. Don) Ludlow & Raven	Cony leuc	Asteraceae	Herb	5	-0.252
52	*Corchorus aestuans* L.	Corc aest	Tiliaceae	Herb	65	0.031
53	*Corchorus capsularis* L.	Corc caps	Tiliaceae	Herb	87	0.031
54	*Cordia dichotoma* Forster	Cord dich	Cordiaceace	Tree	1	-0.019
55	*Costus speciosus* (Koenig.) Sm.	Cost spec	Zingiberacceae	Herb	84	0.001
56	*Curcuma domestica* Valeton.	Curc dome	Zingiberaceae	Herb	4	0.219
57	*Cyanotis vaga* (Lour.) J.A & J.H. Schult	Cyan vaga	Commelinaceae	Herb	58	-0.081
58	*Cynodon dactlylon* (L.) Pers	Cyno dact	Poaceae	Herb	10	-0.682
59	*Cyperus compressus* L.	Cype comp	Cyperaceae	Herb	35	-0.104
60	*Cyperus niveus* Retz.	Cype nive	Cyperaceae	Herb	55	-0.158
61	*Cyperus rotundus* L.	Cype rotu	Cyperaceae	Herb	42	-0.153
62	*Dalbergia sissoo* DC.	Dalb siss	Fabaceae	Tree	11	-0.942
63	*Derris acuminata* Benth.	Derr elli	Fabaceae	Tree	9	-0.105
64	*Desmodium multiflorum* DC.	Desm mult	Fabaceae	Shrub	33	-0.084
65	*Desmostachya bipinnata* (L.) Stapf	Desm bipi	Poaceae	Herb	10	0.008
66	*Digitaria ciliaris* (Retz.) Koeler	Digi cill	Poaceae	Herb	23	0.124
67	*Dillenia pentagyna* Roxb.	Dill pent	Dilleniaceae	Tree	88	0.001
68	*Dioscorea bulbifera* L.	Dios bulb	Dioscoreaceae	Climber	99	0.060
69	*Dioscorea deltoidea* Wall. ex Griseb.	Dios delt	Dioscoreaceae	Climber	42	0.082
70	*Dryopteris cochleata* (D.Don) C. Chr.	Dryo coch	Aspidiaceae	Fern	74	-0.021
71	*Dysoxylum binectariferum* (Roxb.) Hook.f. ex Bedd.	Dyso bine	Meliaceae	Tree	5	0.031
72	*Echinochloa colona* (L.) Link	Echi cola	Poaceae	Herb	1	-0.019
73	*Ehretia acuminata* R. Br.	Ehre acum	Cordiaceae	Tree	9	0.173
74	*Eleocharis retroflexa* (Poir.) Urb.	Eleo retr	Cyperaceae	Herb	2	-0.192
75	*Elephantopus scaber* L.	Elep scab	Asteraceae	Herb	44	0.063
76	*Eleusine indica* (L) Gaertn	Eleu indi	Poaceae	Herb	3	-0.175
77	*Eragrostis tenella* (L.) Beauvois ex Roem. & Sch	Erag tene	Poaceae	Herb	4	-0.201
78	*Ficus hispida* L. f.	Ficu hisp	Moraceae	Tree	2	0.554
79	*Ficus racemosa* L.	Ficu race	Moraceae	Tree	1	-0.800
80	*Ficus religiosa* L.	Ficu reli	Moraceae	Tree	2	-1.013
81	*Fimbristylis dichotoma* (L.) Vahl.	Fimb dich	Cyperaceae	Herb	27	0.236
82	*Flemingia macrophylla* (Willd.) Merrill	Flem macr	Fabaceae	Shrub	15	-0.198
83	*Floscopa scandens* Lour.	Flos scan	Commelinaceae	Herb	20	0.079
84	*Fraxinus floribunda* Wall.	Frax flor	Oleaceae	Tree	7	0.149
85	*Garuga pinnata* Roxb.	Garu pinn	Burseraceae	Tree	5	-0.372
86	*Gmelina arborea* Roxb.	Gmel arbo	Verbenaceae	Tree	9	0.245
87	*Hedychium ellipticum* Buch.-Ham. ex Sm.	Hedy elli	Zingiberaceae	Herb	97	0.031
88	*Helminthostachys zeylanica* L.	Helm zeyl	Ophioglossaceae	Fern	43	-0.147
89	*Holarrhena pubescens* Wall. ex G. Don	Hola pube	Apocynaceae	Tree	8	-0.334
90	*Hypoxis aurea* Lour.	Hypo aure	Hypoxidaceae	Herb	44	-0.005
91	*Hyptis suaveolens* (L.) Poit.	Hypt suav	Lamiaceae	Herb	11	-0.164
92	*Imperata cylindrica* (L.) Raeusch.	Impe cylin	Poaceae	Herb	49	-0.053
93	*Indigofera dosua* Buch.-Ham. ex D. Don	Indi dosu	Fabaceae	Shrub	3	0.026

S.N.	Scientific name	Short form	Family	Life form	Frequency %	NMDS1
94	*Lactuca sativa* L.	Lact sati	Asteraceae	Herb	3	-0.850
95	*Lagerstroemia parviflora* Roxb.	Lage prav	Lythraceae	Tree	61	0.019
96	*Lantana camara* L.	Lant cama	Verbenaceae	Shrub	3	-1.063
97	*Leea crispa* L.	leea cris	Leeaceae	Shrub	2	-1.063
98	*Leea macrophylla* Roxb. ex Hornem	Leea macr	Leeaceae	Shrub	82	0.084
99	*Leucas indica* (L.) R. Br. ex Vatke	lecu indi	Lamiaceae	Herb	2	-0.637
100	*Litsea monopetala* (Roxb.) Pers.	Lits mono	Lauraceae	Tree	112	0.031
101	*Lobelia chinensis* Lour.	Lobe chine	Lobeliaceae	Herb	40	-0.141
102	*Ludwigia hyssopifolia* (G. Don) Exell	Ludw hyss	Onagraceae	Herb	2	0.277
103	*Lygodium japonicum* (Thunb.) Sw.	Lygo japo	Schizaeaceae	Fern	68	0.220
104	*Maesa chisia* Buch.-Ham. ex D. Don	Maes chis	Myrsinaceae	Tree	80	0.031
105	*Mallotus philippensis* (Lam.) Muell.	Mall phil	Euphorbiaceae	Tree	82	0.138
106	*Marsdenia roylei* Wight	Mars royl	Asclepiadaceae	Climber	18	0.003
107	*Mentha spicata* L.	Ment spic	Lamiaceae	Herb	1	-0.637
108	*Mikania micrantha* Kunth.	Mika micr	Asteraceae	Climber	60	-0.014
109	*Miliusa velutina* (Dunal.) Hook.	Mili velu	Meliaceae	Tree	96	0.256
110	*Mitragyna pravifolia* (Roxb.) Korth.	Mitr prav	Rubiaceae	Tree	3	-0.942
111	*Momordica cochinchinensis* (Lour.) Spreng.	Momo coch	Cucurbitaceae	Climber	4	-0.800
112	*Murraya koenigii* (L.) Spreng.	Murr koen	Rutaceae	Tree	78	0.031
113	*Oberonia* sp.	Ober spp	Orchidaceae	Orchid	6	-0.487
114	*Ophioglossum reticulatum* L.	Ophio reti	Ophioglossaceae	Fern	66	0.084
115	*Oplismenus compositus* (L.) P. Beauv	Opli comp	Poaceae	Herb	10	0.296
116	*Oxalis corniculata* L.	Oxal corn	Oxalidaceae	Herb	21	-0.489
117	*Parochetus communis* D. Don	Paro comm	Fabaceae	Herb	8	0.171
118	*Parthenium hysterophorus* L.	Part hyst	Asteraceae	Herb	9	-0.866
119	*Paspalum distichum* L.	Pasp dist	Poaceae	Herb	33	-0.221
120	*Persicaria barbata* (L.) Hara	Pers barb	Polygonaceae	Herb	15	-0.450
121	*Persicaria pubescens* (Blume) H. Hara	Pers pube	Polygonaceae	Herb	20	-0.162
122	*Phoenix sylvestris* Roxb.	Phoe sylv	Palmae	Tree	33	0.039
123	*Phyllanthus amarus* Thonn.	Phyl amar	Euphorbiaceae	Herb	5	-0.931
124	*Phyllanthus emblica* L.	Phyl embl	Euphorbiaceae	Tree	3	0.163
125	*Phyllanthus niruri* L.	Phyl niru	Euphorbiaceae	Herb	93	-0.003
126	*Pilea symmeria* Wedd.	Pile symm	Urticaceae	Herb	3	0.428
127	*Piper logum* L.	Pipe logu	Piperaceae	Climber	15	0.276
128	*Pogostemon benghalensis* (Burm. f.) Kuntze	Pogo beng	Lamiaceae	Shrub	66	-0.182
129	*Pouzolzia hirta* Blume ex Hassk	Pouz hirt	Urticaceae	Herb	50	-0.181
130	*Premna integrifolia* L.	Prem inte	Verbenaceae	Tree	4	0.188
131	*Pteris aspericaulis* Wall. ex. J. Agardh	Pter aspe	Pteridaceae	Fern	15	0.237
132	*Rumex dentatus* L.	Rume dent	Polygonaceae	Herb	1	0.302
133	*Rumex vesicarius* L.	Rume vesi	Polygonaceae	Herb	41	-0.003
134	*Saccharum procerum* Roxb.	Sacc proc	Poaceae	Herb	11	-0.069
135	*Salvia coccinea* Buc'hoz ex Etl.	Salv cocc	Lamiaceae	Shrub	16	-0.632
136	*Schleichera oleosa* (Lour) Oken.	Schl oleo	Sapindaceae	Tree	4	0.027
137	*Scutellaria discolor* Colebr.	Scut disc	Lamiaceae	Herb	33	0.197
138	*Semecarpus anacardium* L. f.	Seme anac	Anacardiaceae	Tree	2	0.216
139	*Setaria pallidefusca* Hubb.	Seta pall	Poaceae	Herb	15	-0.208
140	*Shorea robusta* Gaertn.	Shor robu	Dipterocarpaceae	Tree	116	0.031
141	*Sida acuta* Burm. f.	Sida acut	Malvaceae	Tree	17	-0.242
142	*Sida rhombifolia* L.	sida rhom	Malvaceae	Shrub	18	-0.012

S.N.	Scientific name	Short form	Family	Life form	Frequency %	NMDS1
143	*Smilax aspera* L.	Smil aspe	Liliaceae	Climber	5	0.558
144	*Solanum surattense* Burm. f.	Sola sura	Solanaceae	Shrub	11	-0.393
145	*Spondias pinnata* (L. f.) Kurz.	Spon pinn	Anacardiaceae	Tree	16	0.277
146	*Stephania japonica* (Thunb.) Miers	Step japo	Menispermaceae	Climber	9	-0.764
147	*Strobilanthes atropurpureus* Nees	Stro atro	Acanthaceae	Herb	18	-0.249
148	*Syzygium cumini* (L.) Skeels	Syzy cumi	Myrtaceae	Tree	19	0.099
149	*Terminalia alata* Heyneex. Roth	Term alat	Combretaceae	Tree	41	0.194
150	*Terminalia bellirica* (Gaertn.) Roxb.	Term bell	Combretaceae	Tree	10	-0.011
151	*Terminalia myriocarpa* Van Heurck & Müll. Arg.	Term myri	Combretaceae	Tree	2	-1.063
152	*Themeda arundinacea* (Roxb.) A. Camus	Them arun	Poaceae	Herb	8	-0.376
153	*Thespesia lampas* (Cav.) Dalz	Thes lamp	Malvaceae	Tree	12	0.366
154	*Trewia nudiflora* L.	Trew nudi	Euphorbiaceae	Tree	42	0.016
155	*Trichosanthes anguina* L.	Tric angu	Cucurbitaceae	Climber	10	-0.942
156	*Typha angustifolia* L.	Typh angu	Typhaceae	Herb	1	-0.637
157	*Vanda tessellata* (Roxb.) Hook. ex G. Don.	Vand tess	Orchidaceae	orchid	28	-0.289
158	*Ziziphus mauritiana* Lam.	Zizi maur	Rhamnaceae	Tree	3	-0.433

Appendix 2. Results of generalized linear model.

S. No.	Variable	Residual df	Residual deviance	Deviance	R^2	*F*-value	Pr(>*F*)
1	Sppn ~ NMDS1	19	2204.2				
		18	20.01	2184.2	1.0	2038.2	$<2.2e^{-16}$ ***
2	Climb_rich~NMDS1	19	34.95				
		18	6.314	28.636	0.8	82.204	$3.946\ e^{-08}$ ***
3	Fern_rich~NMDS1	19	17.75				
		18	3.7559	13.994	0.8	67.787	$1.624\ e^{-07}$ ***
4	Herb_rich~NMDS1	19	1342.55				
		18	38.41	1304.1	1.0	638.58	$1.643\ e^{-15}$ ***
5	Orchid_rich~NMDS1	19	19.8				
		18	13.471	6.3289	0.3	10.74	0.0042 **
6	Shrub_rich~NMDS1	19	159.75				
		18	8.229	151.52	0.9	334.8	$4.448\ e^{-13}$ ***
7	Tree_rich~NMDS1	19	80.55				
		18	4.655	75.895	0.9	292.85	$1.394\ e^{-12}$ ***
8	Alt~NMDS1	19	5407.2				
		18	31.2	5376	1.0	3278.3	$<2.200\ e^{-16}$ ***
9	Sppn~NMDS2	19	2204.2				
		18	28.42	2175.8	1.0	1367	$<2.200\ e^{-16}$ ***
10	Climb_rich~NMDS2	19	34.95				
		18	6.333	28.617	0.8	81.913	$4.051\ e^{-08}$ ***
11	Fern_rich~NMDS2	19	17.75				
		18	4.0383	13.712	0.8	63.097	$2.711\ e^{-07}$ ***
12	Herb_rich~NMDS2	19	1342.55				
		18	36.35	1306.2	1.0	626.7	$1.937\ e^{-15}$ ***
13	Orchid_rich~NMDS2	19	19.8				
		18	25.274	-5.4744	-0.3		ns
14	Shrub_rich~NMDS2	19	159.75				
		18	15.406	144.34	0.9	165.66	$1.620\ e^{-10}$ ***
15	Tree_rich~NMDS2	19	80.55				
		18	4.518	76.032	0.9	301.33	$1.094\ e^{-12}$ ***
16	Alt~NMDS2	19	5407.2				
		18	30.4	5376.8	1.0	3366.5	$< 2.200\ e^{-16}$ ***