Biomass-dominant species shape the productivity-diversity relationship in two temperate forests

Yanxia Cheng, Chunyu Zhang, Xiuhai Zhao, Klaus von Gadow

Annals of Forest Science (2018) 75: 97
https://doi.org/10.1007/s13595-018-0780-0

RESEARCH PAPER

Biomass-dominant species shape the productivity-diversity relationship in two temperate forests

Yanxia Cheng[1] · Chunyu Zhang[1] · Xiuhai Zhao[1] · Klaus von Gadow[2,3]

Received: 15 March 2018 / Accepted: 22 October 2018 / Published online: 20 November 2018

Abstract

• ***Key message*** **A negative productivity-diversity relationship was determined for biomass-dominant species at the community level. This study thus supports the hypothesis in which the effects of individual species on the productivity-diversity relationships at the community level are related to their biomass density, an important functional trait.**
• ***Context*** The productivity-diversity relationships have been extensively studied in various forest ecosystems, but key mechanisms underlying the productivity-diversity relationships still remain controversial.
• ***Aims*** The objective of this study is to explore the productivity-diversity relationships at the community level, and to investigate the roles of individual species in shaping the community-level relationships between productivity and diversity under different forest types.
• ***Methods*** The study was conducted in two fully stem-mapped temperate mixed forest plots in Northeastern China: a natural secondary forest plot, and an old-growth forest plot. An individual-based study framework was used to estimate the productivity-diversity relationships at both species and community levels. A homogeneous Thomas point process was used to evaluate the significance of productivity-diversity relationship deviating from the neutral.
• ***Results*** At the species level, most of the studied species exhibit neutral productivity-diversity relationship in both forest plots. The percentage of species showing negative productivity-diversity relationship approaches linearly a peak value for very close neighborhoods (the secondary forest plot: $r = 3$ m, 38%; the old-growth forest plot: $r = 4$ m, 42%), and then decreases gradually with increasing spatial scale. Interestingly, only a few species displayed positive productivity-diversity relationship within their neighborhoods. Dominant species mainly exhibit negative productivity-diversity relationship while tree species with lower importance values exhibit neutral productivity-diversity relationship in both forests. At the community level, a consistent pattern of productivity-diversity relationship was observed in both forests, where tree productivity is significantly negatively associated with local species richness. Four biomass-dominant species (*Juglans mandshurica* Maxim., *Acer mono* Maxim.,*Ulmus macrocarpa* Hance and *Acer mandshuricum* Maxim.) determined a negative productivity-diversity relationship at the community level in the secondary forest plot, but only one species (*Juglans mandshurica*) in the old-growth forest plot.
• ***Conclusion*** The productivity-diversity relationship is closely related to the dominance of individual species at the species level. Moreover, this analysis is the first to report the roles of biomass-dominant species in shaping the productivity-diversity relationship at the community level.

Handling Editor: John M. Lhotka

Contribution of the co-authors Yanxia Cheng and Chunyu Zhang: analyzed the data and led the writing of the manuscript.
Chunyu Zhang and Klaus von Gadow: conceived the ideas and approach.
Xiuhai Zhao: designed the experiments and collected the data.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s13595-018-0780-0) contains supplementary material, which is available to authorized users.

✉ Chunyu Zhang
zcy_0520@163.com

[1] Research Center of Forest Management Engineering of State Forestry and Grassland Administration, Beijing Forestry University, Beijing 100083, China

[2] Faculty of Forestry and Forest Ecology, Georg-August-University Göttingen, Büsgenweg 5, 37077 Göttingen, Germany

[3] Department of Forest and Wood Science, University of Stellenbosch, Stellenbosch 7600, South Africa

Keywords Productivity-diversity relationship · Species dominance · Individual species · Homogeneous Thomas point process

1 Introduction

The influence of species diversity on ecosystem functioning, especially on biomass productivity, has become a major focus of ecological research (Loreau et al. 2001; Hooper et al. 2005). There are no universal relationships between productivity and diversity (hereinafter referred to as PDR). Positive relationships between productivity and diversity appear to be rather common (Schwartz et al. 2000; Hooper et al. 2005; Srivastava and Vellend 2005), whereas U-shaped, negative, and non-significant are also observed (Wardle et al. 1997; Wardle and Lagerström 2008; Ricklefs 1977; Tilman and Pacala 1993; Grace 1999; Mittelbach et al. 2001; Gillman and Wright 2006; Adler et al. 2011; Šímová et al. 2013; Gadow et al. 2016). The relationships between productivity and diversity are usually scale dependent. They are sometimes positive at the global/regional scale, but are often neutral, unimodal, or negative at the local spatial scales (Harrison et al. 2006). The mechanisms shaping the PDR have also received much attention. For example, species diversity may enhance productivity because of facilitation effects and/or niche complementarity among species, and because of the greater probability of including productive species in species-rich communities (Hector 1998; Tilman et al. 1997; Loreau and Hector 2001). But the ecological mechanisms which cause or contribute to a negative PDR remain controversial.

Species diversity affects ecosystem functioning (Tilman 1999; Hooper and Vitousek 1997; Symstad et al. 1998; Lohbeck et al. 2012), but there is no compelling evidence to show that ecosystem functions are consistently and causally connected with species diversity (Grime 1997). Dominant species were found to exhibit an asymmetrical influence on ecosystem functioning (Wardle 1999; Smith and Knapp 2003; Vile et al. 2006). For example, productivity is considered to be driven by a few dominant species that make up a large fraction of the plant biomass (Grime 1997). Ecosystem functioning is determined by functional traits of dominant species such as their relative biomass (Grime 1998; Wardle et al. 2000; Roscher et al. 2012). Numerous studies have demonstrated that ecosystem processes (Lepš et al. 1982) and ecosystem productivity (MacGillivray and Grime 1995; Tilman et al. 1997) are primarily driven by the functional traits of the dominant plants but are independent of species diversity.

The roles of dominant species in shaping PDR are often neglected. The presence of a dominant species may increase the primary production of an ecosystem, because it has higher ecological resource-use efficiency than subdominant individuals (Gong et al. 2011). Dominant species accounting for a relatively small percentage of all species may contribute considerably to total ecosystem functioning. Sala et al. (1996) have shown that the removal of the dominant species, which accounted for 40% of total biomass, had a greater effect on ecosystem functioning than the removal of a constant amount of biomass from each individual species in equal proportions. If most of a particular ecosystem functioning is performed by a few species, and when these species are also dominant, then it may be possible to obtain a negative relationship between ecosystem productivity and species richness (Creed et al. 2009).

Huston et al. (2000) found that there was no consistent effect of species diversity on productivity. Thus, it is necessary to establish fresh approaches to understand the multivariate links between productivity and diversity. On the basis of this need, an individual-based PDR framework was developed to explore relationships between tree productivity and local diversity (Wang et al. 2016). Limited seed dispersal determines the distributions of trees in a forest (Seidler and Plotkin 2006). Conspecifics occurring in distinct patches usually show positive spatial autocorrelation, which has been thought to be a fundamental ecological process influencing local diversity and ecosystem functioning (Pacala and Deutschman 1995; Kühn 2007). A number of theoretical studies have supported the hypothesis that species diversity is dispersal limited (Turnbull et al. 2000; Loreau et al. 2003; Cadotte 2006). The influence of dispersal limitations substantially alters the functions of natural ecosystems (Mouquet and Loreau 2002; Stein et al. 2008). Dispersal limitations contribute to a unimodal PDR not only in a theoretical study (Pärtel and Zobel 2007) but also in natural ecosystems (Stein et al. 2008).However, the spatial autocorrelation of species distributions has been largely neglected in many previous studies. In order to simulate the effects of spatial autocorrelation of species distribution on local diversity and ecosystem functions, a Thomas cluster process (Shen et al. 2009) should be incorporated into the individual-based PDR framework.

This study examines the structuring mechanisms of the community-level PDR in a natural secondary forest and an old-growth forest. We assume that the effects of individual species on the community-level PDR are closely related with an important functional trait, i.e., biomass density. Furthermore, we expect that community-level PDR is consistent in the two forests, but that the shaping roles of individual species should be different. Accordingly, the objective of this study is to explore the pattern of community-level PDR and to investigate the roles of individual species in shaping the community-level PDR in the two forest communities.

2 Materials and methods

2.1 Data collection

The observations for this study were assessed in two large permanent field plots in Northeastern China. The forest type of the study area is a typical temperate conifer and broadleaved mixed forest, in which the average rainfall is 606 mm/year, the average monthly temperature is − 18.6 °C in January and 21.7 °C in July. More details about forest distributions and climate in the Jilin area have been reported by Li et al. (2001). Two experimental field plots were established in the summer of 2010 and remeasured in the summer of 2015: a secondary forest plot and an old-growth forest plot. In each plot, all woody plants with a diameter at breast height (dbh) exceeding 1 cm were tagged and mapped; their species were identified and their dbhs, tree heights, crown widths, and heights to the first live branch were recorded. The two plots have similar woody plant species (Supplementary material Appendix 1 Table A1).

The observational study in the secondary forest plot covers an area of 21.84 ha (420 m × 520 m), and is located at 43° 58.207′ -43° 58.558′ N and 127° 44.092′ -127° 44.541′ E. The plot represents a natural secondary forest. The original vegetation in the secondary forest plot is the same as that in the old-growth forest plot, which emerged after heavy harvesting disturbance several decades ago. The topography in the secondary forest plot is flat with elevations ranging from 468 to 505 m above sea level. In terms of the importance value, the secondary forest plot is dominated by *Juglans mandshurica*, *Acer mandshuricum*, *Acer mono*, *Fraxinus mandschurica* Rupr., *Ulmus davidiana* Plabch. *var. japonica* (Rehd.) Nakai, *Ulmus macrocarpa* and *Betula costata* Trautv. (Supplementary material Appendix 2 Fig. A1). However, the top eight species in biomass density are *Juglans mandshurica*, *Fraxinus mandschurica*, *Pinus koraiensis* Sieb. et Zucc., *Acer mono*, *Ulmus macrocarpa*, *Ulmus davidiana* var. *japonica*, *Acer mandshuricum*, and *Ulmus laciniata* (Trautv.) Mayr. (Fig. 1a).These species with higher biomass density are hereafter referred to as biomass-dominant species. Our analysis in the secondary forest plot includes 24 woody species.

The old-growth forest plot covers an observational study area of 30.0 ha (500 m × 600 m), which is located at 43° 57.928′ -43° 58.214′ N and 127° 45.287′ -127° 45.790′ E. The old-growth forest plot is far away from villages where human disturbance has been virtually unknown. The elevation of the old-growth forest plot ranges from 576 to 784 m above sea level and the topography involves a valley between two slopes. The top ranking species regarding the importance value are *Acer mono*, *Ulmus laciniata*, *Carpinus cordata*, *Acer mandshuricum*, *Tilia amurensis*, *Acer barbinerve*, and *Pinus koraiensis* (Supplementary material Appendix 2 Fig. A1). The top eight species in biomass density are *Ulmus laciniata*, *Acer mono*, *Tilia amurensis* Rupr., *Pinus koraiensis*, *Betula costata*, *Juglans mandshurica*, *Phellodendron amurense* Rupr., and *Quercus mongolica* Fisch. ex Ledeb (Fig. 1a). Again, our analysis in the old-growth forest plot includes 24 woody species.

Although the secondary forest plot has a species composition that is similar to the old-growth forest plot, the dominance, abundance, and productivity of specific species have changed after human disturbance. For example, the importance value of *Fraxinus mandschurica* in the secondary forest plot is greater than that in the old-growth forest (Supplementary material Appendix 2 Fig. A1).

2.2 Species-level relationships between tree productivity and diversity

We evaluated the species-level PDR through the individual-based PDR framework (Wang et al. 2016). The individual-based PDR framework represents a long-recognized tradeoff between competition and facilitation among species. It provides a powerful tool to identify the role of individual species in shaping the PDR. For the combination of tree productivity and species richness surrounding the trees of a focal species, the index of association is calculated as follows:

$$\mathrm{AI}(r) = \frac{1}{N}\sum_{i=1}^{N}\sqrt{SR_i \times P_i} \quad (1)$$

where AI(r) is the index of association; N is the number of individuals. SR_i is the species richness within a circular area with varying radius r around the ith tree; ten circular areas whose radius increase from 1 to 10 m by 1 m ($r = 1, 2 \ldots 10$) are considered for each target tree; P_i is biomass productivity (in kg/year) of the ith tree. To eliminate the dimensional effect of the variable units, SR_i and P_i were standardized by the Min-Max normalization. When using $a = \pi r^2$, the AI(r) function can also be expressed in terms of a circular area a. To avoid the circular area of the focal species being located outside study area, we selected a buffer zone of 10 m along the border of the study area. Only individuals of the focal species within the inner area were used to calculate the P_i values. However, all individuals within the entire area were used to calculate the SR_i values.

There is a growing consensus that ecosystem processes are determined by functional traits of individual species rather than by the number of species (Chapin III et al. 2000; Díaz and Cabido 2001). By considering species richness, other important components of biodiversity are underestimated. Therefore, it is worth trying to calculate the index of association by including a functional diversity index instead of species richness to gain better insights on forest functioning in the future. However, in this study, we still follow the original framework of Wang et al. (2016) due to a lack of particular plant traits.

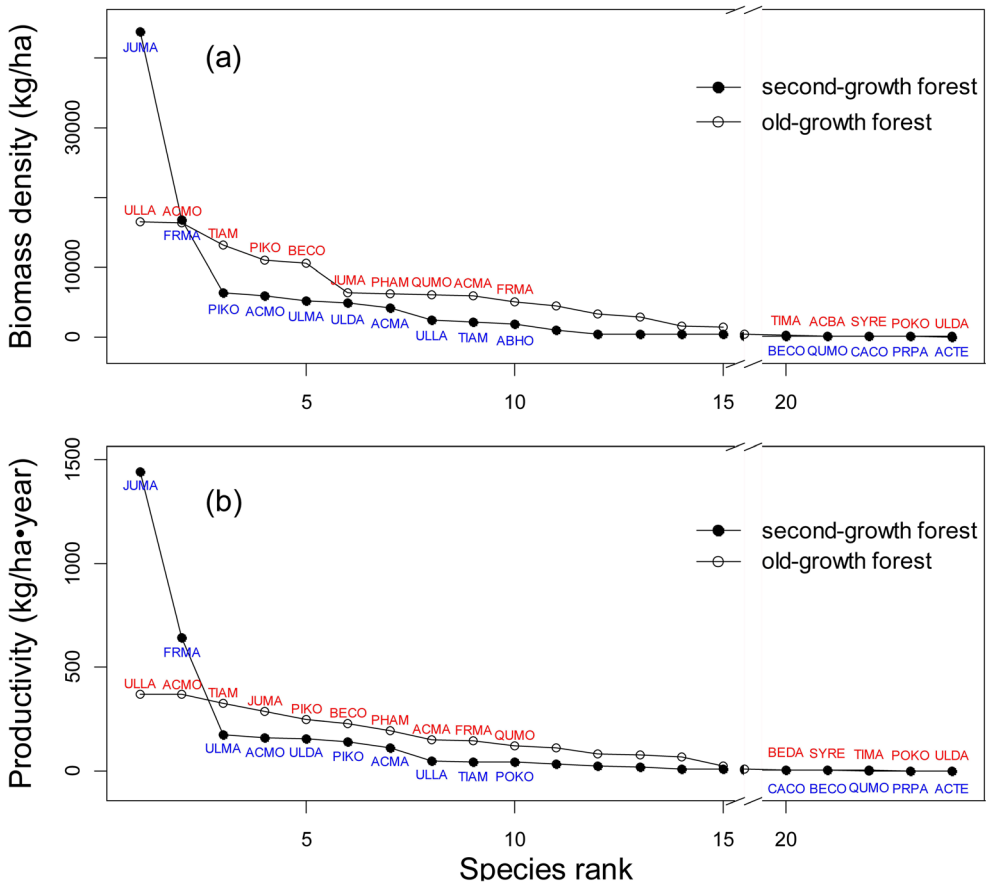

Fig. 1 Species rankings ordered by (**a**) biomass density in 2010 and (**b**) the biomass productivity of individual species. Biomass productivity is the annual increment of aboveground woody biomass from 2010 to 2015. Abbreviated species names in the figure are shown in the Supplementary material Appendix 1 Table A1

2.3 Community-level relationships between tree productivity and diversity

The individual-based PDR framework was also used to estimate the PDR at the community level. All trees within the entire research plot were regarded as focal individuals regardless of the species identity. The biomass productivity of each tree (P_i) and species richness surrounding each tree (SR_i) were included in Eq. (1) to calculate the index of association.

2.4 Estimating tree productivity

Tree biomass productivity, specifically annual aboveground biomass increments between 2010 and 2015, was calculated using the following equation:

$$P_i = \frac{B15_i - B10_i}{5} \quad (2)$$

where P_i is biomass productivity of live tree i between the measurements in 2010 and 2015; $B10$ and $B15$ are the biomass estimates of tree i in 2010 and 2015, respectively. Biomass productivity was calculated using live trees at both measuring times, while recruits and dead trees were excluded in the calculation. Dry biomass of each individual tree was estimated using dbh and aboveground biomass equations, which were described in detail in a previous study (Wang et al. 2016).

2.5 The significance of PDR deviating from neutral

Ripley's method was used to examine the spatial pattern of species distribution (Ripley 1976). The results show that all studied species exhibited a clumped distribution in the two forests (Supplementary material Appendix 2 Fig. A2 and Fig. A3). We assumed that the spatial autocorrelation of species distribution determine local diversity and tree growth. Thus, a Thomas cluster model was performed to examine the significance of PDR deviating from neutral by using AI as a test statistic in the individual-based PDR framework. The Thomas cluster process is a classic Cox process. In the Thomas cluster process, the parents are generated by a homogeneous Poisson process with intensity k and each parent location gives rise to a random number of offspring according to a Poisson distribution with mean μ offspring per parent (Diggle 1978; Thomas 1949).For each parent location y_i, the offspring points x_{ij} are independently and identically distributed, with a probability density of offspring locations estimated by an isotropic Gaussian density (Baddeley et al. 2016).

The confidence envelope was computed using 100 simulated distributions based on the homogeneous Thomas point

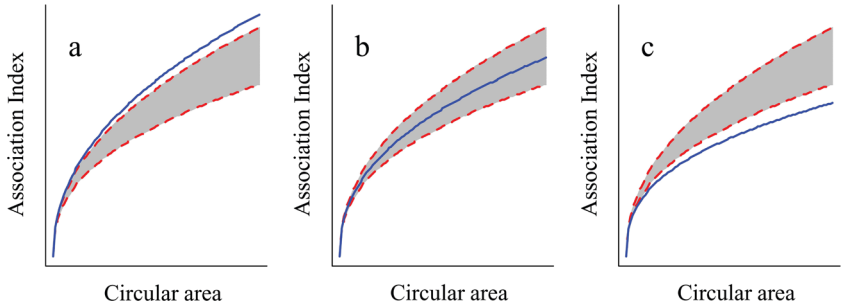

Fig. 2 Conceptual schematic diagram of individual-based PDR framework. The solid line is the index of association which is calculated from the observed dataset; the dashed lines are the confidence envelopes which can be calculated from the Monte Carlo simulation. (**a**) For a positive PDR, the observed line is located above the upper limit of the envelope; (**b**) For a neutral PDR, the observed line is within the envelope; (**c**) For a negative PDR, the observed line is below the lower limit of the envelope

process. If the observed AI is greater/less than that of the fifth largest/smallest value of the 100 realizations, then the observed AI is regarded to differ significantly from a neutral pattern at the 5% level (Fig.2). To satisfy reasonable sample sizes, the analysis was conducted only for the most abundant species comprising at least 30 individuals in each plot.

2.6 The roles of individual species

In order to identify the roles of biomass-dominant species, an individual species or species group are randomly removed from the computation process of the community-level PDR in the sequence of the rankings shown in Fig.1a. Thus, it was possible to identify the relative roles of these tree species in shaping the community-level PDR by comparing the emerging patterns of the community-level PDR.

3 Results

3.1 Species-level relationships between tree productivity and diversity

At the individual species level, the departure of observed PDR from neutrals was tested using a homogeneous Thomas process in the two forests (Supplementary material Appendix 2 Fig. A4 and Fig. A5). The analysis revealed that most species exhibit a neutral PDR in both plots. The percentage of species showing a negative PDR approach a peak value linearly at very close neighborhoods (the secondary forest plot: $r = 3$ m, 38%; the old-growth forest plot: $r = 4$ m, 42%), and then decreases gradually with increasing scale.

Interestingly, very few species displayed a positive PDR within their neighborhoods (Fig. 3). Tree species with higher importance values (i.e., dominant species) mainly exhibit negative PDRs while those with lower importance values tend to exhibit neutral PDRs within the two forests (Supplementary material Appendix 2 Fig. A1).

3.2 The effects of specific species on community-level PDR

The individual-based PDR framework was used to estimate the relationships between productivity and diversity at the community level. Our results show that there was a consistent community-level PDR pattern in the two forests, and that tree productivity is significantly negatively associated with tree species richness (Fig. 4).

The rank-biomass distribution curves reflect the relative contribution of individual species to ecosystem functioning (Fig. 1a). The rank-biomass curve is much steeper in the secondary forest plot than that in the old-growth forest plot. The first seven species account for 89% of total biomass in the secondary forest plot. However, in the old-growth forest plot, the relative regular rank-biomass curve suggests that most dominant species contribute similarly to the total biomass.

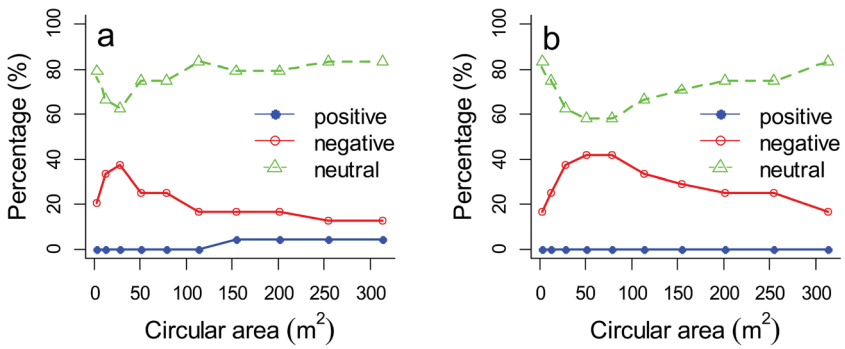

Fig. 3 Proportion of species showing significant positive or negative PDR in the secondary forest plot (**a**) and the old-growth forest plot (**b**). The significant departure from a neutral PDR for focal species was evaluated using a homogeneous Thomas process

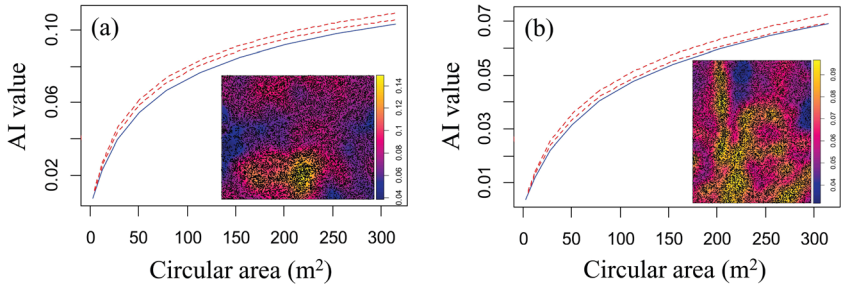

Fig. 4 Relationships between tree productivity and species richness for all living trees greater than 5 cm in dbh within the secondary forest plot (**a**) and the old-growth forest plot (**b**). The dashed lines are the confidence intervals calculated by the homogeneous Thomas process. The solid lines are the observed AI values. The map in each figure shows the distribution density of all living trees greater than 5 cm in dbh

At the community level, the PDR shifts from negative to neutral after removing the biomass-dominant species (Figs. 5 and 6). To identify individual species or species groups which may shape the community-level PDR, biomass-dominant species were sequentially removed during the computation process of the community-level PDR. Our results show that four species (*Juglans mandshurica*, *Acer mono*, *Ulmus macrocarpa* and *Acer mandshuricum*) jointly determine the negative community-level PDR in the secondary forest plot, but it was only one species (*Juglans mandshurica*) in the old-growth forest plot (Supplementary material Appendix 1Table A2 and Table A3).

4 Discussion

The species-level PDR shows significant scale dependence in both study areas. The average spacing between trees, calculated by the square root of 10,000/N (where *N* is number of trees per ha; Nilson 2006), with a dbh greater than 5 cm is 3.4 m in the secondary forest plot and 3.9 m in the old-growth forest plot. Interestingly, up to a circle radius corresponding to that average spacing the percentage of species showing negative PDR achieves the maximum (Fig.3). The average spacing between trees is usually closely related to competition among trees. Competitive interactions will enlarge the average spacing between trees when weaker trees close to others are eliminated

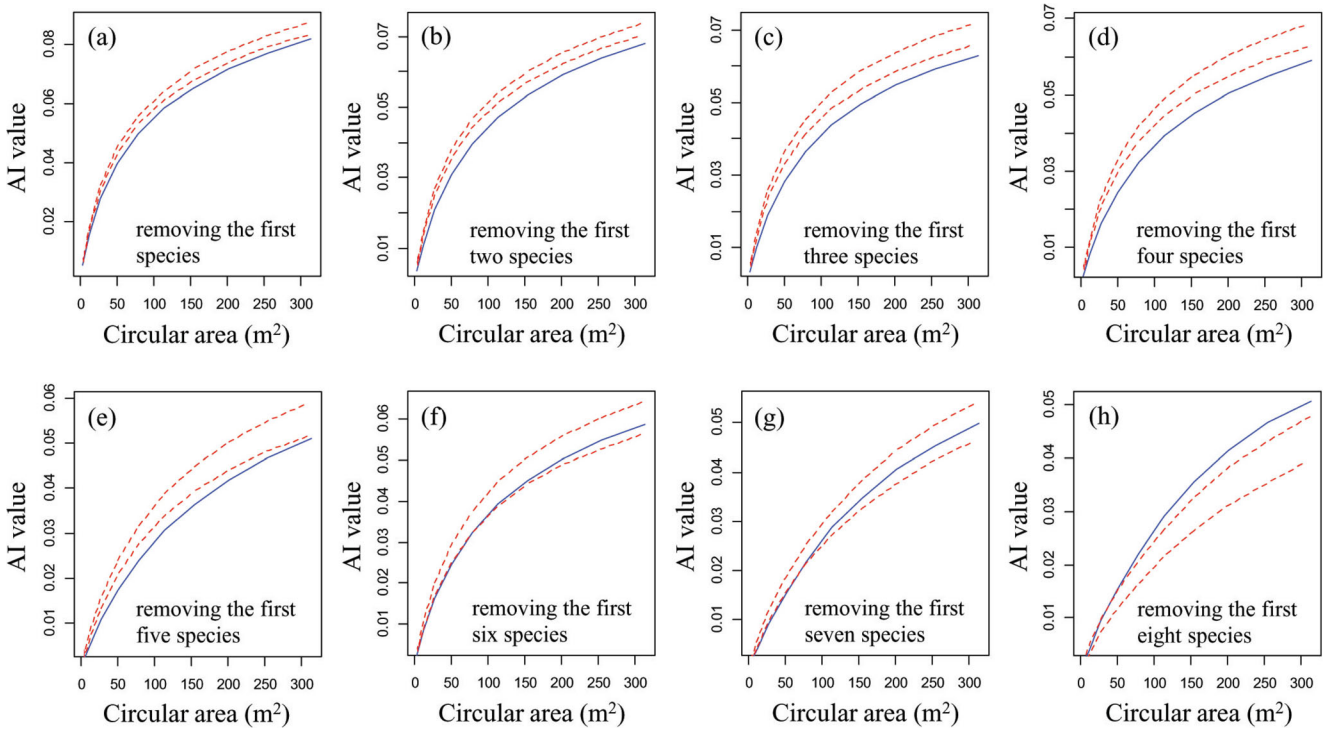

Fig. 5 The effects of biomass-dominant species on community-level PDR in the secondary forest plot. An individual species or a group of individual species was removed during the computation process of the community-level PDR according to the species biomass density rank ordering

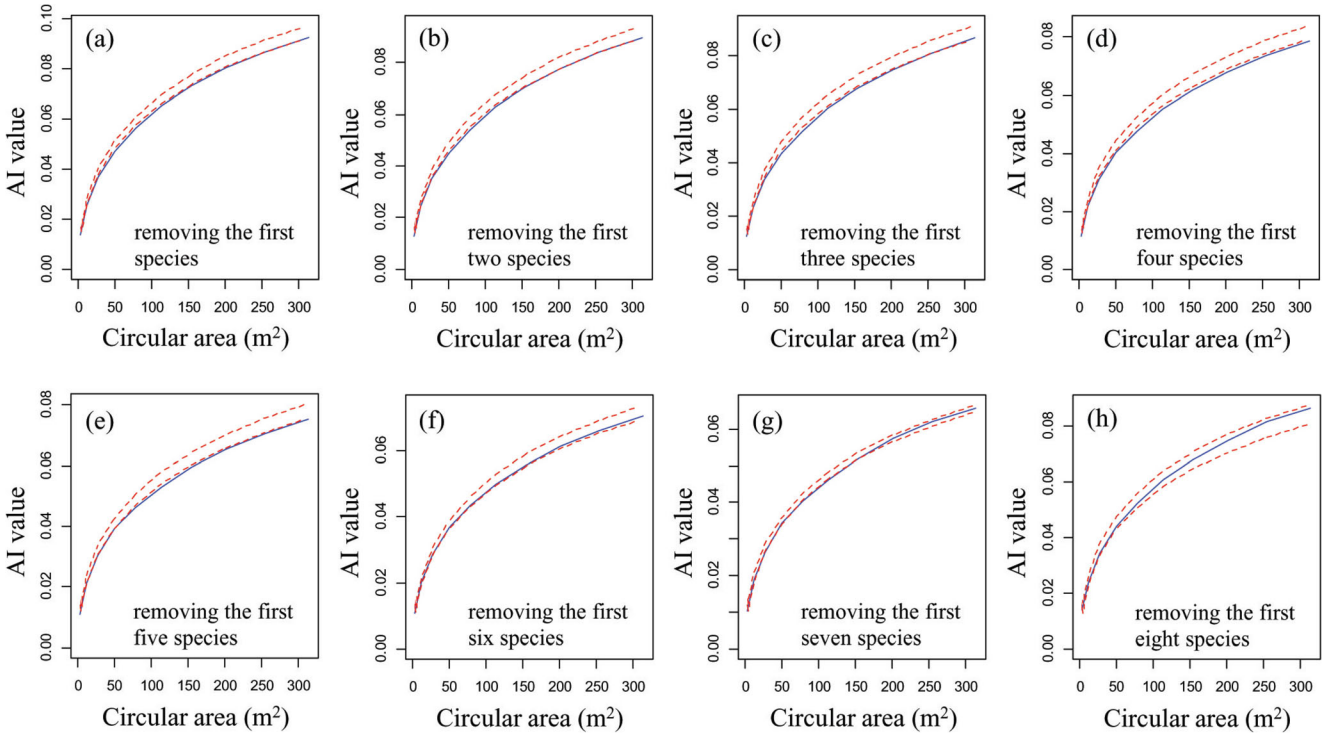

Fig. 6 The effects of biomass-dominant species on community-level PDR in the old-growth forest plot. An individual species or a group of individual species was removed during the computation process of the community-level PDR according to the species biomass density rank ordering

(Meyer et al. 2008). However, the percentages of species showing negative PDR are less than 30% in the majority of the studied scales in both forests. According to the results of the removal analysis, four dominant species showing negative PDR jointly determine the negative community-level PDR in the secondary forest plot, but only one productive species showed a neutral PDR in the old-growth forest plot. This result indicates that competitive effects are the fundamental driving forces influencing PDR's patterns in the secondary forest, but neutral effects in the old-growth forest. This observation is consistent with the fact that the secondary forest plot is still characterized by plant competitive interactions, while the old-growth forest plot is a relative mature and stable forest community. It is worth noting that the two forest plots present different topographies and different altitudinal ranges. Climatic and other abiotic factors are likely to affect productivity in different ways. Therefore, it is hard to conclude the differences in PDR at the community level are completely resulted from the successional stages. The two large forest plots provide a wealth of evidence for assessing the PDR at the community level. However, due to the limited number of plots, the results may be considered exploratory rather than confirmatory.

The species-level PDR and the species dominance are intimately related. Dominant species mainly exhibit a negative PDR while tree species with lower importance values tend to be neutral PDR in both forests. The dominant species have more access to essential resources such as light, water, and soil nutrients. In addition, they usually exhibit a greater interspecific competitive ability (Sala et al. 1996), and may exert greater pressure on other species. Interspecific competition is common in natural communities (Connell 1983; Schoener 1983), and dominant species could negatively affect species richness by competitively excluding other species (Kunte 2008; Tilman 1980).The biomass productivity is mainly generated by a few dominant species in our study (Fig. 1b).

Our study revealed a consistent pattern of negative community-level PDR in the two forests which may further increase the superiority of a few dominant species (Grime 1973; Laughlin and Moore 2009). Dominant species play a decisive role in regulating species diversity and ecosystem productivity. For example, numerically dominant species in a forest community can decrease species diversity by influencing the establishment of new species (Gilbert et al. 2009; Crutsinger et al. 2010). Removing biomass from many species in proportion to their abundance has a smaller effect than removing biomass from only the dominant ones (Sala et al. 1996). We found that the community-level PDR largely depends on a particular subset of biomass-dominant species. In the secondary forest plot, four species presenting higher importance values (*Juglans mandshurica*, *Acer mono*, *Ulmus macrocarpa*, and *Acer mandshuricum*) jointly determine the negative community-level PDR, but only a single species with a relatively lower importance value (*Juglans mandshurica*) in the old-growth forest plot. Therefore, *Juglans mandshurica* seems to be a key species regarding its critical role in shaping the community-level PDR.

The findings of this study are not only interesting to ecologists, but also to foresters who manage multi-species natural forests. For example, structure-based forest management (Li et al. 2014) and near-natural forest management (Gadow et al. 2016; Puettmann et al. 2015) have been proposed to maintain species richness as well as forest productivity. These management practices focus on the cultivation and protection of target trees, but the dominance of tree species is often underestimated. In the future, forest management should take account of the importance of dominant species in shaping the relationships between productivity and diversity in a multi-species uneven-aged forest (Zhang et al. 2014). Similar studies are required to identify the specific competitive role of dominant species (Seifert et al. 2014) and thus improve the effectiveness of management in a natural ecosystem.

Funding information This research is supported by the Key Project of National Key Research and Development Plan (2017YFC0504104) and the Program of National Natural Science Foundation of China (31670643).

Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Adler PB, Seabloom EW, Borer ET, Hillebrand H, Hautier Y, Hector A, Harpole WS, O'Halloran LR, Grace JB, Anderson TM, Bakker JD, Biederman LA, Brown CS, Buckley YM, Calabrese LB, Chu CJ, Cleland EE, Collins SL, Cottingham KL, Crawley MJ, Damschen EI, Davies KF, DeCrappeo NM, Fay PA, Firn J, Frater P, Gasarch EI, Gruner DS, Hagenah N, HilleRisLambers J, Humphries H, Jin VL, Kay AD, Kirkman KP, Klein JA, Knops JM, La Pierre KJ, Lambrinos JG, Li W, MacDougall AS, McCulley RL, Melbourne BA, Mitchell CE, Moore JL, Morgan JW, Mortensen B, Orrock JL, Prober SM, Pyke DA, Risch AC, Schuetz M, Smith MD, Stevens CJ, Sullivan LL, Wang G, Wragg PD, Wright JP, Yang LH (2011) Productivity is a poor predictor of plant species richness. Science 333:1750–1753

Baddeley A, Rubak E, Turner R (2016) Spatial point patterns: methodology and applications with R. Taylor & Francis Group, Florida

Cadotte MW (2006) Dispersal and species diversity: a meta-analysis. Am Nat 167:913–924

Chapin FS III, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynolds HL, Hooper DU, Lavorel S, Sala OE, Hobbie SE, Mack MC, Díaz S (2000) Consequences of changing biodiversity. Nature 405:234–242

Connell JH (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. Am Nat 122: 661–696

Creed RP, Cherry RP, Pflaum JR, Wood CJ (2009) Dominant species can produce a negative relationship between species diversity and ecosystem function. Oikos 118:723–732

Crutsinger GM, Strauss SY, Rudgers JA (2010) Genetic variation within a dominant shrub species determines plant species colonization in a coastal dune ecosystem. Ecology 91:1237–1243

Díaz S, Cabido M (2001) Vive la différence: plant functional diversity matters to ecosystem processes. Trends EcolEvol 16:646–655

Diggle PJ (1978) On parameter estimation for spatial point processes. J R Stat Soc Ser B 40:178–181

Gadow KV, Zhang GQ, Durrheim G, Drew D, Seydack A (2016) Diversity and production in an Afromontane forest. For Ecosyst 3: 15

Gilbert B, Turkington R, Srivastava DS (2009) Dominant species and diversity: linking relative abundance to controls of species establishment. Am Nat 174:850–862

Gillman LN, Wright SD (2006) The influence of productivity on the species richness of plants: a critical assessment. Ecology 87:1234–1243

Gong X, Chen Q, Lin S, Brueck H, Dittert K, Taube F, Schnyder H (2011) Tradeoffs between nitrogen- and water-use efficiency in dominant species of the semiarid steppe of Inner Mongolia. Plant Soil 340: 227–238

Grace JB (1999) The factors controlling species density in herbaceous plant communities: an assessment. Perspect Plant Ecol Evol Syst 2: 1–28

Grime JP (1973) Competitive exclusion in herbaceous vegetation. Nature 242:344–347

Grime JP (1997) Biodiverisity and ecosystem function: the debate deepens. Science 277:1260–1261

Grime JP (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J Ecol 86:902–910

Harrison S, Davies KF, Safford HD, Viers JH (2006) Beta diversity and the scale-dependence of the productivity-diversity relationship: a test in the Californian serpentine flora. J Ecol 94:110–117

Hector A (1998) The effect of diversity on productivity: detecting the role of species complementarity. Oikos 82:597–599

Hooper DU, Vitousek PM (1997) The effects of plant composition and diversity on ecosystem processes. Science 277:1302–1305

Hooper DU, Chapin FS III, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. EcolMonogr 75:3–35

Huston MA, Aarssen LW, Austin MP, Cade BS, Fridley JD, Garnier E, Grime JP, Hodgson J, Lauenroth WK, Thompson K, Vandermeer JH, Wardle DA (2000) No consistent effect of plant diversity on productivity. Science 289:1255a

Kühn I (2007) Incorporating spatial autocorrelation may invert observed patterns. Divers Distrib 13:66–69

Kunte K (2008) Competition and species diversity: removal of dominant species increases diversity in Costa Rican butterfly communities. Oikos 117:69–76

Laughlin DC, Moore MM (2009) Climate-induced temporal variation in the productivity–diversity relationship. Oikos 118:897–902

Lepš J, Osbornová-Kosinová J, Rejmánek M (1982) Community stability, complexity and species life history strategies. Vegetation 50:53–63

Li JD, Wu BH, Sheng LX (2001) Jilin vegetation. Jilin Science and Technology Press, Jilin

Li YF, Ye SM, Hui GY, Hu YB, Zhao ZH (2014) Spatial structure of timber harvested according to structure-based forest management. For Ecol Manag 322:106–116

Lohbeck M, Poorter L, Paz H, Pla L, van Breugel M, Martínez-Ramos M, Bongers F (2012) Functional diversity changes during tropical forest succession. Perspect Plant Ecol Evol Syst 14:89–96

Loreau M, Hector A (2001) Partitioning selection and complementarity in biodiversity experiments. Nature 412:72–76

Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, Tilman D, Wardle DA (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294:804–808

Loreau M, Mouquet N, Gonzalez A (2003) Biodiversity as spatial insurance in heterogenous landscapes. Proc Natl Acad Sci USA 100: 12765–12770

MacGillivray CW, Grime JP (1995) Testing predictions of resistance and resilience of vegetation subjected to extreme events. Funct Ecol 9: 640–649

Meyer KM, Ward D, Wiegand K, Moustakas A (2008) Multi-proxy evidence for competition between savanna woody species. Perspect Plant Ecol Evol Syst 10:63–72

Mittelbach GG, SteinerCF SSM, Gross KL, Reynolds HL, Waide RB, Willig MR, Dodson SI, Gough L (2001) What is the observed relationship between species richness and productivity? Ecology 82: 2381–2396

Mouquet N, Loreau M (2002) Coexistence in metacommunities: the regional similarity hypothesis. Am Nat 159:420–426

Nilson A (2006) Modeling dependence between the number of trees and mean tree diameter of stands, stand density and stand sparsity. In: Cieszewski CJ, Strub M (eds) Second International Conference on Forest Measurement and Quantitative Methods and Management & the 2004 Southern Mensurationists Meeting 15–18 June 2004 Hot Springs, Arkansas USA. University of Georgia, Athens, pp 74–94

Pacala SW, Deutschman DH (1995) Details that matter: the spatial distribution of individual trees maintains forest ecosystem function. Oikos 74:357–365

Pärtel M, Zobel M (2007) Dispersal limitation may result in the unimodal productivity-diversity relationship: a new explanation for a general pattern. J Ecol 95:90–94

Puettmann KJ, Wilson SMG, Baker SC, Donoso PJ, Drössler L, Amente G, Harvey BD, Knoke T, Lu Y, Nocentini S, Putz FE, Yoshida T, Bauhus J (2015) Silvicultural alternatives to conventional even-aged forest management - what limits global adoption? For Ecosyst 2:8

Ricklefs RE (1977) Environmental heterogeneity and plant species diversity: a hypothesis. Am Nat 111:376–381

Ripley BD (1976) The second-order analysis of stationary point processes. J Appl Probab 13:255–266

Roscher C, Schumacher J, Gubsch M, Lipowsky A, Weigelt A, Buchmann N, Schmid B, Schulze E-D (2012) Using plant functional traits to explain diversity–productivity relationships. PLoS ONE 7: e36760

Sala OE, Lauenroth WK, Mcnaughton SJ, Rusch G, Zhang X (1996) Biodiversity and ecosystem functioning in grasslands. In: Mooney HA, Cushman JH, Medina E, Sala OE, Schulze ED (eds) Functional roles of biodiversity: a global perspective. Wiley, Chichester, West Sussex, pp 129–149

Schoener TW (1983) Field experiments on interspecific competition. Am Nat 122:240–285

Schwartz MW, Brigham CA, Hoeksema JD, Lyons KG, Mills MH, van Mantgem PJ (2000) Linking biodiversity to ecosystem function: implications for conservation ecology. Oecologia 122:297–305

Seidler TG, Plotkin JB (2006) Seed dispersal and spatial pattern in tropical trees. PLoS Biol 4:e344

Seifert T, Seifert S, Seydack A, Durrheim G, Gadow K (2014) Competition effects in an afrotemperate forest. For Ecosyst 1:13

Shen G, Yu M, Hu XS, Mi X, Ren H, Sun IF, Ma K (2009) Species–area relationships explained by the joint effects of dispersal limitation and habitat heterogeneity. Ecology 90:3033–3041

Šímová I, Li YM, Storch D (2013) Relationship between species richness and productivity in plants: the role of sampling effect, heterogeneity and species pool. J Ecol 101:161–170

Smith MD, Knapp AK (2003) Dominant species maintain ecosystem function with non-random species loss. Ecol Lett 6:509–517

Srivastava DS, Vellend M (2005) Biodiversity–ecosystem function research: is it relevant to conservation? Annu Rev Ecol Evol Syst 36:267–294

Stein C, Auge H, Fischer M, Weisser WW, Prati D (2008) Dispersal and seed limitation affect diversity and productivity of montane grassland. Oikos 117:1469–1478

Symstad A, Tilman D, Willson J (1998) Species loss and ecosystem functioning: effects of species identity and community composition. Oikos 81:389–397

Thomas M (1949) Ageneralisation of Poisson's binomial limit for use in ecology. Biometrika 36:18–25

Tilman D (1980) Resources: a graphical-mechanistic approach to competition and predation. Am Nat 116:362–393

Tilman D (1999) The ecological consequences of changes in biodiversity: a search for general principles. Ecology 80:1455–1474

Tilman D, Pacala S (1993) The maintenance of species richness in plant communities. In: Ricklefs RE, Schluter D (eds) Species diversity in ecological communities. University of Chicago Press, Chicago, pp 13–25

Tilman D, Knops J, Wedin D, Reich P, Ritchie M, Siemann E (1997) The influence of functional diversity and composition on ecosystem processes. Science 277:1300–1302

Turnbull LA, Crawley MJ, Rees M (2000) Are plant populations seed-limited? A review of seed sowing experiments. Oikos 88:225–238

Vile D, Shipley B, Garnier E (2006) Ecosystem productivity can be predicted from potential relative growth rate and species abundance. Ecol Lett 9:1061–1067

Wang J, Cheng Y, Zhang C, Zhao Y, Zhao X, Gadow KV (2016) Relationships between tree biomass productivity and local species diversity. Ecosphere 7:e01562

Wardle DA (1999) Is sampling effect a problem for experiments investigating biodiversity–ecosystem function relationships? Oikos 87: 403–407

Wardle DA, Lagerström A (2008) The response of plant diversity to ecosystem retrogression: evidence from contrasting long-term chronosequences. Oikos 117:93–103

Wardle DA, Zackrisson O, Hörnberg G, Gallet C (1997) The influence of island area on ecosystem properties. Science 277:1296–1299

Wardle DA, Huston MA, Grime JP, Berendse F, Garnier E, Lauenroth WK, Setälä H, Wilson SD (2000) Biodiversity and ecosystem function: an issue in ecology. Bull Ecol Soc Am 81:235–239

Zhang C, Zhao X, Gadow KV (2014) Analysing selective harvest events in three large forest observational studies in North Eastern China. For Ecol Manag 316:100–109