

Relationship between species richness and biomass on environmental gradient in natural forest communities on Mt. Xiaolongshan, northwest China

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Abstract We analyzed the relationship between species richness and biomass in natural forest communities at two similar sites on Mt. Xiaolongshan, northwest China. At both sites, a wide range of tree layer biomass levels was available by local biomass estimation models. In order to identify underlying mechanism of the species richness–biomass relationship, we included different water resource levels and number of individuals in each plot in our analysis. We sampled 15 and 20 plots (20 m × 20 m), respectively, at both two sites. These plots were sampled equally on the sunny slope and the shady slope. Species richness, number of individuals of each species and diameter at breast height (DBH) as a substitute of biomass of tree layer were recorded in each sample. At one site, the relationship between species richness and biomass was significant on the sunny slope, and this relationship disappeared on the shady slope due to more environmental factors. The relations between species richness and number of individuals and between number of individuals and biomass paralleled the species richness–biomass relation on both slopes. The difference in number of individuals–biomass relationships on the sunny slope and the shady slope revealed “interspecific competitive exclusion” even though the species richness–biomass relationships were not hump-shaped. At the other site, species richness was not related to biomass or to number of individuals. Our study demonstrated the importance of environmental stress and succession of community in the understanding of species diversity–productivity patterns.

Key words biomass, species richness, environmental factors, forest community

1 Introduction

The relationship between species richness and primary productivity has been one of the central issues in plant ecology (Rosenzweig, 1995). The conclusions of these studies, however, were inconsistent. There are three different relationships between species richness and primary productivity that are clearly separated in literature. One is positive relationship (Planka, 1967; Brown, 1975; Kirchner, 1977), one is negative relationship (Rosenzweig, 1971; Silvertown, 1980), and another is hump-shaped relationship (Abramsky and Rosenzweig, 1984; Owen, 1988). Tilman's hump-shaped curve or unimodal model (Tilman, 1982) states that the relationship between species richness and productivity consists of increase, peak, and decline phases along a gradient of increasing resource availability. This unimodal pattern has been confirmed in several plant communities (Rosenzweig, 1995).

The role of species richness in productivity is one of important research topics, and the relationship between biomass and species richness has been studied in varied ecosystems (Grace and Juttila, 1999; Gross et

al., 2000). In natural warm forest communities, many species coexist and each species has its own niche in the community. Some species which favored the environment become dominant and make up the first layer (the topside) of community, the accompanying species make up the second and the third layers, and under these layers are some herbaceous plants and grasses. The layer structure of community allows biomass to increase with species diversity through resources partitioning, in which difference in growth form between layers allows for more complete harvesting of ambient resources such as sunlight (Naeem et al., 1994, 1995). Although theoretically attractive, this mechanism has received little direct support and runs counter to the expectation that a few highly competitive species would usurp the resources (Al-Mufti et al., 1977; Grime, 1977; Goldberg, 1990). Whether stratification of canopy layers promotes coexistence and increases biomass in natural forest communities or not, little direct experimental evidence is available for evaluating these hypotheses (Connell and Lowman, 1989; Parker, 1995).

To test whether the effects of species richness on

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biomass is sensitive to environment in natural forest communities, we chose a natural forest community — *Quercus aliena* var. *acuteserrata* community on Mt. Xiaolongshan in northwest China as the research material. The tree layer is the most important part of the *Q. aliena* var. *acuteserrata* community in the study site, and the shrub layer is very weak. So our study focused on the tree layer of the community.

The main questions we addressed in this study include: 1) what is the relationship between species richness and biomass? 2) does environment play an important role in the richness–biomass relationship? and 3) how environment operates in the richness–biomass relationship?

2 Study sites

The study sites, Maicaogou and Shaba, are two nature reserves 10 km in distance west of Qinling Mountain, 50 km southwest of Tianshui County, Gansu Province. This region is characterized by a transition from the northern part of subtropical zone to the southern part of warm temperate zone in China. The sites are located in the Mt. Xiaolongshan region and the relative height is 500–100 m. The climate is continental monsoon climate with the average daily temperature ranging from -7°C in winter to 22°C in summer and the extremely low temperature -23.2°C . The annual precipitation ranges from 460 to 800 mm in different years and rainfall concentrates from July to September, accounting for 70%–80% of the year. The annual evaporation is 989–1658 mm and the relative air humidity is 68%–78%. There are about 2700 species in the region, which belong to 954 families. Among these species, herbaceous plants share about 1900 species, most of which belong to Gramineae, Compositae, Leguminosae, Ranunculaceae, Orchidaceae, Labiatae and Scrophulariaceae families; trees have about 800 species and most of them are temperate species coming from families of Fagaceae, Betulaceae, Pinaceae, Saxifragaceae, Ulmaceae, Aceraceae and Rosaceae.

Both sites were natural forest communities, which were dominated by *Q. aliena* var. *acuteserrata* and they have been protected for 40 years at least. At the Maicaogou site, the community has been taken as an oak nature reserve for hundreds of years. At the Shaba site, there was a deforestation in the 1960s and large individuals were cleared. For limited rainfall, water resource was a main environmental stress factor for the development of forest communities, especially, on the sunny slope where there was more annual evaporation. Some local forest managers have studied the natural forest community for several years and have booked some achievements in statistics of plant species and biomass estimation. Their work is helpful for the understanding of the relationship between species richness and biomass as well as its environmental effects.

3 Research methods

3.1 Field investigation

The field investigation was conducted in the summer of 2002 and focused mainly in the elevation of 1500–1900 m on both sides of slope facing in two sites. Sample plots of 20 m \times 20 m in size were set during the investigation. At the Shaba site, eight plots were sampled randomly on a south facing slope (sunny slope) and seven on a north facing slope (shady slope); while at the Maicaogou site, 11 plots were set randomly on a sunny slope and nine on a shady slope. All trees bigger than 2.0 cm in diameter at breast height (DBH) were tagged and species names, DBH, height of trees, number of individuals of each species in the tree layer were recorded. Dead trees (standing and fallen) were also measured wherever possible. Plots were subdivided into 25 4 m \times 4 m and 400 1 m \times 1 m quadrats for shrubs and herbs as reference. The elevation, slope aspect and location of each plot were recorded with GPS at the same time.

3.2 Biomass estimation

All tree species that were investigated were divided into three growth groups according to their physiological characteristics, that is, slow growth group such as *Q. aliena* var. *acuteserrata*, fast-medium growth group such as *Populus davidiana*, and coniferous growth group such as *Pinus armandii*. Biomass regression models for tree layer of each group created in the study sites are shown in Table 1.

3.3 Statistical analysis

For statistical analyses, the counts and biomass data were logarithmically transformed. First order (linear) and second order (quadratic) polynomial regressions were used to analyze the shapes of following curves: species richness–biomass, species richness–number of individuals and number of individuals–biomass. In each pair, the first variable was considered as a function of the second one. We present quadratic regressions only if the quadratic term (a of the equation $y=ax^2+bx+c$) is significant. In tables (the results of single species analyses) at least linear regressions are given, and in figures only significant regression lines are drawn.

In order to analyze effects of environment on these relationships, three analyses of covariance (ANCOVA) were performed for each site with slope aspect as a water resource factor. Two ANCOVA were calculated with biomass as the response variable, one with biomass as the covariable, the other with number of individuals as the covariable. In the third ANCOVA num-

Table 1 Biomass models for tree layer in the *Quercus aliena* var. *acuteserrata* community

Growth group	Organ	Regression model	Correlation coefficient	Scope
Slow growth	Stem	$W_s = 0.02231 \times (D^2H)^{0.37755}$	$r = 0.977$	$D = 4.0\text{--}25.0$ cm
	Bark	$W_{bk} = 0.01033 \times (D^2H)^{0.81367}$	$r = 0.962$	$H = 4.0\text{--}20.0$ m
	Branch	$W_b = 0.00616 \times (D^2H)^{0.96951}$	$r = 0.979$	
	Leaf	$W_l = 0.03694 \times (D^2H)^{0.66156}$	$r = 0.921$	
	Root	$W_r = 0.01469 \times (D^2H)^{0.93446}$	$r = 0.969$	
Fast-medium growth	Stem	$W_s = 0.22680 \times (D^2H)^{0.69330}$	$r = 0.960$	$D = 4.0\text{--}28.0$ cm
	Branch	$W_b = 0.02470 \times (D^2H)^{0.73780}$	$r = 0.970$	$H = 4.0\text{--}20.0$ m
	Leaf	$W_l = 0.01080 \times (D^2H)^{0.81810}$	$r = 0.940$	
	Root	$W_r = 0.15530 \times (D^2H)^{0.59510}$	$r = 0.930$	
Coniferous group	Stem	$W_s = 0.02697 \times (D^2H)^{0.91858}$	$r = 0.989$	$D = 4.0\text{--}25.0$ cm
	Bark	$W_{bk} = 0.00604 \times (D^2H)^{0.83368}$	$r = 0.926$	$H = 4.0\text{--}20.0$ m
	Branch	$W_b = 0.01394 \times (D^2H)^{0.92327}$	$r = 0.979$	
	Leaf	$W_l = 0.00760 \times (D^2H)^{0.92464}$	$r = 0.988$	
	Root	$W_r = 0.01373 \times (D^2H)^{0.94785}$	$r = 0.937$	

Source: Han and Ma (1997). In the models, D is the diameter at breast height (DBH), H the height of trees, W_s the biomass of stems, W_{bk} the biomass of bark, W_b the biomass of branches, W_l the biomass of leaves, and W_r the biomass of roots.

ber of individuals was the response variable and biomass the covariable.

4 Results

No unimodal patterns were found in any of the tested relationships between community biomass, species richness and number of individuals (Fig. 1). Linear regression models provided always lower p -values than quadratic ones and the quadratic term was never significant ($p > 0.05$). When there was a significant relationship between species richness and biomass then it was negative.

At the Shaba site, a significantly negative relationship between species richness and biomass was found (Fig. 1). The relationships were very strong. However, they only existed in total and on the shady slope but disappeared completely on the sunny slope. Biomass decreased in plots of high species richness but remained constant in plots of low species richness. In the ANCOVA including all the environments, the effect of species richness on biomass was highly significant but there was also a significant interaction of slope aspect and biomass, which indicated an environmental effect in species richness–biomass rela-

tionship (Table 2).

The species richness–number of individuals curve paralleled that of species richness–biomass but the relationship in total was less strong. There was a significant relationship between species richness and number of individuals on the shady slope. The relation was only marginally significant in total ($p < 0.1$) and disappeared on the sunny slope. The ANCOVA provided a significant effect of species richness on number of individuals and a significant interaction between slope aspect and number of individuals.

The relationship between number of individuals and biomass disappeared in total, but there were two significantly negative relationships on the sunny and shady slopes, which paralleled the one between species richness and biomass (Fig. 1). The effect of number of individuals (covariable) on biomass was not significant in total in the ANCOVA (Table 2). The interaction between biomass and slope aspect was very significant, indicating that on gradient of slope aspect, the change in the relationship between biomass and number of individuals was bigger than that between species richness and biomass. At high productivity levels, the decrease in species richness and number of individuals was similar on the shady slope resulting in a constant number of individuals per surviving species.

Table 2 Analysis of covariance for diversity (species richness) and number of individuals at the Shaba site

	df	Biomass–diversity		Number of individuals–diversity		Biomass–number of individuals	
		MS	F	MS	F	MS	F
Slope aspect	2	0.004	1.83	0.028	6.25*	0.015	1.37
Covariable	1	0.183	62.45***	0.114	29.34***	0.773	38.75***
Slope aspect \times covariable	2	0.018	8.19*	0.029	5.84*	0.007	0.38
Error	23	0.002		0.006		0.013	

Slope aspect is taken as the factor. Each pair in the columns represents response variable–covariable. Significant F -values are labeled: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

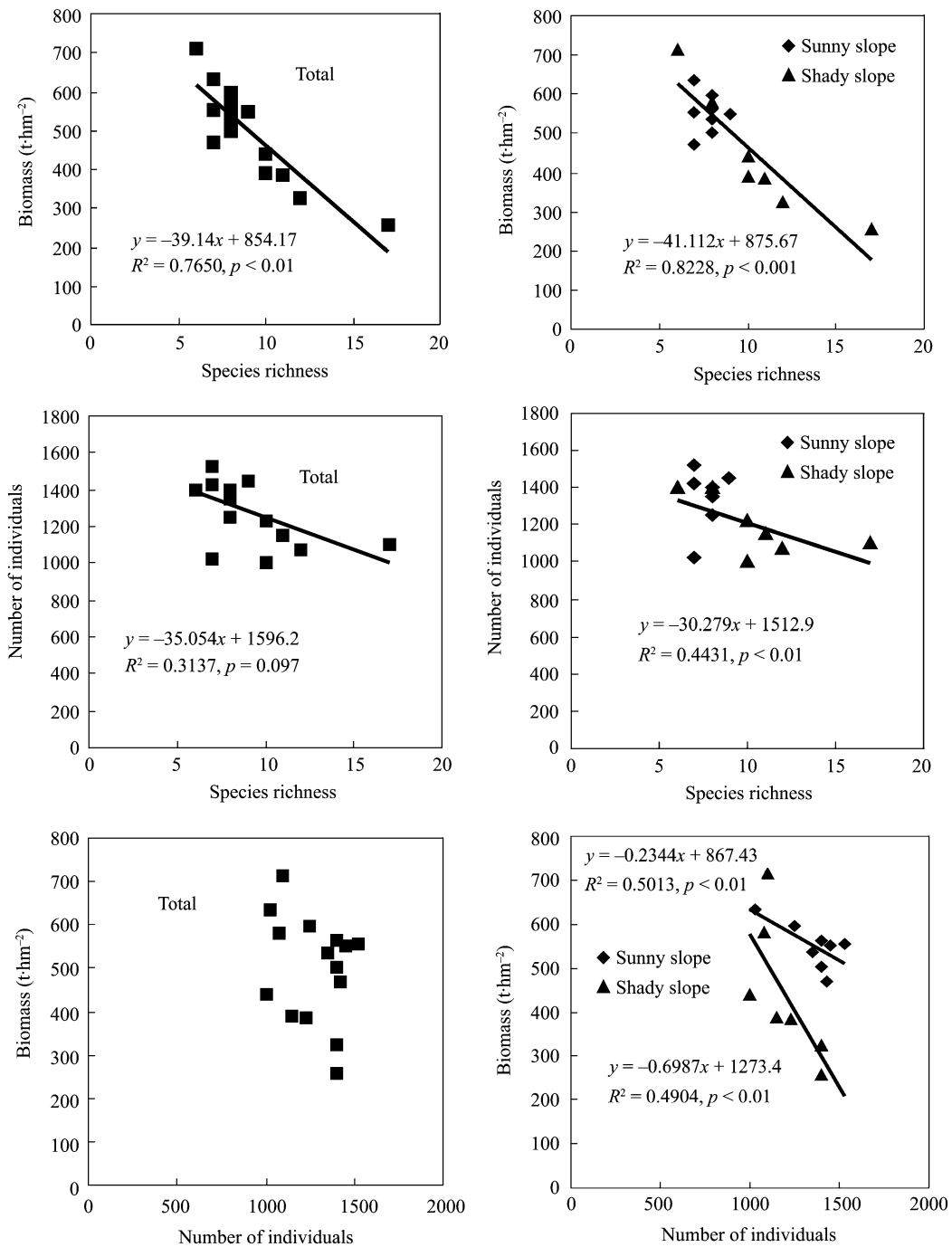


Fig. 1 Relationship between species richness and biomass (top), between species richness and number of individuals (middle) and between number of individuals and biomass (bottom) at the Shaba site. Regression lines and results of regression analyses are presented separately for each group if the relationship is significant ($p < 0.1$).

The fact that some species disappeared but the remaining ones did not lose individuals indicated a biomass-dependent response to species richness. This result could be confirmed by the analysis of the relationship between number of a single species and community biomass. Large of difference in the response of biomass to species richness was found (Table 3). Totally, ten species showed a negative linear

relationship, eight species showed a U-shaped curve and in six species the relationship was not significant. The relationship remained linearly negative for one species, and in three cases the negative relationship disappeared on the sunny slope and one species developed a positive relationship. *Q. aliena* var. *acuteserrata* was already in a senescent stage on the sunny slope but the relationship remained significantly positive.

Table 3 Regression analyses examining the relationship between number of individuals of single species and total biomass of the community at the Shaba site

Species	Relationship	Total		Sunny slope		Shady slope	
		<i>p</i>	<i>R</i> ²	<i>p</i>	<i>R</i> ²	<i>p</i>	<i>R</i> ²
<i>Quercus aliena</i> var. <i>acuteserrata</i>	Linear	0.182 ↑	0.83	0.154 ↑	0.74	0.060 ↑	0.52
<i>Lindera umbellata</i>	Linear	0.050 ↑	0.44	0.009	0.33	0.056 ↑	0.58
<i>Carpinus turczaninowii</i>	Linear	0.152	0.28	0.113	0.12	0.811 ↓	0.42
<i>Tilia dictyoneura</i>	Linear	0.041 ↑	0.54	0.073	0.33	0.050	0.22
<i>Prunus polytricha</i>	Linear	0.005 U	0.61	0.012	0.31	0.224	0.32
<i>Betula platyphylla</i>	Linear	0.032	0.13	0.251	0.24	0.090 ∩	0.52
<i>Cornus hemsleyi</i>	Linear	0.030	0.11	0.009	0.03	0.039	0.18
<i>Pinus armandii</i>	Linear	0.062	0.08	0.030	0.00	0.014	0.00
<i>Populus davidiana</i>	Linear	0.011	0.14	0.061	0.12	0.040	0.02
<i>Ulmus propiqa</i>	Linear	0.003	0.11	0.021	0.01	0.049	0.00

The *p*-value is significant level of the slope in linear regression and of the quadratic term in the quadratic regression. Significant relationships (*p*<0.01) are highlighted in bold face and their shapes indicated positive, negative, U-shaped, and hump-shaped.

At the Maicaogou nature reserve site, the relationship between species richness and biomass was not significant neither in the regression analyses of individuals nor in an ANCOVA combining all the investigated plots. However, the relationship between species richness and biomass was significant on the shady slope but disappeared on the sunny slope. The ANCOVA also provided a significant effect of species richness on biomass on the sunny slope. The interaction between slope aspect and biomass in the ANCOVA on species number was not significant, indicating that there was no productivity-dependent reduction of species richness with slope aspect (Table 4).

There was also no significant relationship between number of individuals and species richness, neither in the regression analyses nor in the ANCOVA. A positive relationship between number of individuals and biomass was only found in the shady slope but disappeared on the sunny slope. In the ANCOVA, the effect of species richness on biomass was highly significant and there was no significant interaction between species richness and biomass on the sunny slope. Like species richness, the number of individuals was not significantly affected by slope aspect although there was a slight decrease between the sunny slope and the shady slope.

Contrary to the Shaba site, the difference for biomass in response to species richness was small at the Maicaogou nature reserve site. At the Maicaogou site, the relationship between number of individuals and

biomass was not significant totally, and that was also not significant at the Shaba site in total (Fig. 2).

5 Discussion

In natural forest communities of different slope aspects that were examined in this study, no relationship between species richness and biomass was found on the sunny slope. While on shady slopes, Shaba site revealed a significantly negative linear relationship between species richness, number of individuals and biomass but that in Maicaogou site did not. There was no evidence for the widely accepted hump-shaped model of species richness–productivity patterns. In a meta-analysis by Waide et al. (1999), the proportion of hump-shaped pattern was 80% but the authors relied only on published statistics without analysis. Mittelbach et al. (2001) reanalyzed the data of a large number of studies and their results could be interpreted differently. On one hand the hump-shaped pattern occurred more frequently than the other tested patterns (positive, negative, U-shaped); on the other hand, the relationship was not hump-shaped in most cases (55%). In a comment on this analysis, Whittaker and Heegaard (2003) argued that unimodal relationship might have been overestimated due to the treatment of scale selection and analysis of data set. Furthermore, the exact number of studies cannot be easily counted and the relationship might be higher because negative

Table 4 Analysis of covariance for diversity (species richness) and number of individuals at the Maicaogou site

	<i>df</i>	Diversity–biomass		Diversity–number of individuals		Number of individuals–biomass	
		<i>MS</i>	<i>F</i>	<i>MS</i>	<i>F</i>	<i>MS</i>	<i>F</i>
Slope aspect	2	0.029	1.42	0.011	0.78	0.018	0.59
Covariable	1	0.023	1.61	0.002	0.24	0.382	14.28***
Slope × covariable	2	0.026	1.65	0.023	1.42	0.005	0.17
Error	53	0.017		0.015		0.033	

Slope aspect is taken as the factor. Each pair in the columns represents response variable–covariable. Significant *F*-values are labeled: **p*<0.05, ***p*<0.01, ****p*<0.001.

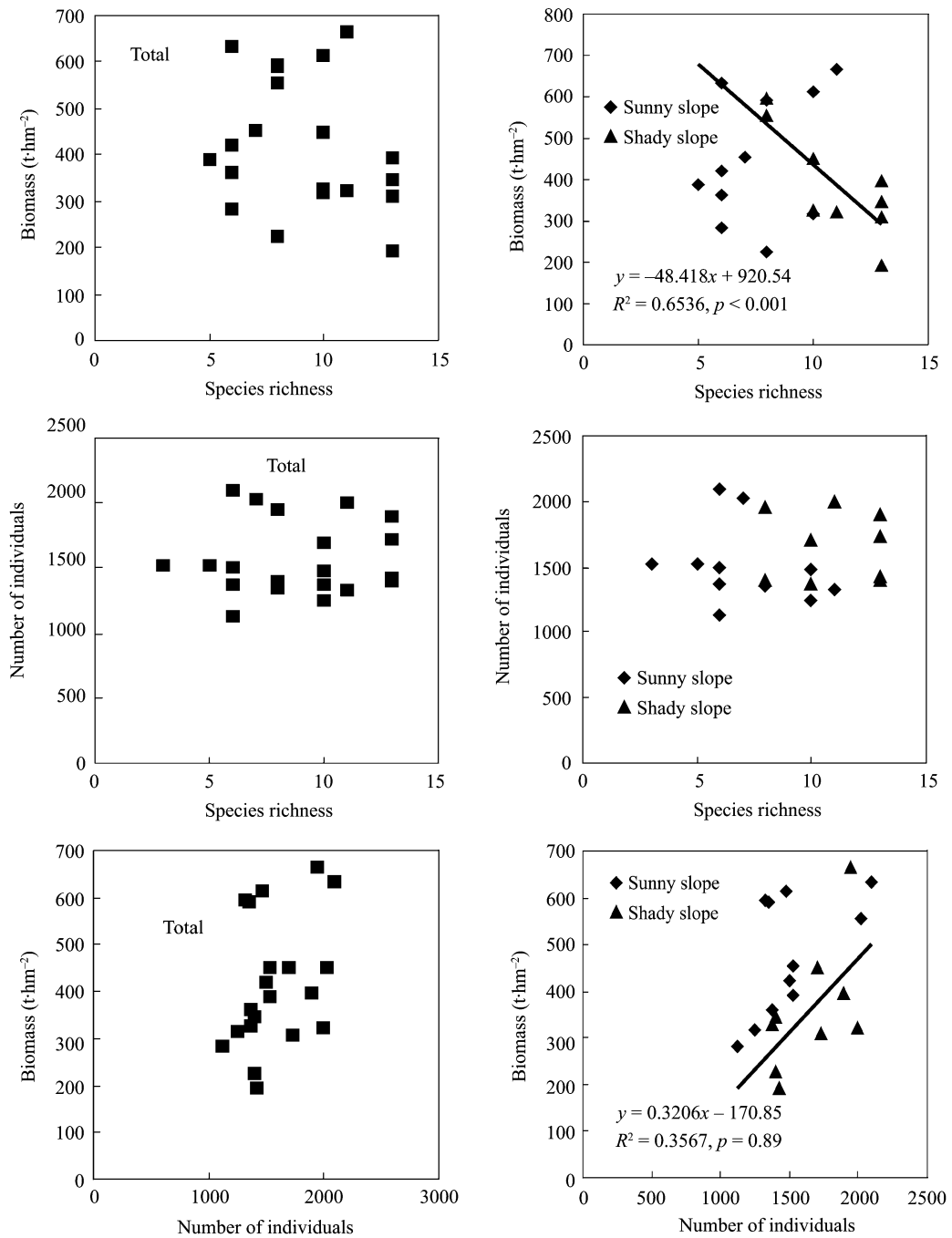


Fig. 2 Relationship between species richness and biomass (top), between species richness and number of individuals (middle) and between number of individuals and biomass (bottom) at the Maicaogou site. Regression lines and result of regression analyses are presented separately for each group if the relationship is significant ($p < 0.1$).

results are often not published (considered less interesting, problems in statistical control of β -error).

At both sites, species richness and biomass were negatively related on the shady slope. In the traditional models of Grime (1973), the descending part of the hump-shaped relationship was explained by the increasing environmental stress that limited productivity at a high species richness. However, in more recent studies that manipulated species richness by sowing and weeding, productivity was found to be a function of species richness (Hector et al., 1999; Tilman et al.,

2001). The negative effect of species richness on productivity usually observed in such experiments is a result of either limited resources competition among species or high probability including low productive species in species-rich communities (Loreau and Hector, 2001). In natural forest communities, the most probable explanation for negative species richness–biomass relationship is limited resources and more extensive competition. A large resources capacity, in turn, carries more species and individuals, and on sunny slopes of the two sites in our study, there

was more water resource stress that limited community productivity in narrow ranges than on sunny slopes.

Two major reasons have been suggested by several studies to explain the absence of a hump shape. 1) An insufficient range of productivity levels prevents the detection of the curve peak which results in a positive or negative relationship (Marrs, 1999; Mittelbach et al., 2001). At both of our sites, the natural forest community was in the late stage of succession and showed a narrow variation in biomass, especially, on the sunny slope, and the biomass was more suppressed by water resources. Insufficient observational studies made the ascending side of the hump be missed and only the descending one left. 2) Hump-shaped relationships are the result of long-term processes like colonization, adaptation and change in species composition (Gough et al., 2000). For instance, the appearance of some new species might enlarge productivity of unsaturated communities. This could be the reason for a positive relationship between productivity and species richness that was often found in natural communities. At our study sites, the plant community was located in nature reserves, and natural succession has made the community teem with species, so we could only observe the community with saturated resources, and more species would increase competition and consume the total community productivity.

The analysis of the change of species richness–biomass relationship with environment revealed a third argument why relationships between productivity and diversity are not always hump-shaped. Tilman (1982) proposed that at low levels productivity was positively related with species richness, but at high levels of productivity a small part of plant species obtained a competitive dominance and excluded other plant species and resulted in a decreased species richness. The only species richness–biomass relationship found in our study was negatively linear. Perhaps there are other relationships, which we did not discover in our study, that were important to natural forest management. But our study was an observational one, which did not allow us to reveal a cause-effect relationship between species richness and biomass.

At the Shaba site, the difference in relationships between species richness and biomass on the two slopes revealed evidence for interspecific competitive exclusion although there was no evidence for a hump-shape or positively linear pattern. On the shady slope, the decrease in biomass with species number added was accompanied by a similar decrease in number of individuals, which resulted in a constant number of individuals per surviving species. That is, some species lost all plants whereas on the average, the remaining species did not lose individuals. The thinning hypothesis, however, would predict an equal change in number of individuals among all species (Oksanen, 1996; Stevens and Carson, 1999). On the sunny slope,

there was less species richness, which was not sensitive to biomass for more water stresses.

At our second observation site in Maicaogou, the relationship between species richness and biomass was significant only on the shady slope. There might be other variables which were not taken into account in our study but correlated with both species richness and biomass. For instance, the community structure, which was an important factor in determining biomass. At the Shaba site, there was a deforestation 40 years ago and in that event some big individuals were cleared in the community. This disturbance avoided influence of large individuals on species richness–biomass relationship. While at Maicaogou, the community has been protected for hundreds of years and there existed many large individuals, which might make the relationship obscure. This may be the reason for the absence of any relationship between species richness and biomass at this site. In conclusion, our study demonstrated that taking environmental changes into account is crucial to understand the productivity–species richness relationship in natural forest communities. Interspecific competition for limited resources can reduce total biomass even though species richness was added. Furthermore, environmental factors and history disturbance might lead to idiosyncratic patterns at different resources capacity levels.

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