

Interannual Variation in Species Interactions of Typical Steppe Communities in Inner Mongolia under Different Land Use Patterns: Postprint

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Abstract

Grazing and mowing, as the primary utilization methods of Inner Mongolia grasslands, exert significant influence on *Stipa grandis* community succession and constructive species replacement. This study focused on the *Stipa grandis* community in the typical steppe of Inner Mongolia, conducting fixed-point observations of small-scale patterns in the *Stipa grandis* community under two utilization methods (grazing and mowing) for three consecutive years from 2013 to 2015; notably, 2014 experienced extreme drought and high temperature conditions. Ecosim 7.72 software was employed to calculate C-score and V-ratio to reflect interspecific interaction relationships within the community, and to analyze the interannual variation of these interactions and their influencing factors. The results demonstrated that: (1) In 2013 and 2015, temperature and precipitation were relatively close to the regional annual means, and interspecific interactions among community plants under both grazing and mowing were competitive; (2) In 2014, an extreme drought and high temperature year, the magnitude and direction of interspecific interactions among community plants under grazing and mowing utilization methods changed substantially, wherein grazing utilization intensified competition among plants, while under mowing utilization, interspecific interactions were facilitative. (3) These results indicate that climate fluctuation is the primary factor influencing interspecific interactions in communities, while in extreme years, utilization methods affect the direction and magnitude of interspecific interactions in communities. This not only provides experimental data for refining the Stress Gradient Hypothesis, but also offers theoretical guidance for the rational utilization of grasslands and the formulation of protection measures in this region.

Full Text

Preamble

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The Annual Variation of Effects Under Different Grassland Utilization Types on Typical Steppe Species Interactions in Inner Mongolia

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Abstract

Grazing and mowing are the most common utilization types in the Inner Mongolia steppe, and they have been proven to play different roles in plant-plant interactions and community succession. In the present study, we conducted a three-year continuous monitoring experiment on the typical steppe community. We compared two different indices of community small-scale patterns using EcoSim 7.72 software. The results were shown as follows: (1) For three consecutive years, the plant species interactions at the community level under grazing were competitive, especially in 2014, the results did not support the stress gradient hypothesis. (2) In 2013 and 2015, the species interactions of community under mowing were competitive, but in 2014, on account of the drought and elevated air temperature, they were facilitative. (3) Different grassland utilization types had distinct effects on plant species interactions, and the effect were also regulated by monthly precipitation and monthly average air temperature in growing season. The present results provided the improvement of stress gradient hypothesis and the theoretical foundation in rational utilization of grassland and the recovery of degraded grassland.

Keywords: typical steppe community; grassland use type; small scale pattern; species interactions

Introduction

Plant community spatial distribution patterns result from past ecological processes, including both biotic and abiotic processes that trigger a series of complex plant-plant interactions. Negative plant-plant interactions (competition) are considered important driving factors determining community structure and diversity in high-productivity communities, and competition can reduce the abundance of competitors, producing negative interspecific associations. The importance of competition for community structure changes with environmental stress levels. Under certain environmental conditions, positive plant-plant interactions (facilitation) play important roles in structuring communities.

Early experiments on plant community spatial patterns focused primarily on neighbor removal experiments, mostly examining only one or a few species pairs rather than community-wide interactions. With deepening research, small-scale spatial pattern association methods that indirectly infer potential effects on community structure and species diversity through species relationships have emerged. This approach can examine relationships among potentially interacting species within a small space, effectively providing a comprehensive understanding of community-wide species interactions and enabling predictions of future community pattern changes based on existing observational data. It has been widely applied in plant community pattern analysis.

Due to global climate change and long-term overgrazing since the 1980s, China's northern ecological barrier—the Inner Mongolia typical steppe—has experienced extensive degradation, manifested as dominant species replacement, reduced species diversity, and decreased aboveground net primary productivity. The representative *Stipa grandis* steppe communities are gradually being replaced by *Stipa krylovii* and *Artemisia frigida* communities, with obvious changes in community structure. Free grazing and mowing are the two main utilization types in Inner Mongolia grasslands. While Chinese scholars have conducted extensive research on species responses to utilization types and adaptation strategies, studies using small-scale spatial pattern methods to explore how land use affects species interactions and entire community patterns have only recently begun. Such research is crucial not only for understanding and predicting community pattern changes but also for guiding rational grassland use and effective conservation.

This study selected grazing and mowing sites in the *Stipa grandis* steppe of Xilingol Grassland for continuous fixed-point monitoring of small-scale patterns from 2013–2015. We aimed to: (1) examine how different utilization types affect plant-plant interactions in *Stipa grandis* communities, and (2) determine whether community interaction relationships are influenced by interannual hydrothermal variations. The results can not only reasonably predict the effects of utilization types and climate change on steppe succession but also provide references for rational grassland use and effective protection measures under climate change.

1. Study Area Natural Conditions

This study was conducted at Mao Deng Pasture, 55 km southeast of Xilinhot City, Xilingol League, Inner Mongolia Autonomous Region (116°20.552 E, 44°16.062 N), at an elevation of 910–1377 m. The region has a typical continental temperate steppe climate with distinct seasons—cold, dry winters and warm summers. The terrain slopes higher in the south and lower in the north. Annual average rainfall is 280–360 mm, annual average temperature is -0.5°C, with maximum temperatures of 37.4°C and minimum of -39.9°C. Annual sunshine is approximately 2800 hours, and the frost-free period is 90–115 days. Annual evaporation is 25%–40% of rainfall. The grassland utilization types include

grazing (summer-autumn grazing at 0.5–0.7 cattle units per hectare) and mowing (harvested in mid-to-late August annually). Community maximum height can reach 87 cm.

2. Research Methods

We established 0.5 m × 0.5 m quadrats both inside and outside fences. Each quadrat was divided into 0.1 m × 0.1 m sub-quadrats (25 total). We recorded each species present in every sub-quadrat, using red-painted chopsticks at the four corners for positioning and GPS to record coordinates for fixed-point monitoring. Surveys were conducted during the growing season (June–August). Species number, height, coverage, and frequency were measured. Community biomass was harvested in 0.5 m × 0.5 m quadrats, oven-dried at 65°C to constant weight. Soil samples (0–10 cm) were collected from 5 quadrats per community. Soil total carbon and nitrogen were measured with an Elementar analyzer, and total phosphorus by molybdenum-antimony colorimetry. Growing season rainfall and temperature data were provided by the research station.

[FIGURE:1] Three years (2013–2015) monthly precipitation and monthly average temperature in June to August

3. Data Analysis

3.1 C-score and V-ratio Calculation

Species presence-absence data from sub-quadrats were compiled into binary matrices (1 = present, 0 = absent). Species occurring fewer than 5 times were excluded. We used EcoSim 7.72 software with null models to calculate C-score and V-ratio, analyzing species distribution patterns through Monte Carlo random simulations (5000 iterations). Three algorithms were compared: Fixed-Fixed (FF, both rows and columns fixed with equiprobable randomization), Fixed-Equiprobable (FE, rows fixed with equiprobable column randomization), and Fixed-Proportional (FP, rows fixed with non-equiprobable column randomization).

C-score is an index of checkerboard distribution proposed by Stone & Roberts (1990), calculated as: $C_{ij} = (R_i - S)(R_j - S) + S$

where M is the number of species in the community, S is the number of quadrats where species i and j co-occur, R_i is the number of quadrats where species i occurs, and R_j is the number of quadrats where species j occurs.

V-ratio is an index using the ratio of column sum variance to row sum variance to represent community structure (Schluter 1984).

3.2 Standard Effect Size

To facilitate comparison, we calculated the Standard Effect Size (SES) for C-score and V-ratio matrices:

$$SES = (\bar{C} - \mu) / \delta$$

where \bar{C} represents the observed C-score or V-ratio, μ represents the mean from 5000 Monte Carlo simulations, and δ represents the standard deviation of simulated values. SES values between -2 and 2 indicate random distribution. For C-score, $SES > 2$ indicates non-random segregation (negative association/competition), while $SES < -2$ indicates non-random aggregation (positive association/facilitation). For V-ratio, the interpretation is opposite: $SES > 2$ indicates facilitation dominance, $SES < -2$ indicates competition dominance.

3.3 Statistical Analysis

Community quantitative characteristics and soil properties were analyzed using independent samples t-tests in SPSS 21.0.

1. Effects of Utilization Type on Community Structure, Species Composition, and Soil Properties

Different utilization types significantly affected community species number, frequency, biomass, and soil total nitrogen, but not average coverage, soil total carbon, or total phosphorus. Grazing communities had significantly higher species numbers than mowing communities, while mowing communities had significantly higher community height, coverage, biomass, and soil total nitrogen than grazing communities.

Community quantitative characteristics and soil conditions under the two utilization types

Plant species composition and species frequency under the two utilization types

2. Effects of Utilization Type on C-score and V-ratio

Under grazing, both C-score and V-ratio values were significantly greater than simulated results ($P < 0.05$), indicating competition-dominated species interactions. The values showed a bell-shaped trend across years, with strongest competition in 2014 (the drought year), suggesting drought altered species interaction relationships.

Under mowing, species interactions were competitive in 2013 and 2015 (no significant difference from null models), but facilitative in 2014. The C-score values fell below the double-dashed line ($SES < -2$), indicating a shift from competition to facilitation. V-ratio values also showed this pattern, with competition weakening in the dry year.

Comparison of C-score and V-ratio values of plant community binary matrices with null models under different grassland utilization types

[FIGURE:2] Interannual variance of three algorithms on standard effect size of communities' C-score under different grassland utilization types

[FIGURE:3] Interannual variance of two algorithms on standard effect size of communities' V-ratio under different grassland utilization types

Discussion

1. Different Responses of Two Utilization Types to Climate Change

Callaway and Bertness proposed the Stress Gradient Hypothesis (SGH), which predicts that species interactions shift from competition to facilitation as stress increases. This has been supported in subarctic, alpine, tundra, and Mediterranean ecosystems. Our study found that climate variation, particularly in the extreme drought year of 2014, had greater impact on species interactions than utilization type. Under grazing, both C-score and V-ratio SES values indicated competition-dominated interactions, with competition intensifying during drought and high temperature—contradicting SGH predictions.

Under mowing, however, the pattern reversed: 2014 showed facilitation while other years showed competition, supporting SGH. This suggests that in high-productivity environments, disturbance (grazing) can reduce competitive dominance of tall, dominant plants, allowing other species to grow rapidly and resulting in overall competitive patterns. Mowing, being a single annual harvest, leaves the community largely undisturbed during the long growing season, maintaining soil structure and water retention, which may enhance facilitative effects under stress.

2. Intrinsic Mechanisms of Different Climate Fluctuation Responses

Many studies support that abiotic factors are crucial in altering community patterns, with interannual climate fluctuations often having greater impact than utilization type. Research on Australian semi-arid shrublands found drought effects far exceeded grazing disturbance. Similarly, our results show different community responses to 2014' s extreme drought: grazing intensified competition while mowing reduced it. This aligns with studies on Canadian prairies showing that different dominant species respond differently to drought, changing interaction directions and intensities.

The mowing regime' s minimal disturbance (except for small herbivores like *Ochotona daurica* and *Lasiopodomys brandtii*) allows *Stipa grandis* dominance while preserving soil structure and water-holding capacity. In contrast, continuous grazing pressure reduces dominant species' competitive advantage, balancing species relative status but potentially increasing overall competition.

3. Advantages of Small-Scale Pattern Analysis and Study Significance

Small-scale spatial pattern methods offer advantages over neighbor removal experiments by maintaining plant integrity and studying the community as an organic whole, reducing information loss from focusing only on common species. Medium- to long-term monitoring better reflects climate change impacts. Our

results show that during extreme drought and high temperature, grazing intensifies competition while mowing promotes facilitation, supporting previous findings that annual mowing benefits *Stipa grandis* steppe restoration more than grazing. The results provide experimental data for refining SGH and offer theoretical guidance for rational grassland use and protection measures in this region.

References

- [1] Reitalu T, Prentice H C, Sykes M T, Lonn M, Johansson L J, Hall K. Plant species segregation on different spatial scales in semi-natural grasslands. *Journal of Vegetation Science*, 2008, 19(3): 407–416.
- [2] Pottier J, Marrs R H, Bédécarrats A. Integrating ecological features of species in spatial pattern analysis of a plant community. *Journal of Vegetation Science*, 2007, 18(1): 223–230.
- [3] Badano E I, Cavieres L A, Molina-Montenegro M A, Quiroz C L. Slope aspect influences plant association patterns in the Mediterranean matorral of central Chile. *Journal of Arid Environments*, 2005, 62(1): 93–108.
- [4] Forrester D I. The spatial and temporal dynamics of species interactions in mixed-species forests: from pattern to process. *Forest Ecology and Management*, 2014, 312: 282–292.
- [5] Grubb P J. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews*, 1977, 52(1): 107–145.
- [6] Pacala S W, Levin S A. Biologically generated spatial pattern and the coexistence of competing species. In: Tilman D, Kareiva P, eds. *Spatial Ecology: the Role of Space in Population Dynamics and Interspecific Interactions*. Princeton: Princeton University Press, 1997: 204–232.
- [7] López R P, Valdivia S, Rivera M L, Rios R S. Co-occurrence patterns along a regional aridity gradient of the subtropical Andes do not support stress gradient hypotheses. *PLoS One*, 2013, 8(3): e58518.
- [8] Travis J M J, Brooker R W, Clark E J, Dytham C. The distribution of positive and negative species interactions across environmental gradients on a dual-lattice model. *Journal of Theoretical Biology*, 2006, 241(4): 896–902.
- [9] Callaway R M, Walker L R. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology*, 1997, 78(7): 1958–1965.
- [10] Tewksbury J J, Lloyd J D. Positive interactions under nurse-plants: spatial scale, stress gradients and benefactor size. *Oecologia*, 2001, 127(3): 425–434.
- [11] Maestre F T, Callaway R M, Valladares F, Lortie C J. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology*, 2009, 97(2): 199–205.

- [12] López R P, Squeo F A, Armas C, Kelt D A, Gutiérrez J R. Enhanced facilitation at the extreme end of the aridity gradient in the Atacama Desert: a community-level approach. *Ecology*, 2016, 97(6): 1593-1604.
- [13] Chen L P, Zhao N X, Zhang L H, Gao Y B. Responses of two dominant plant species to drought stress and defoliation in the Inner Mongolia steppe of China. *Plant Ecology*, 2013, 214(2): 221-229.
- [14] [Note: Reference appears to be missing from original]
- [15] Pamela G, Martin R. Do species' strategies and type of stress predict net positive effects in an arid ecosystem? *Ecology*, 2017, 98(3): 794-806.
- [16] Zhang J, Hao Z Q, Song B, Li B H, Wang X G, Ye J. Fine-scale species co-occurrence patterns in an old-growth temperate forest. *Forest Ecology and Management*, 2009, 257(10): 2115-2120.
- [17] Jiménez J J, Decaëns T, Rossi J P. Soil environmental heterogeneity allows spatial co-occurrence of competitor earthworm species in a gallery forest of the Colombian 'Llanos' . *Oikos*, 2012, 121(6): 915-926.
- [18] Stone L, Roberts A. The checkerboard score and species distributions. *Oecologia*, 1990, 85(1): 74-79.
- [19] Luzuriaga A L, Sánchez A M, Maestre F T, Escudero A. Assemblage of a semi-arid annual plant community: abiotic and biotic filters act hierarchically. *PLoS One*, 2012, 7(7): e41270.
- [20] Schluter D. A variance test for detecting species associations, with some example applications. *Ecology*, 1984, 65(3): 998-1005.
- [21] Bertness M D, Callaway R. Positive interactions in communities. *Trends in Ecology & Evolution*, 1994, 9(5): 191-193.
- [22] He Q, Bertness M D. Extreme stresses, niches, and positive species interactions along stress gradients. *Ecology*, 2014, 95(6): 1437-1443.
- [23] Reisner M D, Doescher P S, Pyke D A. Stress-gradient hypothesis explains susceptibility to invasion and community stability in North America's semi-arid ecosystems. *Journal of Vegetation Science*, 2015, 26(6): 1212-1224.
- [24] Brooker R W, Maestre F T, Callaway R M, Lortie C L, Cavieres L A, Kunstler G, Liancourt P, Tielbörger K, Travis J M J, Anthelme F, Armas C, Coll L, Corcket E, Delzon S, Forey E, Kikvidze Z, Olofsson J, Pugnaire F, Quiroz C L, Saccone P, Schiffers K, Seifan M, Touzard B, Michalet R. Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology*, 2008, 96(1): 18-34.
- [25] Schöb C, Michalet R, Cavieres L A, Pugnaire F I, Brooker R W, Butterfield B J, Cook B J, Kikvidze Z, Lortie C J, Xiao S, Al Hayek P, Anthelme F, Cranston B H, García M C, Le Bagousse-Pinguet Y, Reid A M, le Roux P C,

- Lingua E, Nyakatyá M J, Touzard B, Zhao L, Callaway R M. A global analysis of bidirectional interactions in alpine plant communities shows facilitators experiencing strong reciprocal fitness costs. *New Phytologist*, 2014, 202(1): 95–105.
- [26] Bulleri F, Xiao S, Maggi E, Benedetti-Cecchi L. Intensity and temporal variability as components of stress gradients: implications for the balance between competition and facilitation. *Oikos*, 2014, 123(1): 47–55.
- [27] Michalet R, Schöb C, Lortie C J, Brooker R W, Callaway R M, Bailey J K. Partitioning net interactions among plants along altitudinal gradients to study community responses to climate change. *Functional Ecology*, 2014, 28(1): 75–86.
- [28] Michalet R, Brooker R W, Cavieres L A, Kikvidze Z, Lortie C J, Pugnaire F I, Valiente-Banuet A, Callaway R M. Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecology Letters*, 2006, 9(7): 767–773.
- [29] Michalet R, Pugnaire F I. Facilitation in communities: underlying mechanisms, community and ecosystem implications. *Functional Ecology*, 2016, 30(1): 3–9.
- [30] Connell J H. Diversity in tropical rain forests and coral reefs. *Science*, 1978, 199(4335): 1302–1310.
- [31] Bruno J F, Stachowicz J J, Bertness M D. Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution*, 2003, 18(3): 119–125.
- [32] Zeidler M, Duchoslav M, Banáš M, Lešková M. Impacts of introduced dwarf pine (*Pinus mugo*) on the diversity and composition of alpine vegetation. *Community Ecology*, 2012, 13(2): 213–220.
- [33] Alados C L, Navarro T, Komac B, Pascual V, Martínez F, Cabezudo B, Pueyo Y. Do vegetation patch spatial patterns disrupt the spatial organization of plant species? *Ecological Complexity*, 2009, 6(2): 197–207.
- [34] Howard K S C, Eldridge D J, Soliveres S. Positive effects of shrubs on plant species diversity do not change along a gradient in grazing pressure in an arid shrubland. *Basic and Applied Ecology*, 2012, 13(2): 159–168.
- [35] Maalouf J P, Le Bagousse-Pinguet Y, Marchand L, Touzard B, Michalet R. The interplay of stress and mowing disturbance for the intensity and importance of plant interactions in dry calcareous grasslands. *Annals of Botany*, 2012, 110(4): 821–828.
- [36] Le Bagousse-Pinguet Y, Maalouf J P, Touzard B, Michalet R. Importance, but not intensity of plant interactions relates to species diversity under the interplay of stress and disturbance. *Oikos*, 2014, 123(7): 777–785.
- [37] Martorell C, Almanza-Celis C A I, Pérez-García E A, Sánchez-Ken J G. Coexistence in a species-rich grassland: competition, facilitation and niche struc-

ture over a soil depth gradient. *Journal of Vegetation Science*, 2015, 26(4): 674–685.

[38] Bennett J A, Cahill J F Jr. Evaluating the relationship between competition and productivity within a native grassland. *PLoS One*, 2012, 7(8): e43703.

[39] Baldwin A H, Jensen K, Schönfeldt M. Warming increases plant biomass and reduces diversity across continents, latitudes, and species migration scenarios in experimental wetland communities. *Global Change Biology*, 2014, 20(3): 835–850.

[40] [Note: Chinese reference - likely about grazing effects on soil properties]

[41] Smit C, Vandenberghe C, den Ouden J, Müller-Schärer H. Nurse plants, tree saplings and grazing pressure: changes in facilitation along a biotic environmental gradient. *Oecologia*, 2007, 152(2): 265–273.

[42] Jeschke M, Kiehl K. Effects of a dense moss layer on germination and establishment of vascular plants in newly created calcareous grasslands. *Flora*, 2008, 203(7): 557–566.

[43] Hacker S D, Gaines S D. Some implications of direct positive interactions for community species diversity. *Ecology*, 1997, 78(7): 1990–2003.

[44] Chu C J, Maestre F T, Xiao S, Weiner J, Wang Y S, Duan Z H, Wang G. Balance between facilitation and resource competition determines biomass-density relationships in plant populations. *Ecology Letters*, 2008, 11(11): 1189–1197.

[45] [Note: Chinese reference - likely about restoration effects of different management practices]

Figures

Source: ChinaXiv – Machine translation. Verify with original.

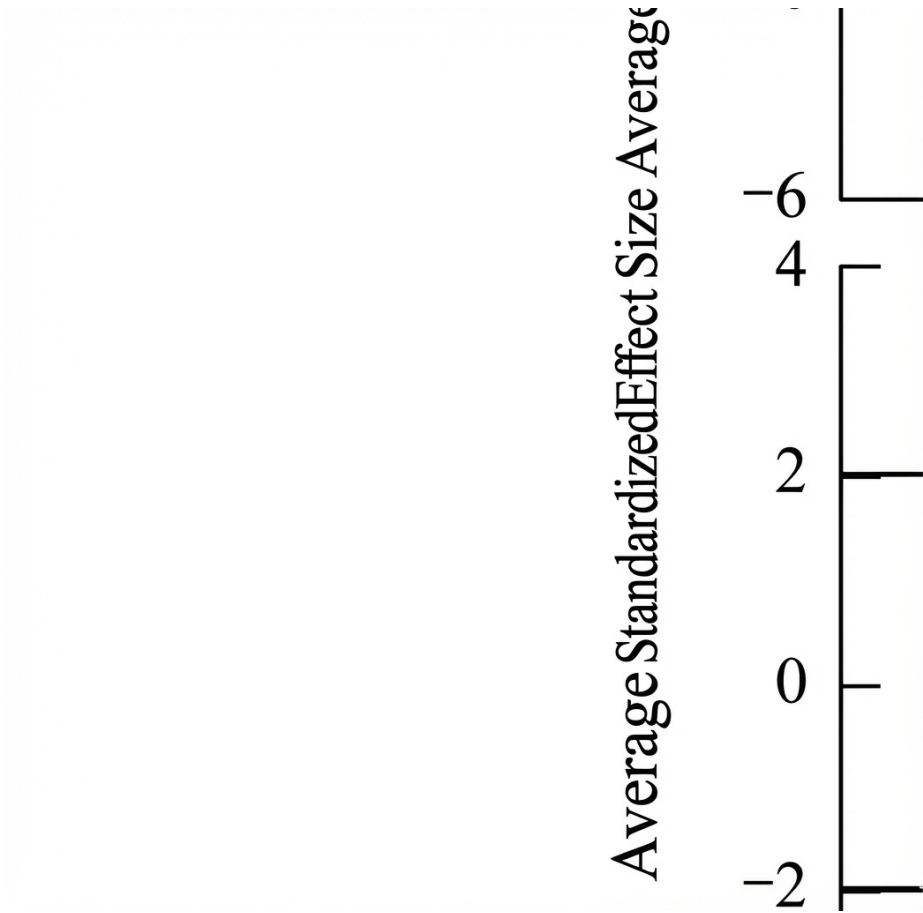


Figure 1: Figure 5

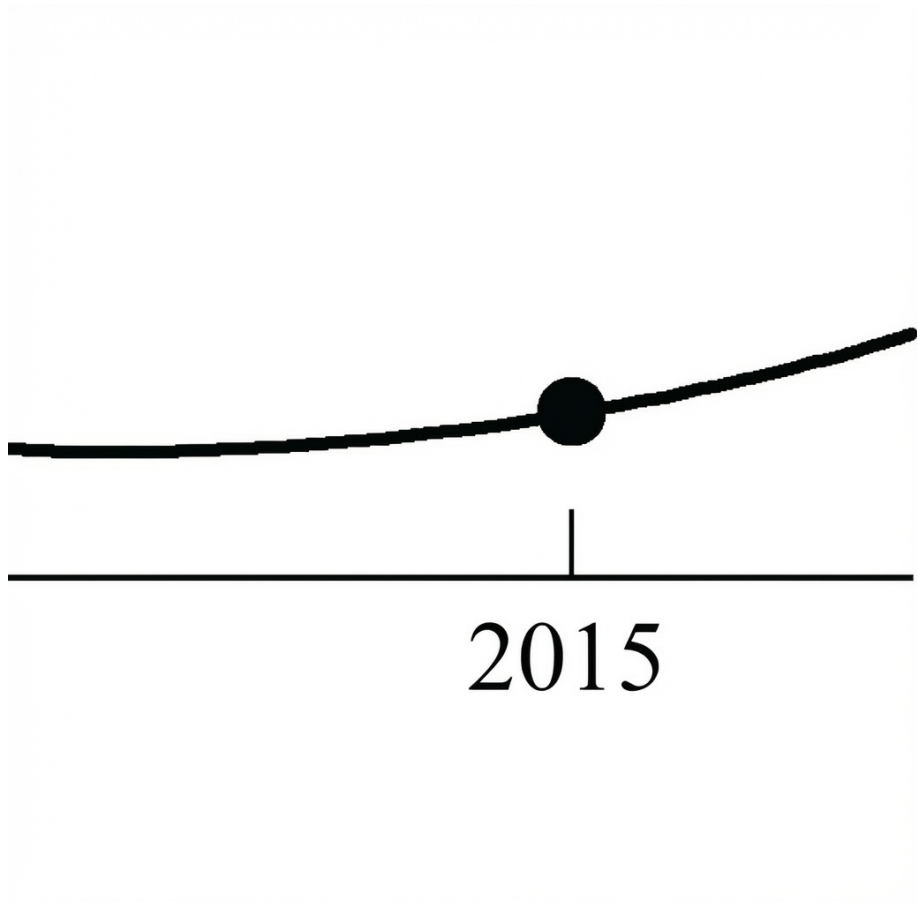


Figure 2: Figure 8

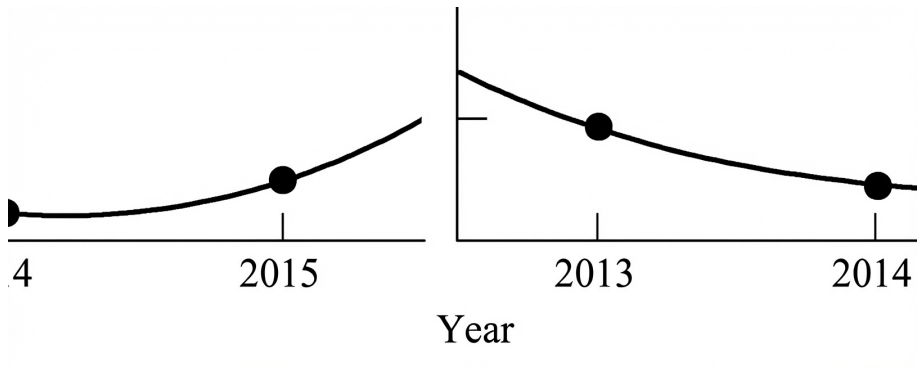


Figure 3: Figure 9