

A reexamination of the relationships among phenological complementarity, species diversity, and ecosystem function

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Abstract. Interest in the effects of species diversity on ecosystem function has been rapidly increasing, and many studies have concluded that increasing species diversity improves ecosystem function. Theories predict that phenological complementarity, the asynchrony of species resource use and growth, may explain how species diversity enhances ecosystem function but it remains largely untested. In this paper, we tried to determine: (i) whether, in a species-rich natural assemblage, increasing species diversity enhances ecosystem function by increasing phenological complementarity, and (ii) how phenological complementarity was related to the scales of alpha-diversity. Over a three-year period, we conducted the experiment in 55 permanent plots with a relatively homogeneous environment in natural alpine grasslands, and estimated percent cover of each plant species present in each plot three times in each growing season. Species diversity in each permanent plot was quantified in two ways, the total number of species, and the evenness of species abundance. Phenological complementarity was quantified as the negative logarithm of the variance ratio. Ecosystem function was measured as total annual cover (i.e. the sum of maximum cover values recorded for each species in a growing season). Statistical analysis of the relationships between total annual cover, species diversity, and phenological complementarity found that total annual cover increased with species diversity, and phenological complementarity was responsible for the positive effects of species diversity on total annual cover. Phenological complementarity, however, was not significantly related to species diversity. These results indicate that phenological complementarity was critical to the maintenance of total annual cover in our studied alpine plant communities. However, considering different mechanisms of species coexistence (e.g. local similarity), phenological complementarity is not necessarily linearly correlated with the scales of alpha-diversity in species-rich plant assemblages. In addition, other mechanisms, for example, the sampling effect for phenological complementarity, may simultaneously act on how phenological complementarity enhances ecosystem function. Therefore, greater understanding of how diversity and phenological complementarity influence ecosystem function will require more extensive experiments that control the effects of composition.

Keywords: Alpine grassland; Ecosystem function; Evenness; Phenological complementarity; Species diversity; Variance ratio.

Introduction

Recently, interest in the effects of species diversity on ecosystem function has been rapidly increasing, and researchers studying experimental terrestrial ecosystems (Naeem et al., 1995, 1996; Tilman et al., 1996, 1997a; Hector et al., 1999) have recently concluded that increasing species diversity improves ecosystem function. However, these studies have generated considerable criticism based upon their experimental methodology (Huston, 1997; Wardle, 1999), analysis (Aarssen, 1997), and general conclusions (Grime, 1998). As a result, understanding the mechanisms underlying the relationship between species diversity and ecosystem function remains important. Complementarity, where ecological differences (e.g., phenology) among species lead to more complete utilization

of resources, may explain the biological effects of species diversity on ecosystem function (Tilman et al., 1997b; Loreau, 1998). Though theoretically attractive, few empirical diversity-ecosystem function studies have been constructed to test this mechanistic hypothesis (Hooper, 1998; Fridley, 2001).

Phenological complementarity, the asynchrony of species resource use and growth, may enhance ecosystem function when phenological differences allow different species to peak at different times throughout a growing season (Gulmon et al., 1983; Hooper, 1998). A previous empirical work showed that naturally occurring variation in species diversity had little effect on whether phenological complementarity can enhance ecosystem function (Stevens and Carson, 2001). This result emerged even though experimental manipulations of resources created contrasting environmental conditions analogous to larger scale environmental variation, thereby hopefully improving the generality of the findings (Stevens and Carson,

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2001). Nonetheless, how phenological complementarity manifests itself in natural species-rich plant communities still remains unclear and needs to be experimentally explored. Here we hypothesize that, in species-rich plant assemblages, phenological complementarity is critical to the maintenance of ecosystem function. Considering different mechanisms of species coexistence, for example, local similarity, which allows for species coexistence in that the rate of competitive displacement slows as species become increasingly locally similar (Hubbell, 1979; Hubbell and Foster, 1986), however, phenological complementarity may not be significantly related to the scales of alpha-diversity.

We collected data from a natural alpine grassland containing species with a variety of phenologies. Over the three-year period of this study, we measured percent cover of each plant species three times in each growing season in 55 permanent plots with a relatively homogeneous environment. Our aim was to test whether increasing species diversity enhances ecosystem function by increasing phenological complementarity in natural species-rich plant assemblages and how phenological complementarity was related to the scales of alpha-diversity.

Materials and Methods

Site Location

Our study site, a natural alpine grassland, is located in the eastern region of the Qing-Hai Tibetan Plateau (latitude 35°58'N, longitude 101°53'E, altitude about 3,500 m) in northwestern China. The climate is alpine humid, mean annual temperature is 1.2°, with the monthly average ranging from below -10° in January to 11.7° in July. Mean annual rainfall is 620 mm, and mean annual growing degree days are less than 150 days. The main soil type is sub-alpine meadow soil. The soil horizon is about 80 cm. The vegetation consists mainly of arctic alpine and Chinese Himalayan plants (Wu, 1995) and is dominated by Sedges (e.g. *Kobresia* spp.), Graminoids (e.g. *Festuca* spp., *Poa* spp., *Agrostis* spp.), Composite (e.g. *Saussurea* spp.), and Buttercup (e.g. *Anemone* spp.).

Sampling Design and Parameters Estimated

In September 1998, 55 0.5 m × 0.5 m permanent plots separated by at least 5 m were established along a transect line within the same microhabitat type where the environmental conditions and species composition are relatively homogeneous. From 1999 to 2001, we conducted this experiment three times at the end of June, July, and August in each plant growth season.

In each plot, the plant species richness and plant species cover of each plant species were recorded. Ecosystem function was measured as total annual cover (TAC), which is the sum of the maximum cover values recorded for each plant species within each plot for each year. Introduced by Stevens and Carson (2001), this approach of calculating total annual cover uses a technique originally designed to calculate aboveground net primary productiv-

ity (ANPP) from biomass samples (Malone, 1968). ANPP of herbaceous plant assemblages is best estimated by sampling biomass multiple times throughout the growing season and summing the maximum biomass values for each species (Stevens and Carson, 2001). Here total annual cover was calculated in an analogous manner.

We quantified species diversity in each permanent plot with two indices, the total number of species occurring at any time during a single season, *S*, and the evenness of species abundance, *E*, calculated by Simpson's measure of evenness ($1/\sum_{i=1}^S p_i^2$)/*S* (Krebs, 1997), where p_i is the relative abundance of species *i* based on the maximum cover value recorded for each species in a given year.

We quantified phenological complementarity (PC) as the negative logarithm of the variance ratio (Frost et al., 1995;

Klug et al., 2000), i.e. $PC = -\ln\left(\frac{\text{Var}\left\{\sum_{i=1}^n S_i\right\}}{\sum_{i=1}^n \text{Var}\{S_i\}}\right)$,

where S_i is the percent cover of species *i*, and $\text{Var}\{\}$ is the sample variance among June, July, August samples. $PC > 0$ results when the sum of covariances among species is negative and indicates complementarity. In contrast, $PC < 0$ occurs when the sum of covariances among species is positive and indicates synchronous. Finally, $PC = 0$ occurs when the sum of the covariances of species is zero and indicates that species vary independently.

Data Analysis

We used backward selection to build a multiple regression model to explain variation in total annual cover (TAC). Species richness (*S*), evenness (*E*), phenological complementarity (*PC*), and their third order polynomial expressions were used as explanatory variables in the analysis. After the model was determined, we used type III sums of squares to determine the effects of each explanatory variable in the model on total annual cover.

Results

Our study site contained species with a variety of phenologies that peaked through the growing season (Figure 1), indicating that phenological complementarity could, in principle, enhance total annual cover. Multiple regression of total annual cover on species diversity and phenological complementarity showed that total annual cover was the third order polynomial expressions of number of species and linear functions of evenness and phenological complementarity (analyses from data collected in 2001; analyses using data collected during the other two years yielded similar results) (Table 1). The regression model explained 58.9% of the variation in total annual cover (Table 1). The third order polynomial expressions of number of species together explained 15.51% of the variation in total annual cover (Table 2), indicating that the positive effects of number of species on total annual cover was nonlinear (Figure 2B). Evenness of species abundance and phenological complementarity can explain 11.33% and 32.06% of

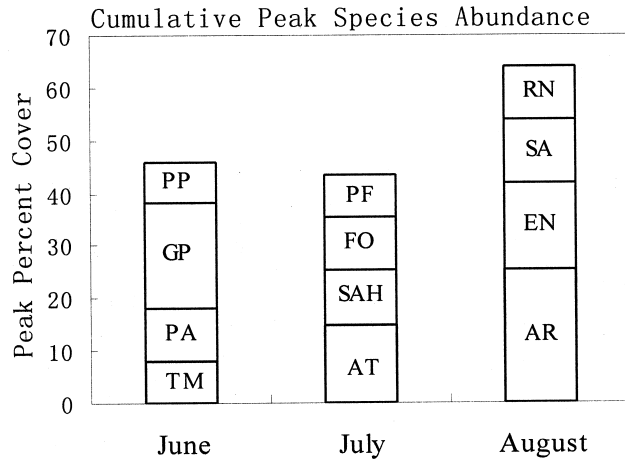


Figure 1. The 12 most common species' peak abundance. Averaging each species' percent cover across all plots for each observation time, and the maximum of the three observation times was diagrammed for the 12 most common species. Species abbreviations: PP—*Poa pratensis*; GP—*Geranium pylzowianum*; PA—*Potentilla anserina*; TM—*Taraxacum mongolicum* Hand.-Mazz.; PF—*Potentilla fragarioides* L.; FO—*Festuca ovina* L.; SAH—*Saussurea hieracioides* Hook. f.; AT—*Anemone trullifolia* Hook. f. et Thoms. var. *Linearis* (Bruhl) H.-M.; RN—*Roegneria nutans* (Keng) Keng; SA—*Stipa aliena* Keng; EN—*Elymus nutans* Gruseb.; AR—*Anemone rivularis* Buch.-Ham. var. *barbulata* Turcz.

variability in total annual cover, respectively, and their positive effects on total annual cover appeared linear (Figure 2A, 2C). Phenological complementarity itself had more than half the explanatory power of the model, and it was uncorrelated to two indices of species diversity (Figure 3).

Discussion

We found that phenological complementarity could explain the observed positive relationships between number of species, evenness, and total annual cover. The result was consistent with theoretical predictions about the effect of phenological complementarity on how species diversity enhances ecosystem function. It was different from Stevens and Carson's findings (2001) in an early successional plant assemblage, where they found no evidence that phenological complementarity was the mechanism responsible for the observed positive relationships between species diversity and ecosystem function, and increasing diversity did not enhance phenological complementarity. They suggested that, indeed, phenological complementarity may be critical to the maintenance of ecosystem function in their studied plant assemblage, but sufficient complementarity may be achieved at low levels of diversity. However, in our studied species-rich plant communities, we found that, phenological complementarity could be achieved at high levels of diversity, but as the experiment of Stevens and Carson showed, it was also uncorrelated with species diversity. These results in different ecological contexts indicate that phenological com-

Table 1. The multiple regression model of total annual cover on listed variables.

Variable ^a	Parameter	Student's T	P
S	25.845	2.343	0.023
S ²	-0.902	-2.528	0.015
S ³	0.0101	2.741	0.009
E	126.098	3.763	<0.0001
PC	20.287	6.331	<0.0001

^aOverall F_{5,49}=14.019, P<0.0001, R²=0.589. S: number of species per plot; E: evenness of species abundance per plot; PC: phenological complementarity.

Table 2. The effects (Type III sums of squares) of each variable in the multiple regression model on total annual cover.

Source ^a	DF	SS	% SS explained
S	1	1591.123	4.39%
S ²	1	1852.161	5.11%
S ³	1	2177.106	6.01%
E	1	4103.818	11.33%
PC	1	11615	32.06%
Residual	49	14200.19	41.1%

^aS: number of species per plot; E: evenness of species abundance per plot; PC: phenological complementarity.

plementarity was critical to the maintenance of ecosystem function, but natural variation in phenological complementarity was not necessarily linked linearly to the scales of alpha-diversity in species-rich plant assemblages.

Vandermeer (1990) showed that, given the restricted suite of fundamental plant resources, even in very different species or functional groups, resource use is still only partially complementary. Nonetheless, partial complementarity may increase ecosystem function, at least marginally (Hooper, 1998). Reduced competition by this mechanism has been suggested to be a primary reason for improved yields in intercropping (Vandermeer, 1990) as well as for allowing species coexistence in diverse natural communities (Grubb, 1977). However, because the resource requirements of all plants are fairly similar, the effects of complementary resource use on ecosystem function at the scales of alpha-diversity are thought to saturate at relatively low species richness (Vitousek and Hooper, 1993). McNaughton (1993) showed that phenologies are more synchronous in communities with only one or a few species. This might suggest that, in species-rich plant assemblages, the effects of phenological complementarity on ecosystem function at the scales of alpha-diversity may be achieved at much higher levels of diversity than other types of complementary resource use (e.g. in space, or in types of resource used). In fact, our results confirmed that the effects of phenological complementarity on ecosystem function, indeed, can be achieved at very high levels of diversity (average 34 species per plot, ranging from 15 to 49).

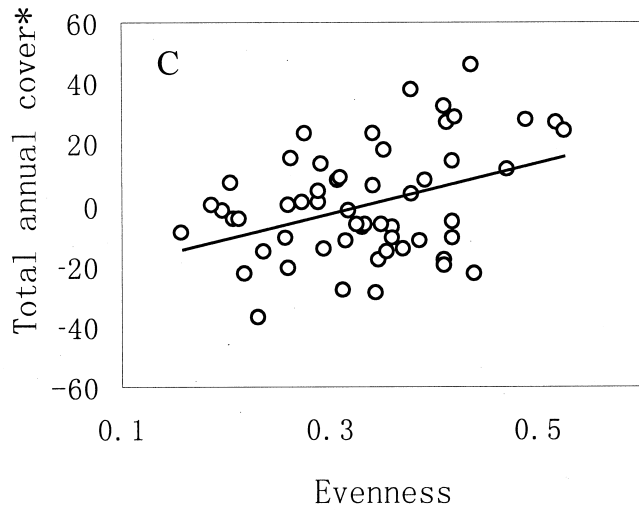
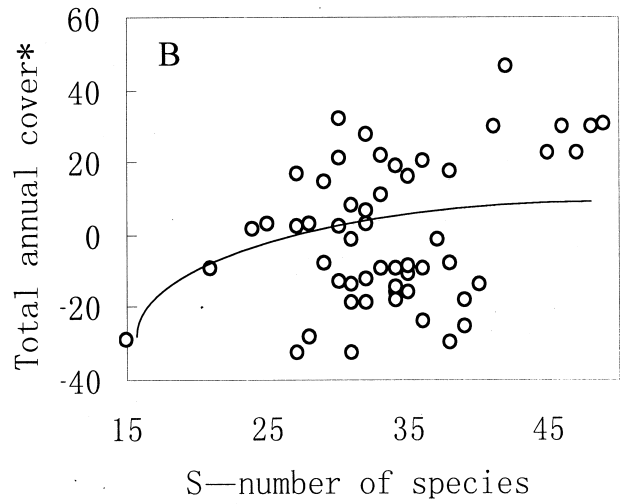
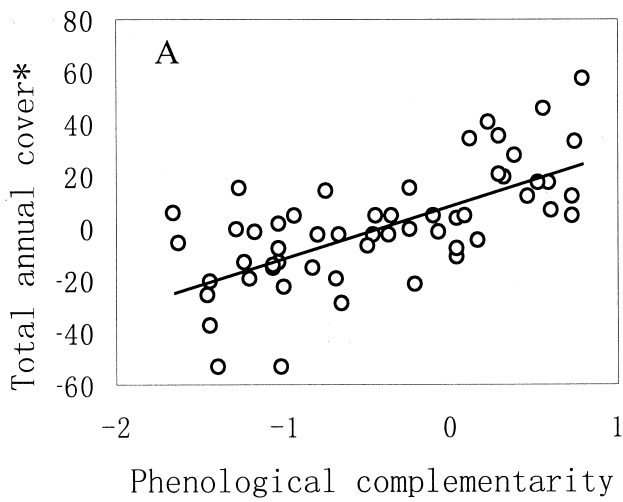


Figure 2. Relationships between total annual cover and all variables in the determined model. (A-C) Partial residual plots show the relationships between each explanatory variable and the variation in total annual cover not explained by all other variables in the determined model. (Total annual cover* in A-C are the partial residuals of total annual cover.)

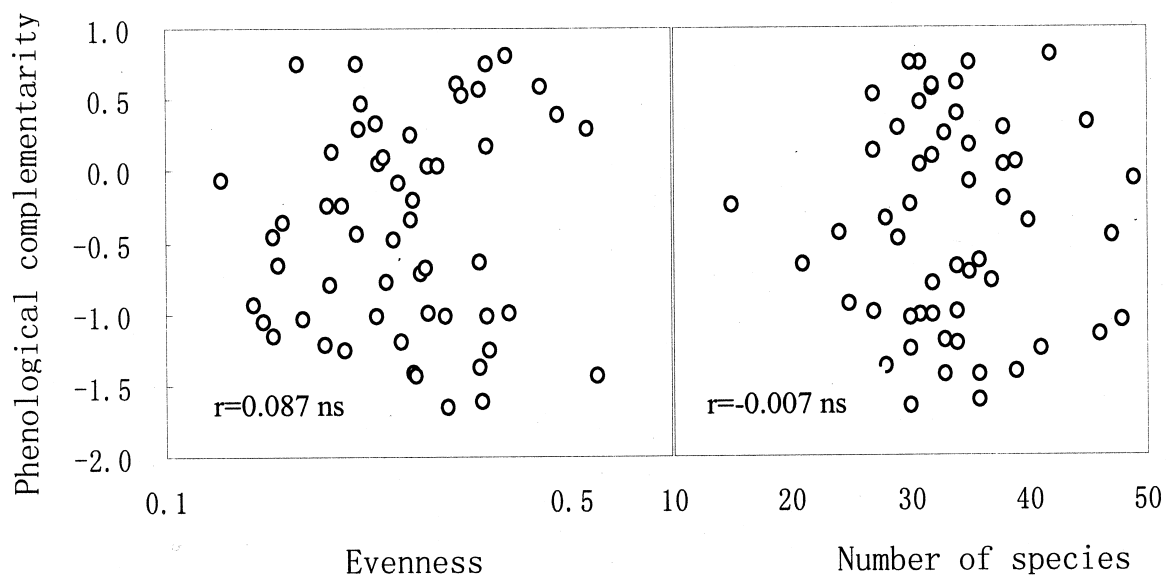


Figure 3. Relationships between phenological complementarity and two measures of species diversity, evenness of species abundance and number of species.

However, because of asynchronous resource use, the effects of competition are weaker so that noncomplementary (i.e. synchronous) species are able to coexist (Petchey, 2000). Local similarity has also been invoked to explain coexistence between competitive species (Hubbell, 1979; Hubbell and Foster, 1986), and here it also means that more synchronous species, i.e. species with high resource use overlap, are able to coexist. Thus, coexistence of more synchronous species accounts for the increased species diversity, but it may make little contribution to phenological complementarity. Consequently, it may not be surprising that phenological complementarity was uncorrelated with the scales of alpha-diversity (see also Stevens and Carson's, 2001).

In addition, different mechanisms may be connected with phenological complementarity by operating simultaneously or sequentially. For example, the sampling effect for phenological complementarity (Fridley, 2001) may simultaneously act on how phenological complementarity enhances ecosystem function because of the greater probability of including more phenologically complementary species in more species-rich communities. Also, the life history of species (winter annuals, summer annuals, biennial, and perennials) may allow temporal partitioning of the growing season (for example, Carson and Barrett, 1988), so the contrasting life history may enhance the effect of phenological complementarity in plant communities, and this deserves further exploration. Greater understanding of how diversity and phenological complementarity influence ecosystem function will require extensive experiments that allow for the control of species composition separate from species that are temporarily separated phenologically.

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Literature Cited

- Aarssen, L.W. 1997. High productivity in grassland ecosystem: effected by species or productive species? *Oikos* **80**: 183-184.
- Carson, W.P. and G.W. Barrett. 1988. Succession in old-field plant communities: effects of contrasting types of nutrient enrichment. *Ecology* **69**: 984-994.
- Fridley, J.D. 2001. The influence of species diversity on ecosystem productivity: how, where, and why? *Oikos* **93**: 514-526.
- Frost, T.M., S.R. Carpenter, A.R. Ives, and T.K. Kratz. 1995. Species compensation and complementarity in ecosystem function. In C.G. Jones and J.H. Lawton (eds.), *Linking Species and Ecosystems*, Chapman and Hall Press, London, pp. 224-239.
- Grime, J.P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* **86**: 902-910.
- Grubb, P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* **52**: 107-145.
- Gulmon, S.L., N.R. Chiariello, H.A. Mooney, and C.C. Chu. 1983. Phenology and resource use in three co-occurring grassland annuals. *Oecologia* **58**: 33-42.
- Hector, A., B. Schmid, C. Beierkuhnlein, M.C. Caldeira, M. Diemer, P.G. Dimitrakopoulos, J. Finn, H. Freitas, P.S. Giller, J. Good, R. Harris, P. Högberg, K. Huss-Danell, J. Joshi, A. Jumpponen, C. Körner, P.W. Leadley, M. Loreau, A. Minns, C.P.H. Mulder, G. O'Donovan, S.J. Otway, J. S. Pereira, A. Prinz, D.J. Read, M. Scherer-Lorenzen, E.-D. Schulze, A.-S.D. Siamantziouras, E.M. Spehn, A.C. Terry, A.Y. Troumbis, F.I. Woodward, S. Yachi, and J.H. Lawton. 1999. Plant diversity and productivity experiments in European grasslands. *Science* **286**: 1123-1127.
- Hooper, D.U. 1998. The role of complementarity and competition in ecosystem responses to variation in plant diversity. *Ecology* **79**: 704-719.
- Hubbell, S.P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. *Science* **203**: 1299-1309.
- Hubbell, S.P. and R.B. Foster. 1986. Biology, chance, and history and the structure of tropical rain forest tree communities. In J. Diamond, T.J. Case, Harper, and Row (eds.), *Community Ecology*. New York, pp. 314-329.
- Huston, M.A. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* **110**: 449-460.
- Klug, J.L., J.M. Fischer, A.R. Ives, and B. Dennis. 2000. Compensatory dynamics in planktonic community responses to pH perturbations. *Ecology* **81**: 387-398.
- Krebs, C.J. (eds.). 1997. *Ecological methodology*. Columbia University press, Columbia, 449 pp.
- Loreau, M. 1998. Biodiversity and ecosystem functioning: A mechanistic model. *Proc. Natl. Acad. Sci. USA* **95**: 5632-5636.
- Malone, C.R. 1968. Determination of peak standing crop biomass of herbaceous shoots by the harvest method. *Am. Midl. Nat.* **79**: 429-435.
- McNaughton, S.J. 1993. Biodiversity and function of grazing ecosystems. In E.-D. Schulze and H.A. Mooney (eds.), *Biodiversity and Ecosystem Function*. Springer-Verlag, Berlin, Germany, pp. 361-383.
- Naeem, S., L.J. Thompson, S.P. Lawler, J.H. Lawton, and R. M. Woodfin. 1995. Empirical evidence that declining species diversity may alter the performance of terrestrial ecosystems. *Proc. Roy. Soc. Lond. B* **347**: 249-262.
- Naeem, S., K. Håkansson, J.H. Lawton, M.J. Crawley, and L.J. Thompson. 1996. Biodiversity and plant productivity in a model assemblage of plant species. *Oikos* **76**: 259-264.
- Petchey, O.L. 2000. Species diversity, species extinction, and ecosystem function. *Am. Naturalist* **155**: 696-702.
- Stevens, M.H.H. and W.P. Carson. 2001. Phenological complementarity, species diversity, and ecosystem function. *Oikos* **92**: 291-296.
- Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* **379**: 718-720.
- Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. 1997a. The influence of function diversity and composition on ecosystem processes. *Science* **277**: 1300-1302.
- Tilman, D., C.L. Lehman, and K.T. Thomson. 1997b. Plant diversity and ecosystem productivity: theoretical

- considerations. Proc. Natl. Acad. Sci. USA **94**: 1857-1861.
- Vandermeer, J.H. 1990. Intercropping. In C.R. Carrol, J.H. Vandermeer, and P.M. Rosset (eds.), *Agroecology*. McGraw-Hill, New York, pp. 481-516.
- Vitousek, P.M. and D.U. Hooper. 1993. Biological diversity and terrestrial ecosystem biogeochemistry. In E.-D. Schulze and H.A. Mooney (eds.), *Biodiversity and Ecosystem Function*. Springer-Verlag, Berlin, Germany, pp. 3-14.
- Wardle, D.A. 1999. Is "sampling effect" a problem for experiments investigating biodiversity-ecosystem function relationships? *Oikos* **87**: 403-407.
- Wu, Z.Y. (eds.). 1995. *Vegetation of China*. Academic Press, Beijing, China, 643 pp.

物候互補、物種多樣性與生態系統功能之間關係的再檢驗

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物種多樣性對生態系統功能的影響近來引起了人們極大的興趣，許多研究得出結論：多樣性的增加能夠促進生態系統功能。理論預測：物候互補，即物種在資源利用和生長上的不同步，可以解釋多樣性是如何提高生態系統功能的，但還沒有得到充分驗證。本文試圖弄清，在物種豐富的自然植物群落中，①是否多樣性的增加促進生態系統功能是通過增加物候互補實現的；②物候互補與 α 多樣性的關係如何。為此，我們在天然的高寒草場一個相對同質的環境中建立的55個永久樣方中進行實驗觀測，估計了每個生長季中每個樣方中出現物種的百分蓋度，實驗為期三年。每個樣方的物種多樣性用總物種數和均勻度兩種方式度量，物候互補用方差比的對數的負數來表示，生態系統功能用年總蓋度（即一個生長季中每個物種所記錄下的最大蓋度之和）來衡量。年總蓋度，物種多樣性，物候互補關係的統計分析表明：年總蓋度隨著物種多樣性的增加而增加；物候互補能夠用來解釋物種多樣性對年總蓋度的正效應，但它與物種多樣性沒有顯著相關關係。這些結果表明：在我們研究高寒植物群落中，物候互補對年總蓋度的維持是關鍵的，然而，考慮到不同的物種共存機制（比如，局域相似性等），在物種豐富的植物群落中，物候互補可能與 α 多樣性不必線性相關。此外，其他機制，比如物候互補的取樣效應，可能也在物候互補促進生態系統功能中同時發揮著作用。因此，更好地理解物候互補、物種多樣性對生態系統功能的影響將需要更廣泛的實驗以控制構成效應。

關鍵詞：高寒草場；生態系統功能；均勻度；物候互補；物種多樣性；方差比。