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Title: Daytime warming lowers community temporal stability by reducing the abundance of dominant, stable species

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subordinate species.

Abstract

Daytime and nighttime warming have the potential to influence plant community structure and ecosystem functions. However, their impacts on ecological stability remain largely unexplored. We conducted an eight-year field experiment to compare the effects of daytime and nighttime warming on the temporal stability of a temperate steppe in northern China. Our results showed that the cover and stability of dominant species, stability of subordinate species, and compensatory dynamics among species strongly influenced

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community-level stability. However, daytime, but not nighttime, warming significantly reduced community temporal stability mainly through the reduction in the abundance of dominant, stable species. These findings demonstrate the differential effects of daytime and nighttime warming on community stability, and emphasize the importance of understanding the changes of dominant species for accurately predicting community dynamics under climate warming.

Introduction

Temporal stability, defined as the constancy (i.e., the inverse of variability) of the ecological variables over time (Pimm, 1984), is a fundamental property of any ecological system.

Elucidating its regulatory mechanisms is not only important for understanding how nature operates, but also critical for maintaining the sustainability of managed ecosystems that provide ecological goods and services for humanity (Tilman *et al.*, 2014). Species diversity is often thought as a critical determinant of community temporal stability. Ecological theory predicts that increasing species diversity could enhance community temporal stability via several mechanisms, including the overyielding effect (Lehman & Tilman, 2000), the portfolio effect (Doak *et al.*, 1998; Lehman & Tilman, 2000), and compensatory population dynamics among species (i.e., the increases in the abundance of some species are compensated by the declines in the abundance of other species; Loreau & de Mazancourt, 2008; Gonzalez & Loreau, 2009; Hautier *et al.*, 2014). A growing number of empirical studies have reported positive effects of biodiversity on the temporal stability of community biomass (McNaughton, 1977; Tilman & Downing, 1994; Steiner *et al.*, 2005; Tilman *et al.*,

2006; van Ruijven & Berendse, 2007; Isbell *et al.*, 2009; Hector *et al.*, 2010; Yang *et al.*, 2012; de Mazancourt *et al.*, 2013; Hautier *et al.*, 2014). Nevertheless, other studies have identified the importance of other factors other than species diversity in regulating community temporal stability. For example, the stability properties of dominant species could have substantial influence on community stability if the dominant species behave differently from the other species in the community, or synergistic interactions (e.g., complementary effect or facilitation) become unimportant in the assemblages characterized by high dominance (Hillebrand *et al.*, 2008; Wilsey *et al.*, 2014). Subordinate and/or rare species may also contribute largely to ecological stability (Downing *et al.*, 2014) if, for example, their presence promotes weak trophic interactions (McCann *et al.*, 1998; Jiang *et al.*, 2009; Downing *et al.*, 2014). However, irrespective of the increased understanding on the role of various ecological factors in influencing community temporal stability (Polley *et al.*, 2007; Grman *et al.*, 2010; Sasaki & Lauenroth, 2011; Yang *et al.*, 2011; Hallett *et al.*, 2014; Wilsey *et al.*, 2014), little consensus on their relative roles across different ecosystems has been reached.

The Earth's land surface has experienced substantial climate warming over the past five decades, with the magnitude of the temperature increase being notably greater during nighttime than daytime (Zhou *et al.*, 2009; Xia *et al.*, 2014). Daytime and nighttime warming have been demonstrated to influence plant photosynthesis and respiration differentially (Wan *et al.*, 2009; Xia *et al.*, 2009), with possibly subsequent effects on stability. For example, net primary productivity could increase under daytime warming that tends to enhance the rate of carbon (C) assimilation, and decline under nighttime warming that tends to accelerate C loss through increased respiration (Xia *et al.*, 2014). This could

potentially lead to a positive effect of daytime warming and a negative effect of nighttime warming on community temporal stability via the warming-induced changes in productivity (i.e., changes in the overyielding effect). Moreover, climate warming may influence community stability by altering the abundance and/or stability of component species. For example, the abundance and stability of dominant species may change under warming if they suffer largely from the detrimental effect of warming-induced drought stress (Mariotte *et al.*, 2013; Mariotte, 2014), which could subsequently influence community-level stability. The contributions of subordinate and rare species to community temporal stability are likely to be augmented under warming if they benefit most from enhanced facilitation associated with water deficit induced by warming (Callaway *et al.*, 2002; Thompson *et al.*, 2010).

Community stability may also be affected by warming-induced changes in compensatory dynamics among species, as the abundance of cold-adapted species may decline whereas that of warm-adapted species may increase under climate warming (Gottfried *et al.*, 2012). Mesic species may also become progressively more restricted as warming dries the soil (Price & Waser, 2000). Finally, given the possible dependence of community stability on species diversity, warming may affect community stability indirectly by changing species diversity.

The temperate steppe is the typical biome of arid and semiarid regions and stretches across the Eurasian continent, providing valuable goods and services for people living in the region.

However, both productivity and biodiversity of this ecosystem are sensitive to climate warming (Wan *et al.*, 2009; Yang *et al.*, 2010) and it is critical to understand the climate warming effects on its long-term provisioning capacity. Here, we report on an 8-year (2006-2013) field experiment of daytime and nighttime warming in a temperate steppe of

Northern China to examine their impacts on community temporal stability and the associated mechanisms. Our results showed that daytime, but not nighttime, warming reduced the temporal stability of plant communities mainly through reducing the abundance of dominant species, which exhibited greater stability than subordinate and rare species.

Materials and Methods

Study site

This study was carried out in a semiarid temperate steppe (42°02'N, 116°17'E, 1324 m a.s.l.) in Inner Mongolia, China. Mean annual temperature in the study area is 2.1 °C, with the mean monthly temperature ranging from -17.5°C in January to 18.9 °C in July. Mean annual precipitation over the previous 60 years is 383 mm, with the majority of annual rainfall occurring during the growing season (from May to October). The soil at the study site is of the chestnut type, with average bulk density of 1.31 g cm⁻³ and pH of 7.7. The dominant species in this temperate steppe, which has relatively low aboveground primary productivity (approx. 100-200 g m⁻² yr⁻¹), are perennial plants, including *Artimesia frigida*, *Stipa capillata*, *Leymus chinensis*, *Cleistogenes caespitosa*, and *Potentilla acaulis*. The study site was subjected to cattle grazing prior to 2001, and has been fenced since 2001 to exclude large herbivores (Wan *et al.*, 2009).

Experimental design

The experiment used a random block design with four treatments, including the control (C), daytime (6:00 am-6:00 pm, local time) warming (D), nighttime (6:00 pm-6:00 am, local time) warming (N), and continuous (24 h) warming (D+N); each treatment had four replicates. The plot size is 3×4 m with a 3-m distance between any two adjacent plots. All the warmed plots were heated by MSR-2420 infrared radiators (Kalglo Electronics Inc, Bethlehem, PA, USA), suspended 2.25 m above the ground. In order to simulate the shading effects, we also placed “dummy” heaters with the same shape and size as the infrared heaters in the control plots. All the heaters under the warming treatments were set at an electrical power output of 1,600 W (Xia *et al.*, 2009). We acknowledge that our experiment lacked an ambient control treatment, which would allow us to compare treatments with and without heaters. However, the effects of the physical presence of heaters, such as those on shading, bird densities and wind exposure, appeared limited in our study, and we were able to assess the effect of warming by comparing results of the dummy heater treatment and the real heater treatment. Daytime and nighttime warming increased daily mean soil temperature by 0.34 and 0.52 °C, respectively (Figure S1). In contrast, neither daytime nor nighttime warming affected air temperature. Daytime warming reduced soil moisture by 0.43 V/V% (absolute difference), whereas nighttime warming had little effect on soil moisture (Figure S1). The warming treatment started from 23 April, 2006 and ran continuously in the first two years (2006 and 2007). Beginning from 2008, the heaters were turned on from March 15 to November 15. In the winter, there was no living aboveground biomass. Therefore, the effect of winter heating was likely limited, as supported by the lack of differences in community

cover and species richness between the first two years and remaining years of our experiment (Fig. 3).

Vegetation monitoring

From 2006 to 2013, we estimated plant cover in two 1 ×1 m permanent quadrats in each plot in August when plant biomass reached its peak level (Yang *et al.*, 2010). As in many previous studies (e.g., Knapp *et al.*, 2001; Lan & Bai, 2012; Mouillot *et al.*, 2013; Xu *et al.*, 2015; Isbell *et al.*, 2015), we used plant cover as a proxy of plant biomass. Direct estimation of aboveground biomass by clipping the permanent quadrat would bring disturbance to the quadrat and therefore was not used. The cover of each species in each quadrat was estimated using a canopy interception technique based on 100 equally distributed grids (10×10 cm). The mean of plant cover of the two quadrats in each plot was used for statistical analyses. We recorded species richness in each quadrat, and limited this estimate to species that rooted within the quadrat; species with parts overhanging the plot were excluded. Within each quadrat, the community cover was calculated as the summed cover of plant species present in the quadrat. The summed cover of all species may exceed 100%. Plant species were also categorized based on their relative abundances. A species was classified as 'dominant' if its mean relative abundance in the control plots exceeded 5%, as 'subordinate' if its mean relative abundance was between 1% and 5%, and as 'rare' if its mean relative abundance was <1% (Mouillot *et al.*, 2013; Mariotte *et al.*, 2013). This classification regime yielded 5 dominant species, 11 subordinate species, and 32 rare

species. The names of the dominant, subordinate, and rare species were included in Table S1.

Statistical analysis

Temporal stability (S) of dominant species, subordinate species, rare species, and communities at the plot scale was calculated as the ratio of the mean (μ) to the standard deviation (σ) of the cover values from 2006 to 2013. The degree of species compensatory dynamics was quantified using the community-wide synchrony index of species abundance developed by Gross *et al.* (2014), defined as

$$\eta = \left(\frac{1}{n} \right) \sum_i \text{corr}(Y_i, \sum_{j \neq i} Y_j) \quad (1)$$

where Y_i and Y_j are the cover of species i and j , respectively, and n is the number of species.

η reaches its minimum value of -1 when species are maximally asynchronized, and maximum of +1 when species are perfectly synchronized; it attains the values of 0 when species fluctuate independently (Gross *et al.*, 2014). There were no significant temporal trends in community cover from 2006 to 2013, hence detrending was not necessary.

We used separate repeated-measures ANOVAs to assess the effects of daytime and nighttime warming on species richness, total community cover, and cover of dominant species, subordinate species, and rare species across 2006 to 2013, where year was considered as within-subjects effects and daytime and nighttime as a fixed between-subjects effect. Two-way ANOVAs were performed to test the effects of daytime and nighttime warming on community temporal stability, temporal stability of dominant species, subordinate species, and rare species, and community-wide synchrony, where

daytime and nighttime warming were considered as fixed factors, community temporal stability, temporal stability of dominant species, subordinate species, and rare species, and community-wide synchrony were viewed as dependent variables. Paired-samples t-tests were used to compare stability across dominant, subordinate, and rare species.

Multiple regressions were used to examine factors that may influence community temporal stability, including community cover, species richness, community synchrony, stability of dominant, subordinate, and rare species, to community temporal stability. Furthermore, we used structural equation modeling (SEM) to identify causal linkages between explanatory variables and community temporal stability. Based on the linear regression results, we estimated the strength of direct and indirect relationships among the considered variables.

We checked the bivariate relationships between variables to ensure that linear models were appropriate. We then constructed SEM models based on the known effects and potential relationships among the drivers of community temporal stability (Fig. S5), and estimated the strength of total, direct and indirect effect of these variables (Table S2, S3, S4). We evaluated the fit of each model using the χ^2 -test (Grace & Bollen, 2005). SEM analyses were performed using AMOS 18.0 (Amos Development Co., Greene, Maine, USA). Other statistical analyses were conducted using SPSS 16.0 (SPSS, Inc., Chicago, Illinois, USA) and SAS (SAS Institute Inc., Cary, NC, USA).

Results

Temporal stability and community-wide synchrony

Daytime warming ($F_{1,15}=4.5$, $p=0.05$), but not nighttime warming ($F_{1,15}=0.0$, $p=0.96$), reduced temporal stability of community cover (Fig. 1). The temporal stability of dominant species was higher than that of subordinate species ($t_{1,15}=6.7$, $p<0.001$) and rare species ($t_{1,15}=11.4$, $p<0.001$). However, neither daytime nor nighttime warming influenced dominant species stability or subordinate species stability (Fig. 1). In contrast, daytime warming marginally reduced rare species stability ($F_{1,15}=4.0$, $p=0.06$), whereas nighttime warming enhanced it ($F_{1,15}=4.6$, $p=0.05$).

Neither daytime nor nighttime warming affected population synchrony. The values of the synchrony index did not differ among the experimental treatments, regardless of whether considering the whole communities or considering dominant, subordinate, and rare species separately (all $p>0.05$; Fig. 2).

Plant community response

Species richness fluctuated within a relatively small range (from 14 to 17), and did not differ between the control and warmed plots (daytime warming, $F_{1,27}=0.02$, $p=0.88$; nighttime warming, $F_{1,27}=0.24$, $p=0.63$; Fig. 3a). Neither daytime ($F_{1,27}=0.11$, $p=0.75$) nor nighttime warming ($F_{1,27}=0.70$, $p=0.42$) affected total community cover (Fig. 3b). Daytime warming marginally reduced the cover of dominant species (by 15.6%, $F_{1,27}=3.1$, $p=0.09$; Fig. 3c), but marginally increased the cover of subordinate species (by 29%, $F_{1,27}=3.2$, $p=0.08$; Fig. 3d).

Rare species cover was not affected by either daytime warming ($F_{1,27}=2.8$, $p=0.12$; Fig. S2d) or nighttime warming ($F_{1,27}=0.3$, $p=0.60$; Fig. S2d). By contrast, nighttime warming had no effects on the cover of the three groups (dominant species, $F_{1,27}=0.05$, $p=0.83$; subordinate species, $F_{1,27}=0.48$, $p=0.50$; rare species, $F_{1,27}=0.3$, $p=0.60$; Fig. 3).

Factors influencing stability

Linear regressions showed that community-level stability was positively correlated with the stability ($r^2=0.55$, $P<0.001$; Fig. 4d) and cover ($r^2=0.18$, $P<0.1$; Fig. 4g) of dominant species, but negatively correlated with community synchrony ($r^2=0.27$, $P<0.05$; Fig. 4c). Other variables that may potentially contribute to community temporal stability (e.g., total community cover, species richness, the cover and stability of subordinate species, and the cover and stability of rare species) showed no relationships with community stability (Fig. 4, S3).

The best SEM model ($\chi^2 = 14.07$, $P = 0.30$, $df = 12$, $GFI = 0.90$, $RMSEAR = 0.08$) explained 72% of the variations in community temporal stability (Fig. 5). This model revealed that daytime rather than nighttime warming suppressed community temporal stability through reducing the cover of dominant species (Fig. 5). Standardized total effect coefficients of daytime and nighttime warming on community stability were -0.32 and 0.13, respectively (Table S2), which can be entirely attributed to indirect, rather than direct effects of warming on stability (Table S3, S4). Dominant species stability, subordinate species stability, and community-level synchrony contributed to community temporal stability, but were not affected by either daytime or nighttime warming.

Discussion

Our results demonstrated that daytime warming, but not nighttime warming, lowered community temporal stability by reducing the abundance of dominant species that are comparatively more stable than subordinate and rare species. This result, together with those of several other studies on the asymmetric effects of daytime and nighttime warming on ecosystem functions (Wan *et al.*, 2009, Peng *et al.*, 2013; Xia *et al.*, 2014; Fu *et al.*, 2014; Piao *et al.*, 2015), suggests that research ignoring different ecological consequences of daytime and nighttime warming may not realistically predict community dynamics under future climate change scenarios. Moreover, our finding provides the rare evidence for the important role of dominant species, not species diversity, for regulating the stability of plant communities in the face of environmental change (see also Xu *et al.*, 2015).

Species richness and community stability

Anthropogenic perturbations that decrease diversity could suppress community-level stability (Tilman & Downing, 1994; Yang *et al.*, 2012). However, we found little support for the linkage between species diversity and community stability in our study. This finding is contradictory with the generally positive diversity-stability relationships reported by experimental studies that directly manipulated species diversity to examine its effect on community temporal stability (Tilman *et al.*, 2006; Isbell *et al.*, 2009; Hector *et al.*, 2010; Jiang & Pu, 2009; Campbell *et al.*, 2011; Gross *et al.*, 2014). One possible reason for the lack of diversity effects in our study is the relatively small gradient of species richness, which was unaffected by the warming treatments. Thus, our results are inconsistent with those of

experiments establishing large diversity gradients through soil nutrient manipulations (e.g., Tilman & Downing, 1994; Yang *et al.*, 2012) or direct diversity manipulations (e.g., Tilman *et al.*, 2006; Isbell *et al.*, 2009; Hector *et al.*, 2010). Some studies, however, have shown that the presence of small diversity gradients may not necessarily prevent diversity effects on stability from being detected (Sasaki & Lauenroth, 2011). Alternatively, the lack of diversity-stability relationships observed in our study may well reflect the fact that a variety of other factors, including the stability of dominant species that we considered here, could also influence community stability (Ives & Carpenter, 2007). The results of our study, which explored stability patterns of natural communities subjected to different climate warming scenarios, support the assumption that species diversity, despite the considerable attention it has received, is only one of many possible factors that influence community stability (Ives & Carpenter, 2007).

Dominant species and community temporal stability

Several previous studies have reported that the stability of dominant species is more important than species richness in determining community-level stability (Polley *et al.*, 2007; Grman *et al.*, 2010; Sasaki & Lauenroth, 2011; Yang *et al.*, 2011; Wilsey *et al.*, 2014). Consistent with these studies, we found that dominant species stability constituted the major contributor to community temporal stability. In particular, *A. frigida*, a semi-shrub (SS), contributed to up to 55% of community cover and community stability was positively associated with its stability in our study (Fig. S3c, S4). The effects of dominant specie

stability on community temporal stability are conceptually linked to the sampling effect (Aarssen, 1997; Huston, 1997; Tilman, 1999), where dominant species contribute predominantly to ecosystem functioning. Note that daytime and nighttime warming had little effect on the stability of dominant species, possibly due to the lower sensitivity of semi-shrubs than herbaceous plants to warming (Lin *et al.*, 2010). Daytime warming, however, resulted in the reduced abundance of dominant species, probably because the dominant species suffered largely from the detrimental effect of water deficit under daytime warming, due to their high canopy height and large specific leaf area (Yang *et al.*, 2013; Mariotte, 2014). Reduced abundance of the dominant, stable species is thus primarily responsible for reduced community stability under daytime warming.

Non-dominant species and community temporal stability

Subordinate and/or rare species can have substantial impacts on ecosystem functions, which are disproportionate to their abundance (Power *et al.*, 1996; Lyons *et al.*, 2005). In a fluctuating environment, the importance of subordinate and/or rare species to ecosystem functions may be further strengthened (Walker *et al.*, 1999; Yachi & Loreau, 1999). Therefore, ignoring the potential contribution of non-dominant species could lead to a biased understanding of the determinants of community temporal stability and projections of ecological service under climate change scenarios in the future (Lyons & Schwartz, 2001; Downing *et al.*, 2014). In stability and cover of dominant species, the stability of subordinate species constitutes the third most important contributor to community temporal stability

(see Fig. 5). Although the stability of subordinate species influences community temporal stability, it was not affected by either daytime or nighttime warming. Instead, daytime warming stimulated the abundance of subordinate species. Note that although the increased abundance of the less stable subordinate species in response to daytime warming may be associated with reduced community stability, this pathway was statistically insignificant in our SEM. The enhanced cover of subordinate species under daytime warming may be explained by the decreased competition from dominant species and increased synergistic effects among subordinate species due to exacerbated thermal and water stress under daytime warming (Callaway *et al.*, 1997, 2002).

Compensatory dynamics and community temporal stability

Compensatory dynamics can be driven by a variety of mechanisms (Gonzalez & Loreau, 2009), and the relative importance varies widely across different communities (Bai *et al.*, 2004, Houlahan *et al.*, 2007). In our study, compensatory dynamics (i.e., low species synchrony) are the fourth most important contributor (behind stability and cover of dominant species, and stability of subordinate species, see Fig. 5) to community temporal stability. A possible explanation for the significant compensatory dynamics observed in this system is competition between dominant and non-dominant species. The temperate steppe in this region was severely degraded due to over-grazing prior to 2000. Given the national policy of ecological restoration in China, the experimental area was fenced to exclude grazing in 2001. *A. frigid*, a semi-shrub with high tolerance to grazing, dominated early in

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this system (Niu & Wan, 2008). Without grazing disturbance, grasses and perennial forbs with greater growth rate and/or regeneration ability (most were non-dominant species), which confer greater competitive advantages (Gough *et al.*, 2012), increased in abundance via vegetative growth at the sacrifice of *A. frigida* over the experimental period (Fig. S2), leading to significant compensatory dynamics at the community level. Note that these temporal changes in the relative abundances of the dominant and non-dominant species were robust to our daytime warming treatments, which was reflected in our finding that neither daytime nor nighttime warming altered the community-level asynchrony. Therefore, the changes in compensatory dynamics cannot account for the reduced community temporal stability under daytime warming.

The lack of nighttime warming effects

No changes in the stability and cover of dominant species, the stability of subordinate species, or community-level synchrony were observed under nighttime warming, despite the fact that nighttime warming had greater impacts on soil temperature than daytime warming.

One possible explanation for the neutral effect of nighttime warming is that the positive effect of nighttime warming on plant growth via increasing minimum temperature and extending the length of growing seasons may have been mitigated by increased plant respiration under nighttime warming (Alward *et al.*, 1999; Xia *et al.*, 2009; Peng *et al.*, 2013).

Further investigations are needed to assess the robustness of our results.

The effects of warming on different stability properties

In the present study, we showed that daytime, but not nighttime, warming lowered community temporal stability by reducing the abundance of dominant, stable species. A recently published study (Yang *et al.*, 2016), conducted in the same study system, reported that nighttime, but not daytime, warming enhanced drought resistance via stimulating carbon sequestration. These results thus point to the differential responses of different stability properties to daytime and nighttime warming. In addition, given that resilience, in addition to resistance, also contributes to temporal stability (i.e., greater resilience and resistance leading to greater temporal stability), our findings indicate that the warming effects on resilience and resistance may differ from each other, which remains to be explored by future work.

Our study provides direct evidence that daytime, but not nighttime, warming reduced the temporal stability of plant communities. This result suggests that experiments and models that assume symmetric effects of daytime and nighttime warming on ecosystem processes may not realistically predict the effects of rising temperature on ecological stability, emphasizing the need to assess ecological consequences of climate warming at finer temporal resolutions. The generality of this result needs to be assessed by experiments in other ecosystems based on realistic warming scenarios in the future. Moreover, our findings highlight the importance of dominant species for community stability under climate warming, providing strong argument for the idea that factors other than species diversity may contribute dominantly to ecosystem functions (Grime, 1998; Ives & Carpenter, 2007).

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Figure legend

Figure 1. The effects of daytime and nighttime warming on the temporal stability of communities, dominant species, subordinate species, and rare species. C, D, N, and D + N represent control, daytime warming, nighttime warming, and daytime + nighttime warming, respectively. Error bars indicate \pm SE.

Figure 2. The effects of daytime and nighttime warming on species synchrony at the level of whole communities, dominant, subordinate and rare species. See Fig. 1 for abbreviations.

Error bars indicate \pm SE.

Figure 3. The effects of daytime and nighttime warming on species richness (a), community cover (b), relative cover of dominant species (c), and relative cover of subordinate species across 2006-2013 (d). See Fig.1 for abbreviations. Error bars indicate \pm SE.

Figure 4. Linear regressions of the temporal stability of community cover against community cover (a), species richness (b), community synchrony (c), dominant species stability (d), subordinate species stability (e), rare species stability (f), dominant species cover (g), and subordinate species cover (h).

Figure 5. The results of final structural equation modelling showing the causal relationships among daytime warming, nighttime warming, cover and stability of dominant species, stability of subordinate and rare species, and community-level synchrony to community temporal stability. Arrows indicate significant (solid, $P < 0.05$) and nonsignificant (dashed, $P > 0.05$) relationships. The width of arrows indicates the strength of the causal effect.

Numbers above the arrows indicate path coefficients (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

R^2 values represent the proportion of variance explained for each variable. Model fit

summary: $\chi^2 = 14.07$, $P = 0.30$, $df = 12$, GFI = 0.90, RMSEAR = 0.08.



