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Research Article

Ecological Problem of Diversity-productivity Relationship Elucidated Through Statistical Analysis of Experimental Microcosmic Plant Communities

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Abstract

Background: Augmented anthropogenic activities are posing a direct threat to species diversity at regional and global scale for past many decades. Ecologists are very much alarmed about the serious repercussions of diversity-loss and predicting depauperate and poor functioning ecosystems in near future. However, the results of many such studies have been questioned too, on the basis of faulty inclusion of high productive species in experiments that rendered the relationship between diversity and ecosystem functioning debatable. **Objective:** Present study tries to find out the answer and deals exclusively with the effects of species diversity and richness on the productivity of plant communities in microcosms. **Methodology:** Pearson correlation and analysis of variance (ANOVA) carried out across all communities to observe the effect of species diversity and richness on herb productivity, indicated a highly significant and positive relationship ($r = 0.85$, $F = 20.93$, $p<0.001$), ($r = 0.76$, $F = 11.23$, $p<0.01$), respectively. **Results:** The results lend support to diversity-productivity hypothesis even at smaller scale ecosystems. This study comes to a new finding that at smaller scale ecosystems, the role of growth forms proves to be redundant and what matters most is species diversity and richness on the functioning of ecosystems. **Conclusion:** The present study accentuates the issues of ecological conservation and elucidates that more diverse and species rich areas are prerequisite for better functioning ecosystems. Therefore, this study recommends the conservation of biodiversity and that the productivity and functioning of an ecosystem can be enhanced by conserving and promoting its alpha diversity.

Key words: Species diversity, species richness, ecosystems, ecosystem functioning, biomass, productivity, microcosms

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Data Availability: All relevant data are within the paper and its supporting information files.

INTRODUCTION

Augmented anthropogenic activities for past several decades have elevated concern for the existence of species and populations and its impact on ecosystems. These concerns have initiated a lot of observational and experimental studies on the relationship between species richness and ecosystem functioning and restoration ecology[1-7]. In many ecological studies, the impact of species richness on ecosystem functioning was investigated by comparing different ecosystem types varying in species numbers or alike ecosystems distributed at different geographical locations[8,9]. There are different parameters to study the functioning of an ecosystem, out of which productivity is considered as one of the excellent indicator of ecosystem functioning[6,10]. Topical studies which were performed in different ecosystems have shown that several communities and ecosystem processes are positively correlated with species diversity[1,11,12]. Yet many objections were also raised about the generality of these biodiversity effects[13-15]. As a result, it has been squabbled that the consequences of biodiversity loss are likely to be idiosyncratic, differing quantitatively and qualitatively between trophic groups and ecosystems[16,17]. Previous studies have shown that change in species equitability occurs much before does occur species extinction in ecosystem under anthropogenic influence. Therefore, it warrants increased and immediate attention[18].

There are no exact available data about the current rates of species extinction. Yet some scientific estimates place it somewhere between two and three orders of magnitude higher than rates found in fossil records[19,20]. So, the concern over the effect of diversity-loss on ecosystem functioning is a hot topic in contemporary ecological studies.

In order to study the effects of community indices on ecosystem functioning and stability, experimental microcosms have been very successful. Many latest and significant developments in community ecology have been derived from experiments conducted in microcosms. Studies with microcosms have addressed a broad variety of phenomena, including climate change, biodiversity, assembly rules, habitat restoration, trophic dynamics and mycorrhizal associations. The common factor linking these studies are that they manipulate an individual environmental axis and explore the role that axis plays in structuring communities[21]. It has also been suggested that microcosms and mesocosms can be a useful approach for apparently intractable global problems, such as ecosystem responses to climate change or managing biodiversity through the design of nature reserve[22].

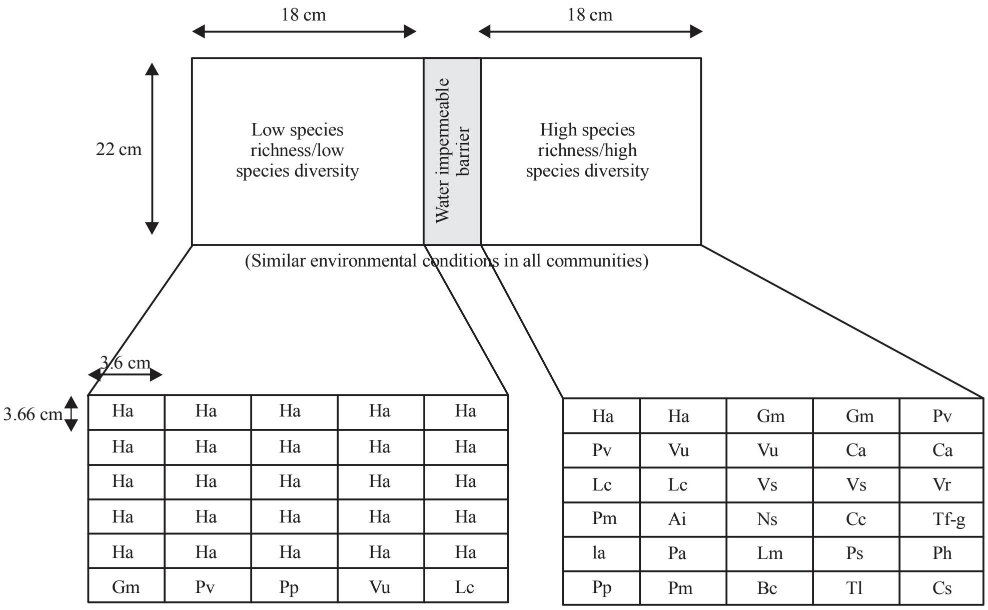
The main objective of this study was to observe the effect of species diversity and richness on the functioning of experimental plant communities in microcosms. The study was designed in such a way that adjoining plots of a pair did not differ significantly in their immediate environmental conditions, whereas they differed significantly in their species richness and diversity values. Present experimental setup allowed us in correlating and understanding the relationship among diversity, richness, growth forms and microcosm functioning even with similar environmental conditions.

MATERIALS AND METHODS

Establishment of experimental microcosms: This study was conducted from May, 2011 to January, 2012 and a total of ten experimental plant communities with 300 seeded individuals in microcosms were raised in the greenhouse of Higher College of Technology, Muscat (Sultanate of Oman). The dimensions of microcosms were $36\times22\times5$ cm^3 and were almost same as designed and studied in a species richness and drought effect study in experimental plant communities[23]. Each microcosm was then filled with 500 g of commercial compost (Total N = 100 ppm, P_2O_5 = 185 ppm and K_2O_5 = 250 ppm). Furthermore, each microcosm was divided into two equal plots (18×22 = 396 cm^2) by water impermeable barriers following[23]. In this way we maintained similar environmental conditions in all adjoining plots of pair in the studied microcosms (Fig. 1).

Species heterogeneity in plant communities (pairs of low and high species richness and diversities): For the establishment of plant communities, a total of 25 different herbs were used and chosen randomly for each plot. The herbs used for present study were of different mean stem length. Examples of studied herbs were *Glycine max*, *Phaseolus vulgaris* L., *Vigna ungiculata* (L). *Walp.*, *Cicer arientinum*, *Lens culinaris*, *Vigna radiata*, *Nigella sativa* L., *Cuminum cyminum*, *Pimpinella anisum* L., *Pisum sativum*, *Coriandrum sativum*, *Trigonella foenum-graecum*, *Macrotyloma uniflorum* and *Thymus vulgaris* etc. (Table 1 and Fig. 1).

In each pair of microcosms, one plot was labeled as Low Species Richness (LSR) while other as High Species Richness (HSR). As a result, a total of 10 adjoining LSR and HSR plots were created in the experimental setup. Each plot was further divided into 30 smaller areas of 3.66×3.60 cm (13.2 cm^2 area), having 1 seed/13.2 cm^2. That's how, this study could ensure that throughout all microcosms each individual was interacting with other in a defined area of available ecological



Ha	Ha	Ha	Ha	Ha
Ha	Ha	Ha	Ha	Ha
Ha	Ha	Ha	Ha	Ha
Ha	Ha	Ha	Ha	Ha
Ha	Ha	Ha	Ha	Ha
Gm	Pv	Pp	Vu	Lc

Ha	Ha	Gm	Gm	Pv
Pv	Vu	Vu	Ca	Ca
Lc	Lc	Vs	Vs	Vr
Pm	Ai	Ns	Cc	Tf-g
Ia	Pa	Lm	Ps	Ph
Pp	Pm	Bc	Tl	Cs

Fig. 1: Schematic representation of experimental design showing two plant communities in a pair of plots. See the low species richness or diversity with tall stem class species i.e., *Helianthus annus* and high species richness or diversity with comparatively smaller stem class species. The diagram is just an example of two adjoining communities composition. Other communities were raised by various other species compositions as per the diversity gradient of present study

Table 1: Description of herb species in experimental plant communities in microcosms

Species name	Species code	Plant family	Mean stem length (cm)
Pisum sativum	Ps	Fabaceae	15
Coriandrum sativum	Cs	Apiaceae	12
Vigna radiata	Vr	Fabaceae	16
Glycine max	Gm	Fabaceae	30
Lens culinaris	Lc	Fabaceae	15
Phaseolus vulgaris	Pv	Fabaceae	18
Brassica campestris	Bc	Brassicaceae	15
Vigna sinensis	Vs	Fabaceae	20
Phaseolus mungo	Pm	Fabaceae	16
Vigna ungiculata	Vu	Fabaceae	30
Cicer arietinum	Ca	Fabaceae	25
Petunia parviflora	Pp	Solanaceae	20
Trigonella foenum-graecum	Tf-g	Fabaceae	25
Nigella sativa	Ns	Ranunculaceae	15
Iberis amara	Ia	Brassicaceae	30
Cuminum cyminum	Cc	Apiaceae	25
Pimpinella anisum	Pa	Apiaceae	21
Helianthus annus	Ha	Asteraceae	30
Chrysanthemum morifolium	Cm	Asteraceae	22
Macrotyloma uniflorum	Mu	Fabaceae	30
Thymus vulgaris	Tv	Lamiaceae	22
Petunia hybrida	Ph	Solanaceae	17
Lobularia maritima	Lm	Brassicaceae	15
Tagetes lucida	Tl	Asteraceae	28
Asystasia intrusa	Ai	Acanthaceae	23

resources. In this way, 30 seeds of different species ($30\times13.2 = 396$ cm^2) were sown in each plot according to desired equitability or evenness to maintain adjoining low and high diverse ecosystems in each microcosmic pair (Table 2 and Fig. 1).

Growth form (stem length classes) and their significance: The stem lengths of each species was also recorded and distributed in 3 different growth form classes viz., short herbs (0-14 cm), medium herbs (15-20 cm) and tall herbs (21-30 cm). The percent share of these growth forms was found to be

Table 2: Paired t-test between High Species Richness (HSR) and adjoining Low Species Richness (LSR) communities in all 5 pairs of experimental microcosms

Parameters	HSR (Mean)	LSR (Mean)	Mean difference	t-value	Significance level (df = 4)
Species richness (S)	15.20	4.00	11.20	4.16	$p<0.01$
Shannon-Weiner index of species diversity (H')	2.38	0.45	1.93	7.85	$p<0.001$
Evenness/Equitability (E)	0.903	0.326	0.577	12.95	$p<0.001$
Productivity/Biomass (g)	115.28	60.87	54.41	4.41	$p<0.01$

4, 40 and 56%, respectively among the species pool thus showing somewhat equal distribution between medium and tall herbs. The stem lengths of various herbs are of great significance in present microcosm study. In a recent study in experimental grassland, high community mean values of shoot length also contributed to high community biomass[24]. Since, it has been shown that the stem height or growth is positively related to aboveground biomass production[25,26]. This study took the stem length as an indicator of species biomass. The data were collected in order to observe the apparent effect of diversity, richness and growth forms on microcosm productivity. In some previous experimental studies, it was argued that higher diversity plots had more productive species which made it difficult to explain the effect of diversity on productivity. As according to a study of Huston[27] in ECOTRON study[1] the highly productive species were only included in the highest diversity treatment, rendering detection of a relationship between diversity and productivity inevitable. In the Cedar Creek diversity experiment[28] the apparent diversity effect was because of greater probability of containing the most productive species in the high species richness treatment.

Species diversity and equitability: Diversity is the combination of two factors, species richness i.e., number of species and distribution among species, referred as equitability or evenness[29]. This study established ten different levels of diverse communities by manipulating the richness and equitability of different species per plot. Equitability or evenness was measured by equation[30]:

$$E = \frac{H'}{\ln(S)}$$

where, E is equitability or evenness index, H' is Shannon-Weiner diversity index and S is total species richness at the site. Species diversity of adjoining plant communities was calculated by Shannon-Weiner diversity index:

$$H' = -\sum_{i=1}^{S} p_i \ln p_i$$

where, S is the total number of species or species richness, p_i is relative abundance of each species and ln is natural log[31]. Each plot was irrigated at an interval of 48 h with an equal amount of distilled water (500 mL).

Estimation of aboveground community biomass: After 6 weeks of treatment, peak aboveground community biomass was calculated by harvest method, where clipping was done by hand with the help of sharp scissors. In order to obtain a valid estimation of the herbage, the vegetation was harvested very close to surface level[32]. The harvested plants were put in hot air oven at 80°C for 48 h to get biomass values[6], which were expressed in terms of grams (g).

Statistical analysis of data: In order to understand the effect of community indices i.e., species diversity and richness on the functioning of microcosms, the data was statistically analyzed for Mean ± Standard Error, linear regression, one way analysis of variance (ANOVA), Pearson bivariate correlation and paired t-test. All statistical analysis were performed using SigmaPlot (Systat Software, San Jose, California USA) and IBM SPSS Statistics for Windows, Version 20.0. Armonk, NY: IBM Corp.).

RESULTS AND DISCUSSION

Comparison between percent soil moisture and pH: Over the past few decades, accelerating rates of species extinction have prompted an increasing number of studies to reduce species diversity experimentally and examine how this alters the efficiency by which communities capture resources and convert those into biomass[20,33,34]. So, ecologically there is currently much interest in understanding how loss of biodiversity might alter ecological processes vital to the functioning of ecosystems[35]. As an alternative, ecologists have approached this problem by investigating how diversity influences stability and function within a multi-trophic setting in controlled microcosm experiments. The main advantage of microcosms is that they can easily be manipulated and replicated[36]. This study designed to keep the soil environment constant in each microcosm by using the commercial compost. This study also compared percent soil moisture and soil pH between adjoining plots of pairs in each microcosm before and at the end of experiment. For comparing the mean difference between abiotic components of high and low diverse plots of a pair we used paired t-test analysis. The results showed that percent soil moisture ($t = -0.27$, $df = 4$, $\alpha = 0.05$, $p = 0.40$) and pH ($t = 0.84$, $df = 4$, $\alpha = 0.05$, $p = 0.22$) did not differ significantly between high and low species richness plots across all microcosms. This was a good indicator to show that we were able to keep the abiotic environment constant among all studied plots of microcosms. In many earlier studies it was observed that soil nutrients were manipulated among various plant communities that increased variability in correlating diversity and ecosystem functioning[37]. Whereas, keeping the soil environment constant helped us to elucidate the apparent effect of community characteristics on ecosystem functioning.

Significant differences in species richness and diversity among all pairs of plots: Ecologists also found a strong effect of diversity on productivity and evidence suggestive of a simultaneous effect of composition and productivity[4]. The species composition (meaning the particular types and combinations of species present) has been reported to influence ecological processes to a much greater extent than the number of species[27,38-42]. The species richness between adjoining HSR and LSR plots was designed in such a way that all HSR plots (Mean = 15.2) had significantly greater species richness ($t = 4.16$, $df = 4$, $\alpha = 0.05$, $p < 0.01$) than their adjoining LSR plots (Mean = 4) (Table 2). However, the total numbers of individuals for each plot was kept constant at 30 individuals, this was done to observe the apparent effect of diversity and richness on productivity (Fig. 1). Shannon-Weiner index of species diversity between adjoining high and low species richness plots of all pairs showed highly significant differences. The high species diverse plots (Mean = 2.38) had significantly greater diversity ($t = 7.85$, $df = 4$, $\alpha = 0.05$, $p < 0.001$) than their adjoining low species diverse plots (Mean = 0.45). Species evenness or equitability values also exhibited similar trends, where high species even plots (Mean = 0.903) had significantly higher evenness values ($t = 12.95$, $df = 4$, $\alpha = 0.05$, $p < 0.001$) than their adjoining low species even plots (Mean = 0.326) (Table 2).

Relationship between species diversity and community productivity: In community ecological studies also, scientists previously thought species richness was mainly responsible for ecosystem functioning. However later on it was found that equitability and diversity were more influential than mere richness. Many previous studies on grassland plant communities[12,28] and even experimental multi-trophic community[1] were thought to show how productivity increases with species richness[43]. However, in later studies suggested what matters most is species diversity of functional groups, with species number per functional group being less important[40]. It has been suggested that due to human interference, abundance is disturbed first than richness i.e., diversity is disturbed first than richness, which ultimately will definitely affect ecosystem functioning. It was suggested that effects of diversity on productivity must come from interactions among individuals of different species[3]. This underlines the importance of evenness/equitability and abundance pattern among individuals, generating various combinations of species to species interactions, than mere species richness. A paired t-test analysis for biomass values showed that high species diverse community (Mean = 115.28 g) had significantly greater productivity ($t = 4.41$, $df = 4$, $\alpha = 0.05$, $p < 0.01$) than adjoining low diverse community (Mean = 60.87 g) (Table 2). Analysis of Variance (ANOVA), linear regression and correlation across all 10 adjoining plots showed that there is clear positive effect of species diversity on herb productivity, with a highly significant and positive relationship ($r = 0.85$, $F = 20.93$, $\alpha = 0.05$, $p < 0.001$) (Fig. 2).

Significant role of species richness and community productivity: In a heterogeneous habitat each species is a superior performer in only a part of site. As the heterogeneity or diversity increases, the magnitude of effect also increases, resulting in an increased coverage of the range of variations in

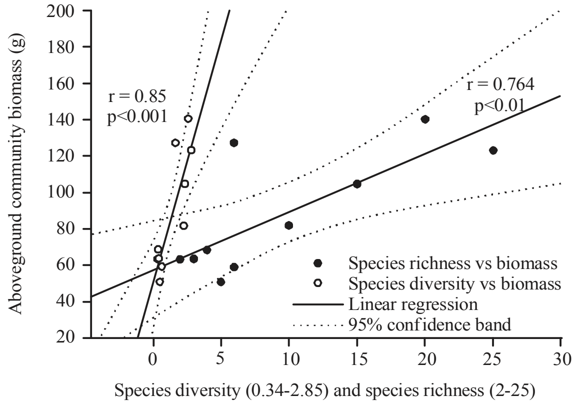


Fig. 2: Linear regression analysis and pearson correlation show that both species diversity and richness are positively correlated with community biomass ($r = 0.85$, $r = 0.76$). The relationship is highly significant at 0.001 and 0.01 levels. The results are shown with 95% confidence band

the condition of habitat. Increased diversity is expected to cause increased efficiency of resource capture and use, because chances increases for the presence of species that are better able to utilize existing conditions. Ecologists found that the significant difference in values of productivity in low species richness and high species richness plots suggests that there is the potential for increasing productivity of a site by realizing its potential α-diversity[5]. Increasing diversity leading to higher productivity may be attributed to 'niche complementarity' theory[40,42]. The niche complementarity theory[39] predicts that differences among species in resource or environmental requirements would allow some combinations of species to more completely capture and use resources and thus have greater productivity than any individual species in monoculture, a phenomenon called over-yielding[44]. Studies investigating the relationship between species diversity and ecosystem functioning have advanced our basic understanding of community dynamics and may ultimately improve conservation by focusing attention on the processes critical to sustaining natural ecosystems[41].

Species richness also had significant positive effect on community productivity in all plots. One way analysis of variance (ANOVA), linear regression and Pearson correlation between species richness and productivity showed that productivity tended to increase with increasing species richness across all 10 experimental plots, exhibiting a significantly positive relationship ($r = 0.76$, $F = 11.23$, $\alpha = 0.05$, $p<0.01$) (Fig. 2).

Species diversity has greater role than species richness on productivity: In the present study, the results of experimental microcosms suggest that species diversity and richness both contribute significantly to microcosm productivity. However, species diversity ($r = 0.85$, $p<0.001$) has the lead over species richness ($r = 0.76$, $p<0.01$) in the functioning of terrestrial microcosms. Results presented in the current study are interesting as this suggests that at smaller levels such as of microcosms the role of growth forms seems to be redundant and what matters most is the diversity and equitability of species. This study found that in the experimental microcosms, percent share of tall herbs was significantly lower in high diversity plots than their adjoining low diversity plots, which reflects the apparent role of species diversity and richness on microcosm productivity. This can be explained by niche complementarity theory[40,42] where more niche model supports more productivity by maximizing the usage of available resources. Similar findings were also reported by community ecologists even in natural ecosystems where a pair by pair survey of plots suggested that majority of HSR plots with higher biomass did not have a greater proportion of tall forbs[5]. It was concluded that when adjacent plots of natural communities are compared, the association between the presence of large and productive species of tall forbs and high species richness and diversity is weak[5,6].

CONCLUSION

The findings of this microcosm study are important as it can be concluded that productivity of sites, even with similar environmental conditions can be increased by promoting and maintaining their alpha diversity. Although, both species diversity and richness contribute to microcosm functioning yet it is the diversity that ultimately regulates the functioning of microcosms and the growth forms may not have a larger role to play at the level of microcosms.

Therefore, this study recommends the need to conserve and maintenance of biological diversity for the better functional microcosms and ecosystems in a larger perspective. In conclusion, this study contributes to understand the unswerving effect of diversity, richness and growth forms on microcosm functioning and accentuates that encouragement must be given for the conservation of species in natural ecosystems.

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