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Species richness pattern of aquatic vascular macrophytes along elevation gradients in Nepal Himalayas

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Abstract. *Siwakoti EA, Nepali B, Mandal TN, Baniya CB. 2023. Species richness pattern of aquatic vascular macrophytes along elevation gradients in Nepal Himalayas. Biodiversitas 24: 6048-6058.* Aquatic vascular macrophytes constitute an important component of aquatic ecosystems. This study aims to determine the species richness pattern of aquatic vascular macrophytes along elevation gradients (100-4900 m asl) in the Nepal Himalayas. We used available published literature on elevational ranges of aquatic vascular macrophytes in Nepal to interpolate the species elevational ranges, thereby providing species richness estimates for 100 m elevational bands. A total of 113 species of aquatic vascular macrophytes belonging to 66 genera under 35 families were recorded from Nepal. Among these macrophytes, dicots were represented by 21 families, monocots with 10 families and pteridophytes with 4 families. Regarding the geographical divisions, the total number of aquatic vascular macrophytes recorded was 76 from the east, 90 from the central and 67 from the west, conclusively central Nepal showed the maximum number of macrophytes. The highest species richness was contributed by Hydrocharitaceae followed by Potamogetonaceae, Plantaginaceae, Lentibulariaceae and Nymphaeaceae. So far, the functional types of macrophytes are concerned, free-floating species were 15, submerged species were 36, floating-leaved species were 18 and emergent species were 44 along elevation gradients in the three geographical divisions in Nepal. The Generalized Linear Model (GLM) was applied to find out the relation between the species richness of aquatic vascular macrophytes with elevation. It showed a statistically significant monotonic declining pattern with increasing elevation. The occurrence of this model was further verified by aquatic vascular macrophyte richness at every 200 m elevation which converged with the general pattern. The study conducted along one of the world's longest bioclimatic elevational gradients led to support the monotonic declining pattern of aquatic vascular macrophytes richness indicating the difference in richness pattern among aquatic and terrestrial ecosystems. It also emphasizes the importance of conserving aquatic ecosystems with their vegetation.

Keywords: Aquatic ecosystems, emergent, floating, geographical division, submerged species

INTRODUCTION

Species richness along elevation gradients has been recognized as a striking ecological phenomenon to explain the geographical variation in the distribution of organisms (Beck et al. 2017). Variations in species richness along elevational gradients have been documented for diverse plant groups and geographical areas (Bhattarai et al. 2014; Bhatta et al. 2018; Liang et al. 2020; Dani et al. 2023; Umair et al. 2023). Species richness along elevational gradients follows three general patterns: a monotonic decrease in species richness with increasing elevation (Khatiwada et al. 2019; Di Musciano et al. 2021), linear increase (Nascimbene and Marini 2015; Kamimura et al. 2017) and a unimodal pattern with mid-elevation peak (Li and Feng 2015; Rawat et al. 2021). Elevational gradient as the main determining factor for aquatic macrophytes richness has been studied in mountain areas such as the Pyrenees (Chappuis et al. 2011; Pulido et al. 2015), Spain (Fernández-Aláez et al. 2018) and Turkey (İkinci and Bayındır 2021). Moreover, elevation has also been shown as a strong influencing factor on aquatic macrophyte diversity irrespective of geographical area (Grimaldo et al. 2016; Alahuhta et al. 2018; Murphy et al. 2019). On the other hand, elevation variation leads to a change in geography (Sun et al. 2019; Pandey et al. 2020), climate, and physico-chemistry of water (Fernández-Aláez et al. 2018; Budhathoki et al. 2021; Chakravarty et al. 2021) and energy-related processes (O'Brien 2006; Vetaas et al. 2019) that contribute to variation in shaping the species distribution and richness pattern. Aquatic macrophytes comprise "aquatic photosynthetic plants", that include some macroalgae, Bryophyta, Pteridophyta and Spermatophyta. Based on their relationships to water level and substrate, aquatic macrophytes are grouped as free-floating, submerged, floating-leaved, and emergent (Chambers et al. 2008). In the present study, we adopted Cook (1996) to define aquatic macrophytes as restricted to Pteridophytes and Spermatophytes.

Aquatic vascular macrophytes, the key components of aquatic ecosystems contribute to the structure and functions of aquatic ecosystems (O'Hare et al. 2018) by altering the physicochemical features of the aquatic environment, nutrient cycling and biotic assemblages and interactions

(Thomaz et al. 2015; Gallardo et al. 2017; Dan et al. 2021). Hence, macrophytes are described as "bio-indicators" of the aquatic environment and are often regarded as "biological engineers" for their contribution to restoring water quality (Ansari et al. 2020). Moreover, freshwater ecosystems rich in macrophytes are recognized as nature's kidneys (Ramachandra et al. 2018). Hence, the preservation of the aquatic macrophytes community in freshwater bodies is considered essential. Low-lying tropical water bodies characterized by average temperatures up to 30°C and less seasonal variation do not significantly affect macrophytes. In contrast, alpine systems where the mean average temperature reaches -20°C or even less, support only stress-tolerant species (Lacoul and Freedman 2006; Kraft et al. 2015; Kreyling et al. 2015). Further, limiting nutrient levels at higher-elevation water bodies represents decreased macrophytes richness (Pulido et al. 2015). Upland aquatic systems are more likely to suffer from exposure to global warming and associated climate change (Önol et al. 2014). Studying elevational gradients in terms of climate change becomes interestingly important because standard temperature decreases at the rate of 0.53°C at every 100 m elevation gradient in Nepal (Bhattarai et al. 2004). Aquatic vascular macrophytes exhibit varying elevational ranges covering either a wide elevational gradient or are extremely restricted (İkinci and Bayındır 2021). In Nepal, only a few studies have addressed the elevational gradients affecting the aquatic vascular macrophytes (Lacoul 2004; Lacoul and Freedman 2006; Upadhyay et al. 2022). Documentation of elevational patterns of vascular macrophytes is of great concern to formulating conservation programs, especially in anthropogenically threatened and climate-affected aquatic ecosystems. The present research hypothesized a monotonically declining pattern of species richness for aquatic vascular macrophytes with increasing elevation. Relating to this hypothesis, the general objective was to assess the species richness pattern of aquatic vascular macrophytes along elevational gradients in three geographical divisions (east, central and west) of Nepal.

MATERIALS AND METHODS

The information for this study came from aquatic environments in Nepal ranging between 26°22' and 30°27'N latitudes and 80°40' and 88°12'E longitudes. (Figure 1). The elevation of the country varies from 60 m asl in the southeastern Tarai to 8,848 m asl in the north at Mt. Everest, the highest peak in the world. Nepal is characterized by a monsoon climate, typical of South Asia (Stacey et al. 2023). Elevation is a complex environmental variable that caused almost 90% of the total variation in surface temperature in this region (Chalise et al. 2003). This study analyzed the species richness of aquatic vascular macrophytes along elevational gradients in three geographical divisions of Nepal. The elevational distribution of macrophytes in Nepal with their geographical divisions was derived from secondary literature such as (Shrestha and Upadhyay1999; Press et al. 2000; Sah et al. 2003; Niroula and Singh 2010; Sharma 2014; Rajbhandari and Rai 2017, 2019; Ghimire et al. 2020; Rajbhandari et al. 2021, 2022; Shrestha et al. 2022). Literature on invasive alien plant species (IAPS) was reviewed by Tiwari et al. (2005); Siwakoti and Karki (2009); Shrestha (2016). Current and valid names were checked through The World Flora Online (WFO) Plant List (2023). WFO Plant List (2023).

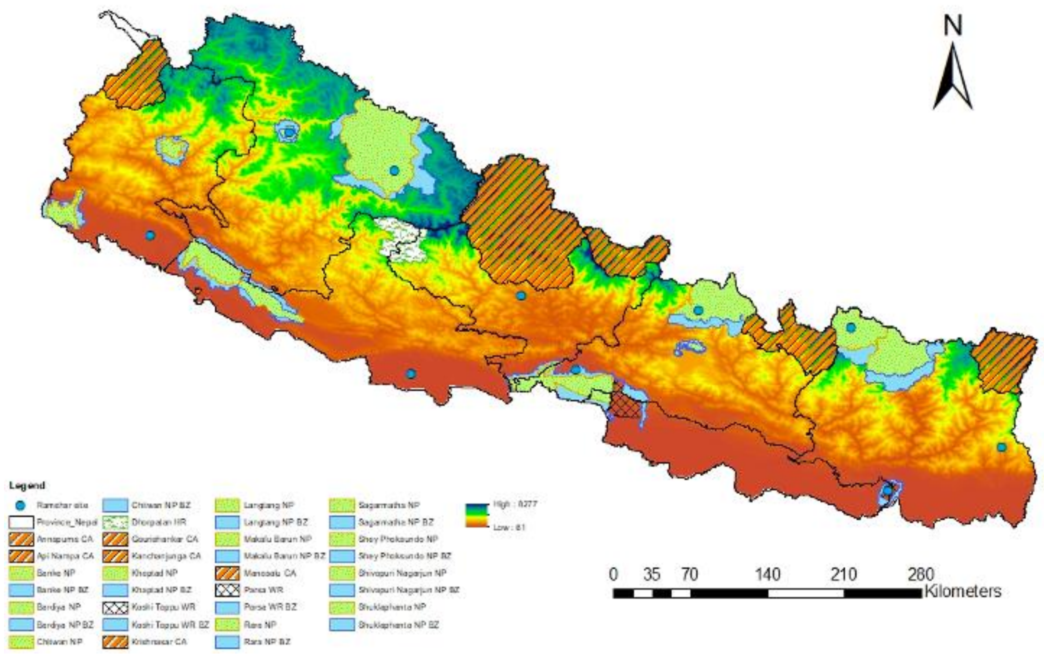


Figure 1. Map of Nepal showing locations of wetlands (•Ramsar sites only)

Aquatic vascular macrophytes are reported from the elevation range of 100-4900 m from Nepal. Elevation was divided equally into 48 bands each with 100 m asl intervals. The elevation range for each species reported in the literature was noted and interpolated at the 100 m asl band. For example, a species named *Potamogeton perfoliatus* L. reported its elevation range of distribution in the published literature as 2800-3400 m asl. During interpolation, this species was considered as distributed through all 2800, 2900, 3000, 3100, 3200, 3300 to 3400 m asl. When a single elevation distribution point comes, that will be considered as a single 100 m. Likewise, all elevations below four, are considered as the lower limit after rounding and equal or above five is considered as the upper limit. For example, a species named *Nymphaea nouchali* Burm. f. was found dispersed between 160-250 m asl. As per the interpolation procedure, this species will occur between 200 to 300 m asl. This procedure of interpolation is similar to earlier studies (Bhattarai et al. 2014; Nepali et al. 2021). Species richness was measured by the species present at every 100 m asl contour. Aquatic vascular macrophytes were categorized as free-floating, submerged, floating-leaved and emergent based on their functional identity in between substrate and water level (Chambers et al. 2008). In this study, the distribution of aquatic vascular macrophytes was looked at on a macroscale covering the entire elevational range within three geographical divisions namely, east, central and west Nepal. Rivers, streams, lakes, ponds, ditches, paddy fields and floodplains were considered the habitat of aquatic vascular macrophytes.

Nomenclature

The nomenclature for vascular macrophytes in this manuscript followed the data presented by the WFO Plant List (2023).

Data analysis

Aquatic vascular macrophyte richness is the discrete response variable. Thus residuals after regression with elevation follow a Poisson distribution that needs a logarithmic log link function (McCullagh and Nelder 2019). This log link function is provided via the Generalized Linear Regression Model (GLM). The Regression models up to the second order were tested after using F-statistics. The best models were presented through graphics. All these analyses were performed through the R program (R Core Team 2022).

RESULTS AND DISCUSSION

Diversity of aquatic vascular macrophytes

Altogether, 113 species of aquatic vascular macrophytes belonging to 66 genera under 35 families were recorded from our study sites in Nepal (Table 1). It contributes 2.13% to the total 5309 flowering plant species of Nepal. Among them, dicots represented 55 species under 31 genera and 21 families and monocots with 51 species under 30 genera and 10 families representing almost equal dicot: monocot ratio (1.08). Aquatic pteridophytes represented by 7 species under 5 genera and 4 families contribute to 1.27% of the total 550 species of Pteridophytes of Nepal. The highest species richness was contributed by Hydrocharitaceae (12 species under 7 genera) followed by Potamogetonaceae (12 species under 3 genera), Plantaginaceae (8 species under 4 genera), Lentibulariaceae (7 species under 1 genus) and Nymphaeaceae (7 species under 2 genera). Similarly, 10 families among dicots and 2 families among monocots were represented by only a single species. Among pteridophytes, Salviniaceae represented the richest family (4 species under 2 genera) while 3 families were represented by a single species. Species richness per genus was the highest in *Potamogeton* (9 species) followed by *Utricularia* (7 species) and *Nymphaea* (6 species). Likewise, 21 dicot, 19 monocot and 3 pteridophyte genera were monospecific. Considering the ecological niche of recorded aquatic vascular macrophytes, free-floatings were 15, submerged were 36, floating-leaved were 18 and emergent were 44. Invasive alien aquatic vascular macrophytes represented by 5 species (18.5%) of the total (27 species) recorded invasive alien plant species in Nepal (Shrestha and Shrestha 2021).

Species richness of macrophytes along three geographical divisions of Nepal

The total number of aquatic vascular macrophytes recorded from different geographical divisions: east, central, and west Nepal were 76, 90 and 67, respectively. Central Nepal showed a maximum number of macrophytes. The number of species confined only to the east, central and west were 10, 16 and 9, respectively. There were 42 vascular macrophytes common among three geographical divisions of Nepal (Figure 2).

The study revealed that the aquatic vascular macrophytes showed a monotonic declining pattern with increasing elevation. The maximum species richness occurred at the beginning of elevation i.e., 100 m asl (Figure 3, Table S1). The occurrence of this model was further verified by analyzing the same species richness at an interval of 200 m elevation. Total aquatic vascular macrophyte richness at every 200 m elevation also showed a similar significant richness pattern as 100 m elevation (Figure 3, Table S2).

Species richness pattern of aquatic vascular macrophytes were further tested as per the geographical divisions in Nepal. In all three geographical divisions, macrophytes richness was found almost similar monotonic declining pattern with elevation (Figure 4 Tables S3, S4, S5). The study revealed 4900 m asl as the highest and 100 m asl as the lowest recorded elevational zones of occurrence of aquatic vascular macrophytes in Nepal. *Ranunculus trichophyllus* Chaix (Ranunculaceae) represented the species that occurred at the highest elevation (2800-4900 m asl) in east, central and west (ECW) Nepal while *Hygrophila difformis* (L.f.) Blume, *Echinochloa picta* (J. Koenig) P.W.Michael and *Salvinia molesta* D.Mitch. were confined to the lowest elevation. The species with a wider range of distribution from the lowest elevational point in all the geographic zones were *Lemna perpusilla* Torr., *Najas gramineae* Delile, *P. nodosus* Poir. and *Stuckenia pectinata* (L.) Borner while *Callitriche palustris* L. showed their widespread occurrence above 2000 m asl.

Table 1. List of aquatic vascular macrophytes in Nepal's east, central and west geographical divisions

Family	Spermatophytes: Dicot species	Functional types (a)	Geographical divisions (b)	Elevation (m asl)	References
Spermatophytes: Dicot species					
Acanthaceae	*Hygrophila difformis* (L.f.) Blume	E	ECW	100-200	Ghimire et al. 2020
Acanthaceae	*Hygrophila polysperma* T.Anderson	E	ECW	100-1200	Rajbhandari et al. 2022
Acanthaceae	*Hygrophila auriculata* (Schumach.) Heine	E	ECW	72-700	Niroula and Singh 2010; Rajbhandari et al. 2022
Asteraceae	*Caesulia axillaris* Roxb.	E	ECW	100-1500	Shrestha et al. 2022
Asteraceae	*Cyathocline purpurea* Kuntze	E	ECW	600-1800	Sharma 2014
Asteraceae	*Enydra fluctans* Lour.	E	ECW	100-1700	Ghimire et al. 2020
Brassicaceae	*Nasturtium officinale* R.Br.	E	ECW	900-3800	Rajbhandari and Rai 2019
Plantaginaceae	*Callitriche palustris* L.	FL	ECW	2300-4200	Sharma 2014
Plantaginaceae	*Callitriche stagnalis* Scop.	FL	ECW	1800-3000	Sharma 2014
Ceratophyllaceae	*Ceratophyllum demersum* L.	S	ECW	80-1700	Ghimire et al. 2020
Convolvulaceae	*Ipomoea aquatica* Forssk.	E	ECW	70-280	Rajbhandari and Rai 2019
Lentibulariaceae	*Utricularia aurea* Lour.	S	ECW	72-1400	Niroula and Singh 2010; Rajbhandari et al. 2022
Lentibulariaceae	*Utricularia scandens* Benj.	S	ECW	1000-3700	Rajbhandari et al. 2022
Nelumbonaceae	*Nelumbo nucifera* Gaertn.	FL	ECW	90-800	Ghimire et al. 2020
Onagraceae	*Ludwigia adescendens* (L.) H.Hara	E	ECW	100-600	Rajbhandari and Rai 2019
Podostemaceae	*Hydrobryum griffithii* Tul.	S	ECW	1000-2000	Ghimire et al. 2020
Ranunculaceae	*Ranunculus trichophyllus* Chaix	S	ECW	2800-4900	Sharma 2014
Amaranthaceae	**Alternanthera philoxeroides* (Mart.) Griseb.	E	EC	72-1310	Niroula and Singh 2010; Sharma 2014
Apocynaceae	*Oxystelma esculentum* (L.f.) Sm.	E	EC	72-200	Niroula and Singh 2010; Sharma 2014
Asteraceae	*Cotula hemisphaerica* (Roxb.) Wall.ex Benth. & Hook.f.	E	EC	1400-1800	Sharma 2014; Ghimire et al. 2020
Lentibulariaceae	*Utricularia bifida* L.	S	EC	350-1300	Ghimire et al. 2020
Lentibulariaceae	*Utricularia gibba* L.	S	EC	100-1600	Ghimire et al. 2020
Lythraceae	*Rotala indica* (Willd.) Koehne	E	EC	100-1500	Ghimire et al. 2020; Rajbhandari and Rai 2019
Lythraceae	*Rotala mexicana* Cham. & Schltdl.	E	EC	200-1400	Sharma 2014; Ghimire et al. 2020
Lythraceae	*Trapa natans* L.	FL	EC	72-800	Ghimire et al. 2020; Sharma 2014
Plantaginaceae	*Dopatrium junceum* (Roxb.) Buch.-Ham.ex Benth.	E	EC	200-1400	Rajbhandari et al. 2022
Plantaginaceae	*Limnophila indica* (L.) Druce	E	EC	200-2300	Rajbhandari et al. 2022
Plantaginaceae	*Limnophila rugosa* (Roth) Merr.	E	EC	115-900	Ghimire et al. 2020
Plantaginaceae	*Limnophila sessiliflora* (Vahl) Blume	E	EC	150-600	Sharma 2014
Sphenocleaceae	*Sphenoclea zeylanica* Gaertn.	E	EW	200-600	Shrestha et al. 2022
Amaranthaceae	*Centrostachys aquatica* (R.Br.) Moq.	E	E	200	Rajbhandari et al. 2021
Cabombaceae	*Cabomba aquatica* Aubl.	S	E	115	Ghimire et al. 2020
Menyanthaceae	*Nymphoides hydrophylla* (Lour.) Kuntze	FF	E	72-600	Niroula and Singh 2010; Sharma 2014
Nymphaeaceae	*Euryale ferox* Salisb.	FL	E	100-500	Sharma 2014
Nymphaeaceae	*Nymphaea odorata* Aiton	FL	E	1600	Ghimire et al. 2020
Nymphaeaceae	*Nymphaea rubra* Roxb.ex Andrews	FL	E	300	Sharma 2014
Lentibulariaceae	*Utricularia australis* R.Br.	S	CW	2300-3800	Ghimire et al. 2020
Nymphaeaceae	*Nymphaea nouchali* Burm.f.	FL	CW	150-250	Rajbhandari and Rai 2017
Nymphaeaceae	*Nymphaea tetragona* Georgi	FL	CW	100-300	Ghimire et al. 2020
Plantaginaceae	*Hippuris vulgaris* L.	E	CW	2850-4700	Sharma 2014
Polygonaceae	*Persicaria amphibia* (L.) Delarbre	FL	CW	2900-3800	Rajbhandari et al. 2021
Ranunculaceae	*Ranunculus natans* C.A.Mey	E	CW	2600-3800	Rajbhandari and Rai 2017; Sharma 2014
Acanthaceae	*Hygrophila salicifolia* (Vahl) Nees	E	C	200-250	Sharma 2014
Ceratophyllaceae	*Ceratophyllum submersum* L.	S	C	183	Ghimire et al. 2020
Haloragaceae	**Myriophyllum aquaticum* (Vell.) Verdc.	FL	C	1350	Ghimire et al. 2020
Lentibulariaceae	*Utricularia minor* L.	S	C	3000-4300	Sharma 2014; Press et al. 2000
Menyanthaceae	*Nymphoides indica* (L.) Kuntze	FF	C	100-1500	Shrestha et al. 2022;
Nymphaeaceae	*Nymphaea alba* L.	FL	C	200-800	Ghimire et al. 2020
Plantaginaceae	*Limnophila heterophylla* (Roxb.) Benth.	E	C	115-200	Ghimire et al. 2020; Rajbhandari et al. 2022

Ranunculaceae	*Ranunculus flavidus* (Hand.-Mazz) C.D.Cook	E	C	2600-4000	Rajbhandari and Rai 2017
Elatinaceae	*Elatine triandra* Schkuhr	E	W	2300	Ghimire et al. 2020
Haloragaceae	*Myriophyllum spicatum* L.	S	W	3000-4000	Ghimire et al. 2020;
Lentibulariaceae	*Utricularia stellaris* L.f.	S	W	200	Ghimire et al. 2020
Menyanthaceae	*Menyanthes trifoliata* L.	E	W	2850–2900	Ghimire et al. 2020; Sharma 2014
Nymphaeaceae	*Nymphaea pubescens* Willd.	FL	W	160-300	Rajbhandari and Rai 2017; Sharma 2014
Spermatophytes: Monocot species					
Alismataceae	*Butomopsis latifolia* (D.Don) Kunth	E	ECW	150-600	Ghimire et al. 2020
Alismataceae	*Sagittaria guyanensis* Kunth	FL	ECW	100-1300	Ghimire et al. 2020
Alismataceae	*Sagittaria trifolia* L.	E	ECW	115-800	Ghimire et al. 2020
Araceae	*Lemna perpusilla* Torr.	FF	ECW	72-2700	Ghimire et al. 2020
Araceae	**Pistia stratiotes* L.	FF	ECW	60-600	Sharma 2014
Araceae	*Spirodela polyrhiza* (L.) Schleid.	FF	ECW	65-1500	Ghimire et al. 2020
Cyperaceae	*Cyperus compactus* Retz.	E	ECW	150-300	Rajbhandari and Rai 2017
Hydrocharitaceae	*Blyxa echinosperma* Hook.f.	S	ECW	700-2000	Ghimire et al. 2020
Hydrocharitaceae	*Hydrilla verticillata* (Roxb.) Royle	S	ECW	100-1600	Shrestha et al. 2022
Hydrocharitaceae	*Najas graminea* Delile	S	ECW	100-2700	Ghimire et al. 2020
Hydrocharitaceae	*Ottelia alismoides* (L.) Pers.	S	ECW	72-270	Niroula and Singh 2010; Sharma 2014; Rajbhandari and Rai 2017
Hydrocharitaceae	*Vallisneria natans* (Lour.) Hara	S	ECW	72-1300	Niroula and Singh 2010; Ghimire et al. 2020
Poaceae	*Echinochloa picta* (J.Koenig) P.W.Michael	E	ECW	150-200	Ghimire et al. 2020
Poaceae	**Leersia hexandra* Sw.	E	ECW	250-1600	Sharma 2014
Poaceae	*Panicum paludosum* Roxb.	E	ECW	200-1100	Sharma 2014
Pontederiaceae	**Pontederia crassipes* Mart.	FF	ECW	75-1500	Ghimire et al. 2020
Pontederiaceae	*Pontederia vaginalis* Burma.f.	E	ECW	150-1800	Sharma 2014
Potamogetonaceae	*Potamogeton crispus* L.	S	ECW	100-2000	Rajbhandari and Rai 2017
Potamogetonaceae	*Potamogeton nodosus* Poir.	FL	ECW	115-3000	Ghimire et al. 2020
Potamogetonaceae	*Stuckenia pectinata* (L.) Borner	S	ECW	100-3000	Niroula and Singh 2010; Ghimire et al. 2020
Potamogetonaceae	*Zannichellia palustris* L.	S	ECW	100-1100	Ghimire et al. 2020
Typhaceae	*Typha angustifolia* L.	E	ECW	72-300	Ghimire et al. 2020
Alismataceae	*Caldesia parnassifolia* (L.) Parl.	E	EC	700	Ghimire et al. 2020
Araceae	*Wolffia globosa* (Roxb.) Hartog & Plas	FF	EC	1300-1400	Rajbhandari and Rai 2017; Sharma 2014
Hydrocharitaceae	*Blyxa japonica* Maxim. ex Asch. & Gürke	S	EC	115-800	Ghimire et al. 2020
Hydrocharitaceae	*Hydrocharis dubia* Backer	FF	EC	115-300	Ghimire et al. 2020
Hydrocharitaceae	*Hydrocharis morsus-ranae* L.	FF	EC	115-2500	Ghimire et al. 2020
Poaceae	*Hygroryza aristata* Nees	FF	EC	80-200	Rajbhandari and Rai 2017
Poaceae	*Hymenachne amplexicaulis* Nees	E	EC	200-1400	Sharma 2014
Pontederiaceae	*Pontederia hastata* L.	E	EC	80-220	Sharma 2014
Aponogetonaceae	*Aponogeton appendiculatus* H.Bruggen	FL	EW	115-225	Ghimire et al. 2020; Sah et al. 2003
Potamogetonaceae	*Potamogeton lucens* L.	S	EW	200-3000	Rajbhandari and Rai 2017
Typhaceae	*Typha elephantina* Roxb.	E	EW	80-300	Rajbhandari and Rai 2017
Aponogetonaceae	*Aponogeton natans* Engl. & K.Krause	FL	E	100-200	Ghimire et al. 2020
Hydrocharitaceae	*Blyxa aubertii* Rich.	S	E	180-1200	Press et al. 2000
Hydrocharitaceae	*Nechamandra alternifolia* Thwaites	S	CW	600-900	Ghimire et al. 2020
Poaceae	*Oryza rufipogon* Griff.	E	CW	100-890	Ghimire et al. 2020; Shrestha and Upadhyay 1999
Potamogetonaceae	*Potamogeton distinctus* A.Benn.	S	CW	900-2900	Sharma 2014
Potamogetonaceae	*Potamogeton natans* L.	S	CW	200-4440	Ghimire et al. 2020
Potamogetonaceae	*Potamogeton pusillus* L.	S	CW	2100-3000	Ghimire et al. 2020
Potamogetonaceae	*Stuckenia filiformis* (Pers.) Börner	S	CW	2000-4700	Ghimire et al. 2020
Alismataceae	*Alisma plantago-aquatica* L.	E	C	200-1000	Ghimire et al. 2020
Eriocaulaceae	*Eriocaulon nepalense* var. *luzulifolium* (Mart.) Praj. & J.Parn	E	C	1300-1400	Rajbhandari and Rai 2017
Hydrocharitaceae	*Najas minor* All.	S	C	700-1700	Ghimire et al. 2020;
Potamogetonaceae	*Potamogeton berchtoldii* Fieber	S	C	800	Ghimire et al. 2020
Potamogetonaceae	*Potamogeton octandrus* Poir.	FL	C	700-1000	Ghimire et al. 2020; Press et al. 2000
Potamogetonaceae	*Potamogeton perfoliatus* L.	S	C	2800-3400	Rajbhandari and Rai 2017
Aponogetonaceae	*Aponogeton crispus* Thunb.	S	W	225	Sah et al. 2003

Aponogetonaceae	*Aponogeton undulatus* Roxb.	S	W	80-200	Ghimire et al. 2020
Araceae	*Lemna minor* L.	FF	W	2000-3000	Rajbhandari and Rai 2017
Hydrocharitaceae	*Vallisneria spiralis* L.	S	W	100-200	Ghimire et al. 2020
Pteridophytes					
Marsileaceae	*Marsilea minuta* L.	E	ECW	58-700	Sharma 2014
Salviniaceae	*Azolla pinnata* R.Br.	FF	ECW	60-1700	Sharma 2014
Salviniaceae	*Salvinia molesta* D.Mitch.	FF	ECW	90-200	Sharma 2014
Isoetaceae	*Calamaria coromandelina* (L.f.) Kuntze	E	E	120	Sharma 2014
Salviniaceae	*Salvinia natans* L. All.	FF	E	100-1600	Ghimire et al. 2020
Polypodiaceae	*Leptochilus pteropus* (Blume) Fraser-Jenk. Subsp. Pteropus	S	C	450	Ghimire et al. 2020
Salviniaceae	*Azolla filiculoides* Lam.	FF	C	58-1300	Sharma 2014

Note: [a]Functional types- FF: free-floating, S: submerged, FL: floating-leaved, E: emergent, [b]Geographical divisions- E: East Nepal, C: Central Nepal, W: West Nepal, *Invasive alien aquatic vascular macrophytes

Table S1. Regression analysis of vascular macrophyte species richness along each 100 m elevation in Nepal

	Species richness		
	normal	*glm: quasipoisson link = log*	
	Null	**Linear first order**	**Linear second order**
Constant	23.47∗∗∗	4.28∗∗∗	2.84∗∗∗
elev	(2.65)	(0.05)	(0.04)
		−0.001∗∗∗	
		(0.0000)	
(elev, 2)1			−5.84∗∗∗
			(0.32)
(elev, 2)2			−0.23
			(0.25)
Observations	49	49	49
Log Likelihood	-213.14		
Akaike Inf. Crit.	428.28		
Residual Deviance	16,526.20 (df = 48)	50.43 (df = 47)	49.55 (df = 46)
Null Deviance (df = 48)	16,526.20	681.57	681.57

Note: ∗p<0.1; ∗∗p<0.05; ∗∗∗p<0.01

Table S2. Regression analysis of vascular macrophyte species richness along 200 m elevation in Nepal

	Species richness		
	normal	*glm: quasipoisson link = log*	
	Null	**Linear first order**	**Linear second order**
Constant	23.16∗∗∗	4.24∗∗∗	2.81∗∗∗
elev	(3.67)	(0.07)	(0.06)
		−0.001∗∗∗	
		(0.0000)	
(elev, 2)1			−4.31∗∗∗
			(0.33)
(elev, 2)2			−0.31
			(0.26)
Observations	25	25	25
Log Likelihood	-108.71		
Akaike Inf. Crit.	219.41		
Residual Deviance	8,083.36 (df = 24)	25.39 (df = 23)	23.82 (df = 22)
Null Deviance (df = 24)	8,083.36	345.79	345.79

Note: ∗p<0.1; ∗∗p<0.05; ∗∗∗p<0.01

Table S3. Regression analysis of vascular macrophyte species richness along elevation in Central Nepal

	Species richness		
	normal	*glm: quasipoisson link = log*	
	Null	**Linear first order**	**Linear second order**
Constant	21.10∗∗∗	4.15∗∗∗	2.74∗∗∗
elev	(2.32)	(0.05)	(0.04)
		−0.001∗∗∗	
		(0.0000)	
(elev, 2)1			−5.76∗∗∗
			(0.32)
(elev, 2)2			−0.33
			(0.25)
Observations	49	49	49
Log Likelihood	-206.65		
Akaike Inf. Crit.	415.29		
Residual Deviance	12,678.49 (df = 48)	47.10 (df = 47)	45.45 (df = 46)
Null Deviance (df = 48)	12,678.49	589.30	589.30

Note: ∗p<0.1; ∗∗p<0.05; ∗∗∗p<0.01

Table S4. Regression analysis of vascular macrophyte species richness along elevation in West Nepal

	Species richness		
	normal	*glm: quasipoisson link = log*	
	Null	**Linear first order**	**Linear second order**
Constant	16.59∗∗∗	3.76∗∗∗	2.58∗∗∗
elev	(1.52)	(0.05)	(0.04)
		−0.0005∗∗∗	
		(0.0000)	
(elev, 2)1		−4.94∗∗∗	
		(0.28)	
(elev, 2)2			−0.61∗∗
			(0.23)
Observations	49	49	49
Log Likelihood	-186.00		
Akaike Inf. Crit.	373.99		
Residual Deviance	5,457.84 (df = 48)	35.24 (df = 47)	30.51 (df = 46)
Null Deviance (df = 48)	5,457.84	341.69	341.69

Note: ∗p<0.1; ∗∗p<0.05; ∗∗∗p<0.01

Table S5. Regression analysis of vascular macrophyte species richness along elevation in East Nepal

	Species richness		
	normal	*glm: quasipoisson link = log*	
	Null	**Linear first order**	**Linear second order**
Constant	17.04∗∗∗	4.28∗∗∗	2.14∗∗∗
elev	(2.47)	(0.04)	(0.04)
		−0.001∗∗∗	
		(0.0000)	
(elev, 2)1			−9.37∗∗∗
			(0.33)
(elev, 2)2			−1.19∗∗∗
			(0.21)
Observations	49	49	49
Log Likelihood	-209.62		
Akaike Inf. Crit.	421.24		
Residual Deviance	14,315.92 (df = 48)	26.71 (df = 47)	15.51 (df = 46)
Null Deviance (df = 48)	14,315.92	819.95	819.95

Note: ∗p<0.1; ∗∗p<0.05; ∗∗∗p<0.01

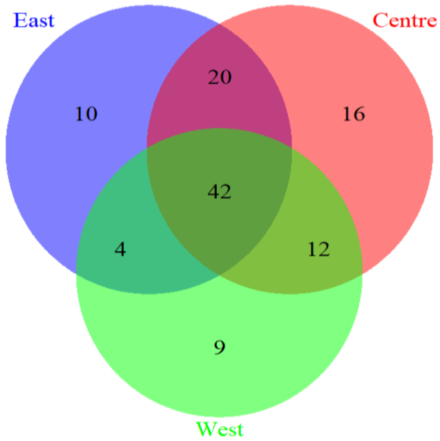
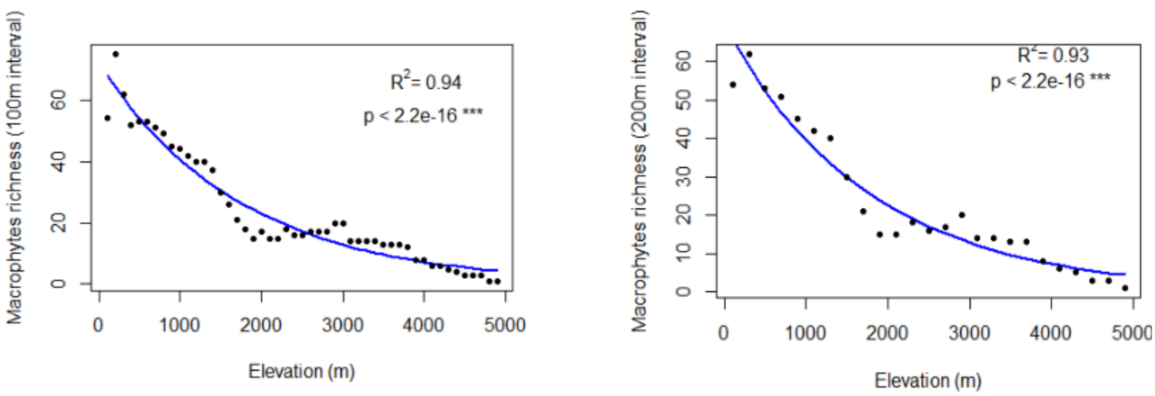
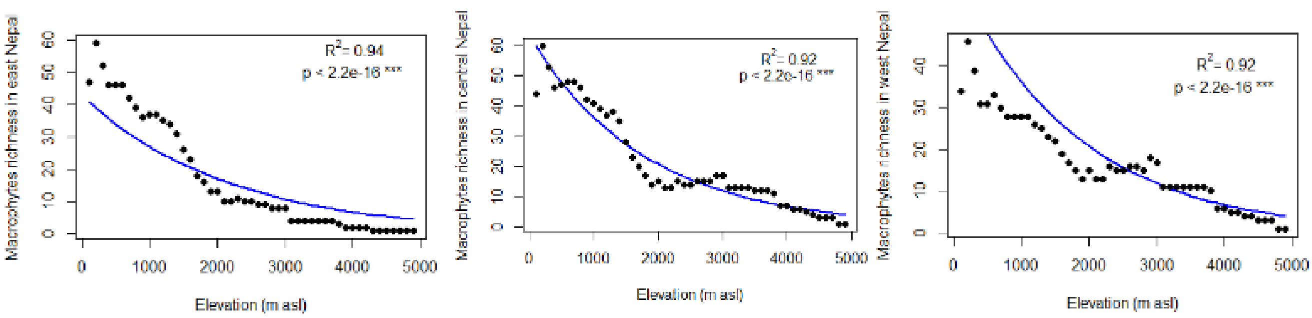


Figure 2. Venn diagram of total aquatic vascular macrophytes species in three geographical divisions, east, central and west of Nepal



A B

Figure 3. Aquatic vascular macrophytes richness pattern in Nepal. A. 100 m elevation range. The fitted line was the statistically significant model after glm regression. B. 200 m elevation range. The fitted line was the statistically significant model after glm regression



A B C

Figure 4. Macrophytes richness pattern along elevation in three geographical divisions of Nepal. A. East Nepal, the fitted line is a statistically significant model after *glm* regression. B. Central Nepal, the fitted line is the statistically significant model after *glm* regression. C. West Nepal, the fitted line is a statistically significant model after *glm* regression

Considering the geographical distribution in east Nepal, *Calamaria coromandelina* (L.f.) Kuntze and *Cabomba aquatica* Aubl. represented as exclusively the lowermost elevation species. *Centrostachys aquatica* (R.Br.) Moq., *Aponogeton natans* Engl. & K. Krause and *N. rubra* Roxb.ex Andrews also showed their restrictions to lower elevation belt while *N. odorata* Aiton represented the highest elevation point. *Blyxa aubertii* Rich. and *S. natans* L. All. showed a wider range of elevational distribution. In central Nepal, *Limnophila heterophylla* (Roxb.) Benth. and *Ceratophyllum submersum* L. were associated with the lowest elevation while *Utricularia minor* L. and *R. flavidus* (Hand.-Mazz) C.D.Cook showed a wider range of distribution at higher elevations. *Azolla filiculoides* Lam. also showed a wider distributional range from low to high elevation. *C. submersum*, *Leptochilus pteropus* (Blume) Fraser-Jenk. subsp. *pteropus*, *P. berchtoldii* Fieber and *Myriophyllum aquaticum* (Vell.) Verdc. represented restricted occurrence at low and high elevations respectively. West Nepal, hosts *A. undulatus* Roxb. and *Vallisneria spiralis* L. found as the lowest altitude species. *A. crispus* Thunb. and *U. stellaris* L.f. showed restrictions exclusively to low altitude while *Elatine triandra* Schkuhr and *Menyanthes trifoliata* L. represented their restrictions to high altitude. *L. minor* L. and *M. spicatum* L. showed their preference over a wide range at higher altitudes. Invasive alien aquatic vascular macrophytes recorded in this study showed heterogenous elevational ranges from 100-1700 m asl. *C. demersum* L., *Pontederia crassipes* Mart, *Leersia hexandra* Sw. and *Pistia stratiotes* L. being common to east, central and west Nepal showed their invasion from low to high altitude. *M. aquaticum* restricted to central Nepal was found at 1400 m asl while *Alternanthera philoxeroides* (Mart.) Griseb. common to east and central Nepal showed its maximum limit to up to 1300 m asl.

Species richness pattern along elevational gradients in Nepal

Nepal could be considered rich in aquatic macrophytes diversity as the wetlands harbored 2.13% of the country's total 5309 flowering plants as reported by Rajbhandari and Rai (2017). The present study has been undertaken to compile information regarding the effect of elevational gradients on the richness pattern of aquatic vascular macrophytes. Similarly, aquatic Pteridophytes contribute to 1.27% of the country's total 550 Pteridophytes species (Kandel and Jenkins 2020). Furthermore, when compared to outside Nepal, aquatic vascular macrophytes accounted for 24.04 % of the macrophytes (470) reported from the Indian subcontinent (Cook 1996) and 3.26 % of the global (3457) aquatic vascular macrophytes (Murphy et al. 2020). A total of 113 species of aquatic vascular macrophytes are reported from Nepal along the elevational gradient of 100-4900 m asl which is almost similar to the report from Catalonia of the Mediterranean area (120 species) along the elevational gradient of 0 to 3000 m asl (Chappuis et al. 2011). Similarly, the highest values in the lowest elevational range (0-250 m asl) are also comparable with Catalonia. The wetlands of Nepal seem to be at matured stage as the ratio of dicot: monocot macrophytes is 1.07. So far the strength of the macrophytes family is concerned Hydrocharitaceae (12 species and 7 genera) and Potamogetonaceae (12 species and 3 genera each) are the largest aquatic families occurring at an elevation range of 100-2700 m and 100-4700 m asl respectively. Potamogetonaceae was also recorded as the family with greater macrophytes species in the Palaearctic (Murphy et al. 2020). This study showed a general trend of a monotonic declining pattern of species richness along elevation, with the highest level of species richness at lower elevations in all geographical regions of Nepal. It contradicts the unimodal (Bhatta et al. 2018; Pandey et al. 2020; Nepali et al. 2021) and linear increase (Kamimura et al. 2017) in richness patterns observed for vascular plants of terrestrial habitat This showed that species richness pattern along elevational gradients differed among taxonomic groups of aquatic and terrestrial ecosystems.

Occurrence of the high level of species richness in the lowland wetlands and decrease with increasing elevation matched with the previous observations (Lacoul and Freedman 2006; Pulido et al. 2015). Ambient bioclimatic conditions, high temperature and eutrophic nature of water bodies at lower altitudes in Nepal might have led to the high richness of aquatic vascular macrophytes in the region. On the other hand, environmental stress associated with the decreased temperature with the estimated lapse rate of about 0.53°C at every 100 m along elevation gradients constitutes an oligotrophic state of water bodies at higher elevations where only variation in nutrient concentration causes the decrease in species richness (Bhattarai et al. 2004; Lacoul and Freedman 2006; Fernández-Aláez et al. 2018). Similarly, a decreasing trend of aquatic macrophytes species was also reported in the studies of high mountain lakes of Pyrenees (Pulido et al. 2015). Optimum energy increases photosynthesis leading to higher biological activity and a consequent increase in species richness (O'Brien 2006). The maximum richness of aquatic vascular macrophytes at 100 m asl may thus be due to the availability of optimum energy at this elevation creating favorable conditions for many aquatic vascular macrophytes. Limited invasions of alien aquatic vascular macrophytes at higher altitudes might be attributed to nutrient-poor habitats, and environmental stress (Zefferman et al. 2015; Guo et al. 2017). They may appear at high altitudes in the near future as the Dark Diversity hypothesis suggests by Partel et al. (2011). So far the invasive species is concerned, invasive alien plant species richness in lower elevation showed a linear decrease in their richness with the elevation increase had also been reported from Nepal (Siwakoti et al. 2016).

Factors influencing species richness along the elevational gradient in Nepal

The factors that influence the species richness may differ among different taxa. Also, a combination of factors may explain the diversity within and among taxa. Therefore, multiple hypotheses have been proposed to explain the patterns in species richness. "Water-energy hypothesis", is one of the most significant hypotheses in defining species richness patterns based on the relationship of available water and energy to the plants along elevation gradients. It states that the richness of species diversity is directly related to the available water and energy in the area (O'Brien 2006; Liang et al. 2020). At lower elevations, the availability of significant water and energy favors the species diversity (Li and Feng 2015). Other hypotheses included the "physical tolerance hypothesis" which proposes that extreme physiological stresses associated with severe climatic extremes can explain the species richness pattern (Currie et al. 2004; Kreyling et al. 2015). Further, the findings of the present study differ from "Rapoport's elevational rule" which suggests a positive correlation between elevation and the elevational range of species. It explains the tolerance of high altitude species over a wide range of climatic conditions leads to more species around the range edges called a 'Rescue effect' (Steven 1992). Aquatic vascular macrophytes are highly sensitive groups of biodiversity. They are predominantly herbaceous annuals growing in water-saturated conditions. Hence, the patterns of their richness along elevational gradients may not be congruent with the amphibious and terrestrial plant taxa studied so far in Nepal. However, the "Species-energy hypothesis" states that the available energy regulates the geographical gradients of biodiversity by controlling population size, extinction rate, food resources and habitats (Li and Feng 2015). "Species-energy hypothesis" fits best to explain variations of aquatic vascular macrophytes species richness suggesting that a wider range of species can be found in habitats with greater energy accessibility. In our study, the highest species richness at lower altitudes with the warmest climate may be due to the high levels of energy availability as those reported in the studies of (Vetaas et al. 2019). Further, the widespread occurrence of *C. palustris* and *S. pectinata* matched with the results of (Chambers et al. 2008; İkinci and Bayındır 2021).

Elevation has also been used to categorize study areas into lowland and upland groups (Sun et al. 2019). Elevation gradient correspondingly varies potent climatic factors like concentration of temperature, nutrient availability and length of growing season. With increasing elevation, the temperature decreases while solar radiation and precipitation increase. A general trend of decrease in freshwater macrophyte species with increasing elevation is attributed to lower temperatures and reduced length of growing season (Jones et al. 2003). Cold and harsh temperatures with short growing seasons which act as filtering agents for species distribution might also be the reason for low species richness in high-altitude freshwater ecosystems (Kraft et al. 2015). Among the three geographical regions, central Nepal harbors the maximum species richness of aquatic vascular macrophytes followed by east and west Nepal. The lowest richness of aquatic vascular macrophytes in west Nepal is in congruence with that of native and invasive plant species richness (Bhattarai et al. 2014). Maximum species richness at the lowermost elevation in all three geographical regions: east, central and west might be supported by a combined effect of biological, climatic and anthropogenic factors (Tanalgo et al. 2015; Budhathoki et al. 2021; Chakravarty et al. 2021; Stefanidis et al. 2021).

This study documents the species richness pattern of aquatic vascular macrophytes along elevational gradients in three geographical divisions in Nepal. Review results showed a good collection of aquatic macrophytes which were maximum at lower elevational zones in all three geographical divisions of Nepal. As the elevation increases, species richness decreases linearly which might be due to low nutrients in high-altitude oligotrophic systems. Moreover, cold temperatures with short growing seasons might also be the reason for the low species richness at high altitudes. *R. trichophyllus* represented the highest elevation species while *H. difformis*, *Echinochloa picta* and *S. molesta* occupied the lowest elevations. *L. perpusilla*, *N. gramineae*, *P. nodosus* and *S. pectinata* ranged widely from the lowest elevations in all geographic divisions while the distribution of *C. pallustris* was widespread above 2000 m asl. It is expected that the researchers interested in exploring more about aquatic vascular macrophytes from broader perspectives can take the review as a reference.

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