Changes in CSR Ecological Strategies of Plants and Communities Following the Introduction and Restoration of Woody Plants in Semi-arid Damaged Steppe Grasslands

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Abstract

Hulunbuir steppe, one of the four largest grasslands in the world, is suffering progressing desertification due to climate change and anthropogenic disturbance. In this study, the plant species and communities were analyzed with CSR ecological strategies for the succession process that occurred following the introduction of woody plants in the restored site in the damaged steppe, and compared with those in the reference site in an attempt to find the lifeform characteristics of plants in grasslands and implications for success in ecological restoration. According to the results, the introduction of woody plants into the damaged land greatly increased the diversity of plant species and CSR eco-functional diversity as the succession progressed. The types of ecological strategies of the temperate typical steppe (TTS) and woodland steppe (WS) in this region are CSR and S/SR, respectively, which means that plants in the temperate Asian steppe are species basically adapted to natural disturbances such as drying and soil movement. As the restoration time elapsed in the damaged lands (R/CR), the ecological strategies were predicted to change in two ways: R/CR→R/CSR→CSR (TSS) in places where only shrubs were introduced, and S/SR→S/SR (WS) in places where trees and shrubs were introduced simultaneously. The results as such mean that the driving force that causes succession in the restoration of temperate grasslands is determined by the lifeform (trees/shrubs) of the introduced woody plants, and therefore, it is judged that trees or shrubs should be selected and introduced bearing the final target vegetation in mind when planning restoration.

Introduction

Grassland ecosystems are the terrestrial biomes that are the most widely distributed throughout the world, and are classified into steppes, prairies, pampas, savannas, and tundra especially based on average annual temperatures and precipitation (Park, 1985; White et al., 2000). Grasslands provide important ecosystem services such as the role of a protective cover for soil, primary production, maintenance of the diversity of ecosystems, and biodiversity (Shantz, 1954; Eyre, 1968; Angerer et al., 2008; Wrage et al., 2011; Li et al., 2022). However, most grasslands are threatened by continuous overgrazing, conversion of farmlands, deforestation, and indiscriminate reclamation that would lead to severe declines of grasslands (Blair et al., 2014; Chen et al., 2012; Chen et al., 2014). At the same time, grassland ecosystems are being devastated due to decreases in precipitation due to climate change, continued forest fires and drought, and deterioration of land conditions (Montanarella et al., 2018) (Blair et al., 2014). In order to preserve grassland ecosystems, which are degraded as environmental changes such as changes in climate and physical environments progress, clarifying the necessity of protection and taking measures to realize restoration for the harmonious development of humans and nature are urgently needed (Li et al., 2017; Deák et al., 2020).

The Hulunbuir temperate steppe in Asia located on the northwest of Hulunbuir is one of the world's four largest steppes in the world, located northwest of Hulunbuir, accounting for 22% of the total area of China (Oikawa and Ito, 2001; Akiyama and Kawamura, 2007; Angerer et al., 2008; Zhang and Huisingh, 2018). The Hulunbuir steppe is one of the types of vegetation that are sensitive to environmental changes such as climate change and has great significance in terms of ecosystem services because of its role as a national green ecological barrier and ecological security (Yang et al., 2019; Li et al., 2022). However, in addition to recent changes in precipitation patterns due to climate change, the land is severely damaged due to the conversion of land use from grasslands to farmlands or from woodland steppe to farms, and rapid increases in the number of livestock (Li et al., 2007). Consequently, the area of grasslands is rapidly decreasing (Akiyama and Kawamura, 2007) and desertification is progressing due to land degradation (Kang et al., 2007; Squires et al., 2009). In order to preserve the Hulunbuir steppe, the Chinese government started a project to prevent desertification and yellow dust damage from the 2000s and to restore the grassland ecosystem together with local residents, and has been making great efforts such as monitoring studies and tree planting until recently (Batunacun et al., 2015).

Meanwhile, the life history strategy of plants is greatly influenced by environmental factors (McIntosh, 1986; Bai et al., 2022), and the interaction between plants and environmental factors as such affects ecosystem functions (Fry et al., 2018). Plants growing in a spatial and temporal microenvironment have similar life history patterns (Barbour et al., 2015), and the characteristics of ecological functional groups among constituent species in the same place can be known (Hunt et al., 2004). Among the methods of evaluating plants' life history strategies according to environmental changes, the analysis of the C-S-R ecological strategy type is usefully used for evaluating plant ecological strategies (Pierce et al., 2017) because it enables understanding the functional characteristics of constituent species of similar environmental factors (Grime and Pierce, 2012).

As such, the analysis of the C-S-R ecological strategy should be an effective method when it is necessary to explain the future state of the grassland ecosystem by revealing the functional characteristics among the community constituent species of the grassland ecosystem, which is gradually declining due to disturbances of climatic, environmental, and physical factors. In addition, since the effect of the changing environment on plant characteristics can be demonstrated with a CSR ecological strategy (Yu et al., 2022), CSR ecological strategies are judged to be useful as a means of evaluating the effectiveness of restoration. However, studies related to CSR ecological strategies of grassland ecosystems are virtually insufficient globally, and there has been no study conducted with the Hulunbuir temperate steppe at all.

Therefore, the purpose of this study is to investigate the CSR ecological strategies of plant species and communities in restored sites where vegetation was introduced into degraded grasslands, desertification areas, and well-conserved reference site grasslands (typical grasslands and woodland steppe), compare and analyze the characteristics of the restored sites and the reference sites in an attempt to find the life historical characteristics of plants in temperate grasslands in order to preserve the Hulunbuir temperate steppe.

Materials And Methods

Overview of the study site

This study was conducted in the steppe (N 48°04'13"~48°27'11", E 119°18'37" to 118°17'18") located in Ganzhuer, Hulunbuir in the north eastern part of Inner Mongolian Autonomy Region, China where trees were planted as part of prevention of desertification from 2014 to 2018. In Hulunbuir, a temperate typical steppe is developed by the Siberian high pressure caused by the western Pacific subtropical high pressure and the East Asian summer monsoon (Zhu et al., 2019). As for the climate of the Hulunbuir Steppe (1981–2010), Walter et al.'s climatic map (1975) was created using data from the China Meteorological Observation Network (http://data.cma.cn/, 2023) measured by the National Meteorological Observatory of Inner Mongolia (Fig. 1 (left)). The average annual temperature was 1.1℃ and the annual precipitation was 422 mm (Fig. 1 (left)). In Whittaker biomes (Whittaker, 1962; Whittaker et al., 1970), Hulunbuir was between temperate grassland/desert and woodland/shrubland (Fig. 1(right)). In addition, in the climate classification standard of Koppen-Geiger, Hulunbuir corresponded to BSh (Steppe climate and hot arid) and thus was classified as a temperate steppe (Kottek et al., 2006).

This research area is a place where the Forestry Bureau of China has carried out a restoration project for grassland devastation and desertification since 2005. Since 2012, Chinese officials have conducted research on monitoring after restoration jointly by the Korea-China-Japan Yellow Dust Joint Research Group WG( ). The restored sites were classified according to the time elapsed after the restoration by planting, and the sites are a total of four points in the sand dune terrain (Table 1). In the case of the point where vegetation was restored in 2005 (R-13 year), 13 years of restoration time had elapsed, and in the case of the point where vegetation was restored in 2008 (R-10 year), about 10 years of restoration time had passed. In addition, in the case of the points where vegetation was restored in 2011 and 2012, respectively (R-7 year and R-6 year), 7 years and 8 years of restoration times had passed, respectively. The reference sites were the non-restoration point (NR) exposed to a floating dune where restoration was not performed, the temperate typical steppe (TTS), and the woodland steppe (WS), which are the terrain of fixed dunes (Fig. 2). The TTS is a natural grassland ecosystem protected in Hulunbuir, China and is called Yilite. TTS is protected with pillars and wire netting and WS is a *P. sylvestris* var. *mongolica* community, a small-scale remnant vegetation, which is still remaining in the region between the forest of Hulunbuir called Nanhui and grasslands (Fig. 2).

Table 1. Characteristics of the study in Hulunbuir

Characteristic of site	Site * name	Topology type	Elevation (m)	Planted method	Introduced or dominant plant
Non restoration	NR	Shifted sandy dune	601	-	*C fruticosum* (Shrub)
Restoration	R-6yr	Sand dune	590	Shrubs planting + seed spray type	*C. fruticosum* (Shrub)
	R-7yr		590	Tree + shrubs planting	*Populus canadensis* (Tree) *C. fruticosum* (Shrub)
	R-10yr		575		*P. sylvestris* var. *mongolica* (Tree) *C. microphylla* (Shrub)
	R-13yr		581	Shrubs planting + seed spray type	*C. fruticosum* (Shrub)
Reference	TTS	Fixed sandy dune	693	-	*G. verum* (Herb)
	WS		729	-	*P. sylvestris* var. *mongolica* (Tree)

The trees selected and planted for vegetation restoration were *P. sylvestris* var. *mongolica* and *Populus canadensis*, which are tree plants that grow wild in Hulunbuir, and *Caragana microphylla* and *Corethrodeneron fruticosum*, which are shrub plants. As for the vegetation restoration method, the seed sowing method or tree planting method was applied (Table 1). In R-6 year, the seed sowing method and shrub planting method were applied simultaneously, and in R-7 year, R-10 year, and R-13 year, trees and shrubs were planted simultaneously (Table 1). The dominant species in individual study sites was *C. fruticosum* in NR and R-6 year, *P. canadensis* in R-7 year and *C. fruticosum* in the underlayer. In addition, *P. sylvestris* was dominant d in R-10 year, and *C. microphylla* was dominant in the underlayer. In addition, in the TTS, *Galium verum*, which is an herb, was dominant, and in the WS, *P. sylvestris* var. *mongolica* was dominant (Table 1).

In order to fix the sand in all restored sites, checkerboard barriers were made using straw and reeds to prevent sand movement. In addition, 1.5m high barbed-wire fences were installed around all the restored sites to protect vegetation from livestock grazing (Park et al., 2013).

CSR Classification and functional group diversity comparison

In order to analyze the types of CSR plant functions by species of the vascular plants that appeared in the Hulunbuir research site, a total of 7 traits; canopy height, leaf dry weight, dry matter content, specific leaf area, lateral spread, flowering start, and flowering period, which are predictor variables, were measured (Hodgson et al., 1999). As for the canopy height (cm), the height of the above-ground part of the target plant was recorded using a ruler or tape measure, and the measurement unit was cm, but was converted to mm for later analysis. As for the leaf dry weight (g), the fresh weights of leaves were measured, the leaves were dried in a 65 ° C natural circulation dryer for 48 hours, the dried leaves were weighed, and the average value was used. As for the dry matter content (%), the ratio of the leaf dry weight to the weight of the leaf saturated with water was obtained and converted into the percentage. The specific leaf area was calculated by dividing the leaf area by the dry weight of the leaf. The lateral spread means the spreading ability of plants, and the distance between creeping stems or ramets was measured, or the life form was applied in some cases. The flowering start and flowering period were observed firsthand in the field or referred to the Illustrated Book of Northern Grassland Plants in China (Gu and Wang, 2009; Gu and Wang, 2011) or the Flora of China in English (2023).

The analysis of CSR ecological strategies of plants used three CSR model systems, and utilized the Global plant CSR analysis (StrateFy tool) provided by Pierce et al. (2017), the C-S-R Signature calculator provided by UCPE Sheffield of Hunt et al. (2004), and the CSR classification tools of Pierce et al. (2013). However, since the StrateFy, newest analysis method of Pierce et al. (2017), which has the largest number of sample data and can be applied to the flora of the world is efficient, it was used as the standard, and other models were used as reference data. The C-S-R ecological strategy type of each plant was identified with the values derived by inputting values suitable for each trait item among the measured values of plant traits using the above tools. According to the CSR model, C, S, and R, which are three basic strategies, are the primary types, the major secondary strategies are classified into CR, SR, CS, and CSR, and as for the tertiary types, the primary and secondary strategies are mixed and classified, resulting in a total of 19 CSR functional types (Hodgson et al., 1999). In addition, to derive the C-S-R ecological strategies of plants, the dominant species of the research site were analyzed preferentially. For those species for which plant characteristic data were not obtained among other species distributed in this research site, data from the sample data of C-S-R analysis models were referred to and used as standards.

To compare vegetations through the arrangement of ecological strategies of communities and track the movements of and changes in the ecological strategies of communities, values were input into the C-S-R comparator provided by UCPE Sheffield of Hunt et al. (2004) based on the C-S-R ecological strategy of each plant species, and the derived C-S-R ecological strategy types were identified. The distances between habitats were calculated with Cartesian distances, and the closer the Cartesian distance to 1, the longer the distance, and the closer the Cartesian distance to 0, the longer the distance (Hunt et al., 2004). Based on the differences in distance, the strategy properties of the communities were identified and compared by community, and the C-S-R ecological strategy direction of the restored site was predicted. Grime's C-S-R triangular system graph was created with the C-S-R ecological strategy type scores using SigmaPlot (Systat Software, Chicago, IL, USA), a statistical analysis program. In addition, the ratios of C-S-R components by plant CSR type and by community were calculated and displayed as a cumulative bar graph to compare the ratios by study site. In addition, to compare eco-functional diversity, the Shannon-Wiener diversity index (H') (1948) was calculated, and the formula used at this time was $H' = -\sum(Pn \ln Pn)$. Pn is the relative abundance, which is the ratio of the nth species within a community, and means the value obtained by dividing the number of individuals of each taxon by the total number of individuals.

Plant Species Composition And Plant Species Diversity

Three permanent quadrats ($4m^2$) were installed at each research site, the names of plant species appearing in the permanent quadrats were recorded every year from 2014 to 2018, and the number of species and the number of individuals were investigated. Shannon-Wiener diversity index (H') (1949) was calculated to compare plant species diversity at NR, resorted sites (R-13 year, R-10 year, R-7 year, R-6 year) and reference sites (TTS and WS) for 5 years. In addition, the total number of species and the average number of species of the appearing plants were compared, and TTS and WS were expressed as one community. At this time, in order to show clear results, the numbers of species that appeared according to the research sites were expressed as log. In addition, plant species were identified referring to the Illustrated Book of Northern Grassland Plants in China (Gu and Wang, 2009; Gu and Wang, 2011) or the Flora of China in English(2023).

Results

Plant CSR ecological strategies

Among the 19 types of plant CSR ecological strategies of plants for 56 taxa, 14 were found in the Hulunbuir research site (Fig. 3, SI. 1). Among them, R/CR type showed the highest ratio at 48.2% with 27 taxa, followed by S/SR type with 14 taxa (25.0%), R type with 12 taxa (21.4%), S type with 8 taxa (14.3%), and SR/CSR type with 6 taxa (10.7%), and other types showed ratios not higher than 10% with 1 ~ 3 species (Fig. 3). Among the CSR types, 5 types (C, C/SC, CR/CSR, SC/SCR, and CSR) were not found in this grassland.

All 61 ecological strategy types were arranged in one triangle diagram, and according to the result, among the primary, secondary, and tertiary C-S-R types, the tertiary (R/CR. S/SR) and primary (S, R) types had large distributions (Fig. 3). All the ecological strategies of the major restored tree species planted in the damaged land were different from each other as they were S type in the case of *P. sylvestris var. mongolica*, CR type in the case of *P. canadensis*, R/CR type in the case of *C. microphylla*, and S/SR type in the case of *C. fruticosum* (Fig. 3).

Changes in the communities CSR ecological strategies

The CSR ecological strategies of the research sites consisted of a total of four types; R/CR (NR, R-7 year), R/CSR (R-6 year, R-13 year), S/SR (WS and R-10 year), and CSR (TTS) (Fig. 4). As the restoration time elapsed in the damaged site (R/CR), the ecological strategies shifted from the strategic type R/CR to R/CSR, and then to CSR at the sites where shrubs were introduced (R-7 year, R-6 year, R-13 year) similarly to the temperate typical steppe (TSS). On the other hand, at the site where trees and shrubs were introduced (R-10 year), the strategic types S/SR→S/SR (WS) appeared quite similarly to the woodland steppe (WS). As such, in the restoration at the damaged sites, succession progress into two different types of ecological strategies according to the life forms (shrub, tree) of the trees introduced in the early stage (Fig. 4).

Among a total of 14 types of C-S-R ecological strategies of plants by study site, S-selective type and R-selective type appeared in all study sites, whereas C-selective type appeared only at the TTS (Fig. 5). The numbers of types of ecology strategies of plants that appeared by research site and the types that occupied the most were 2 and R/CR (75.0%) at NR, 3 and R/CR (50%) at R-6 year, 5 and R/CR and S/SR(28.6% each) at R-7 year, 5 and S/SR (33.33%) at R-10 year, S/SR (33.33%), and 6 and R/CR (45.45%) at R-13 year (Fig. 5). In addition, in TTS and WS, 11 types of CSR ecological strategies appeared, and the most common types were R/CR (29.4%) and S (25.7%), respectively. In NR and R-6 year., 2 to 3 types appeared, which were significantly less compared to the restored sites and reference ecosystems, and the longer the elapsed restoration time and in the reference ecosystem, the greater the number of types of CSR ecological strategies of the species appeared (Fig. 5).

As vegetation was introduced to the damaged sites, the CSR eco-functional diversity of the communities increased in proportion to the elapsed time of restoration (Fig. 6). The CSR eco-functional diversity was higher by up to 2.1 times at the restored sites than at the unrestored sites, and was higher by 1.5 times at the restored site where the longest time of restoration elapsed than at the site that was restored the most recently (Fig. 6). In addition, the CSR eco-functional diversity was lower to 0.8 times and 0.7 times, respectively at the site where the longest restoration time elapsed than at the reference ecosystems (TTS, WS), respectively (Fig. 6).

Changes in eco-functional diversity

After the restoration of vegetation in the damaged sites, the eco-functional diversity and taxonomic diversity increased over time (Fig. 7, SI. 2). The eco-functional diversity (H') was the lowest at the unrestored site (0.45) and the highest at R-13 year (1.64), which was restored first, and the value reached 97% of the value at the steppe (TTS, 1.69) in the reference site. Also, the ecological diversity of the woody steppe (WS, 1.42) in the reference site was lower than that of the temperate typical steppe (TTS, 1.69).

In NR, the total number of species appeared was 11 taxa, and the annual average number of species was the smallest as it did not reach 10. On the other hand, in the reference ecosystems (TTS and WS), a total of 65 taxa appeared and the number of plant species was the largest among the research sites as the annual average number of species appeared was at least 40 (SI. 2). In addition, among the average numbers of species appeared at individual restored sites, those at the 13 years old restored site (13 year) and the 10 years old restored site (10 year), which are the oldest restored sites, were larger by at least two times than those at the 7 years old restored site (7 year), and the 6 years old restored site (6 year), which were restored recently (SI. 2).

Discussion

Types of plant CSR ecological strategies

A total of 14 types of ecological strategies were identified from the 56 taxa that appeared in the research sites in this study, and CSR ecological strategies which are between the S-selective and the R-selective types, accounted for 93% of the entire ecological strategies, and only the remaining three types (CR, C/CR, C/CSR) had the C-selective type (7.1%) (Fig. 3). Among the primary, secondary, and tertiary types of plant CSR ecological strategies at all seven research sites, species with tertiary (R/CR, R/SR, S/SR) and primary (S and R) types were distributed predominantly in order of precedence (Fig. 3, Fig. 5). Meanwhile, three types (CR, C/CR, C/CSR) had the C-selective type (7.1%), and species with the C-selective type were *Belamcanda chinensis*, *Populus canadensis*, *Patrinia rupestris*, and *Saussurea japonica* and appeared only at R-7 year, TTS, and WS where *Populus canadensis* was planted (Fig. 3)

The climate of Hulunbuir is dry in winter, and 70% of the precipitation falls from June to August so that Hulunbuir is somewhat humid only in this period, but the climate is very dry as the annual precipitation is 274mm, and at the same time, temperature differences and interannual fluctuations in precipitation are extremely large. (Fig. 1 (left)). In addition, nutrients are poor since Hulunbuir is a sand dune, and sand movements occurred frequently, and livestock were active as they were grazed in the whole area, except for restored sites and reference ecosystems. Usually, the S-selective type is a stress-tolerant species and lives while maintaining individual survival in habitats subject to resource stress due to severe resource deficiency (Grime, 1977; Grime, 1986; Grime, 2001; Barbour et al., 2015). On the other hand, the R-selective type is a type that opportunistically and rapidly settles down in habitats, where resources are very abundant and external environmental factors change frequently, that are frequently disturbed to invest heavily in breeding (Grime, 1977; Grime, 1986; Grime, 2001; Barbour et al., 2015). As such, many species between S-selective and R-selective types appeared at the research sites in this study and it is considered to be attributable to the fact that environmental stress and disturbances are frequent there (Pierce et al., 2017).

Usually, deep-rooted plants appear in arid areas such as deserts. Since plants' water demand is higher in more arid environments, they must continue to take root in the water table to absorb water (Barbour et al., 2015). Meanwhile, the reason why *Ulmus pumila*, which is a deep-rooted plant, was found extremely rarely in this study is that since this plant is an S/CSR type but has a strategy for environments where C, S, and R coexist, it is a deep-rooted plant, which likes soils with appropriate wettability although it is tolerant to environmental stress and thus its ability to survive in the environments in the research sites in this study decreased over time.

Meanwhile, among the restored species in the research sites in this study, S-selective types are *P. sylvestris var. mongolica* (S) and *C. microphylla* (SR) (Fig. 3). These two species were well established in the early stage and observed every year during the study period. S-selective type plants have low specific leaf area and high dry weight content because they invest energy in leaves or roots. Since legumes such as *C. microphylla* should provide photosynthetic products to bacteria to maintain a symbiotic relationship with nitrogen-fixing bacteria, they should distribute some of their photosynthetic products to other functions. Therefore, they have a characteristic that their growth is generally slow (Grime and Hunt, 1975; Tilman, 1998; Pierce et al., 2013). It is judged that since they have the S ecological strategy as such, in the research sites in this study too, they developed tissues avoided by herbivores such as scale leaves in the case of *P. sylvestris* var. *mongolica*, and thorns in the case of *C. microphylla* to adapt to diverse stress environments thereby increasing the survival rate (Hodgson et al., 1999). In addition, the scale leaves of *P. sylvestris* var. *mongolica* are a strategy to increase the survival rate in dry conditions thanks to their ability to reduce transpiration to the minimum and this is judged to be the reason why *P. sylvestris* var. *mongolica* grows well in the research sites in this study (Liu et al., 2009; Song et al., 2019). On the other hand, *C. microphylla* is judged to have grown well in the research sites in this study because it has a strategy to adapt well to habitats with low productivity or barren environments through symbiosis with nitrogen-fixing bacteria (Bessler et al., 2012). Therefore, it can be seen that these two species were suitable as tree species in the early stage of restoration.

The CSR ecological strategy of *C. fruticosum*, a restored species, was R-selective type, which is an R/CR type (Fig. 3), and *C. fruticosum* was observed in all research sites including NR, restoration sites and reference ecosystems. The reason why *C. fruticosum* could settle down well in the research sites in this study site judged to be the fact that it has the ability to settle down opportunistically and quickly in harsh dry climate environments such as environments where sand movements are frequent, soil resources change frequently, and disturbance (livestock and humans) is frequent given the strategic characteristics of R-selective and CR (competitive ruderal species) types (Grime, 2001). In addition, *C. fruticosum* seems to be highly preferred by animals since its flowering time is early, its flowering period is long, and its leaves are large because a lot of resources are distributed to leaves. Since the forgoing condition is connected to breeding (Barbour et al., 2015), the settlement is expected to be good in all research sites. In addition, it is judged that *C. fruticosum* has been observed every year at unrestored sites, restored sites, and even in reference ecosystems because it had competitive advantage against disturbance or for resources because it had a little more competitive strategies as its ecological strategy type ratio was C:S:R = 19:0:81%. It is judged to have been observed annually with a predominance. Therefore *C. fruticosum* is judged to be appropriate as a species to be restored in the research sites in this study because it endures well even in severe disturbance since it has competitive strategies although it is an R-selective type and is tolerant in competition with later species.

Meanwhile, wasteland is an environment where most organisms can hardly live due to sand movements and the lack of soil nutrients, etc. Nevertheless, pioneer plants that first enter desert areas and live overcoming unfavorable conditions for growth and development such as the lack of nutrients, dryness or dampness, and light (Tang et al., 2020) and nursing plants that helps and protects the resettlement of other plants (Kim et al. 2021) make the environment favorable for other species to live (Barbour et al., 2015). In the restored sites, which are the research sites in this study, both pioneer plants (*Leymus secalinus* and *Corispermum hyssopifolium* (R/CR)) and nursing plants (*C. microphylla* (S/SR) and *C. fruticosum* (R/CR)) utilized as restoration planting species were distributed, and *C. hyssopifolium* and *C. microphylla* appeared even in NR where there was little vegetation (Fig. 3). As such, since there were pioneer and nursing species, it seems that they affected the development of eco-functional diversity according to the restoration period. Considering the aspects of conservation and prevention of desertification of the Hurunbuir grassland ecosystem, which has been undergoing desertification as the grassland area has recently decreased, the preservation and utilization of pioneer species and nursing species with ecological strategies that can lead to increases in ecological functional diversity by helping the introduction and settlement of plants seem to be very important.

P. canadensis with the CR type ecological strategy was planted in R-7 year, a research site in this study, but its rooting not good and even withering individuals appeared (Author's observation). The C-selective species as such live in resource-rich places, distribute most of the photosynthetic products to growth, have broad leaves, have large amounts of biomass, and have strategies highly competitive for resources (Grime, 1977; Grime, 1986; Grime, 2001). Therefore, the reason why they did not grow well and did not survive to the end is judged to be the fact that their vitality gradually decreased due to their low ecological status in the research sites in this study, where there were many environmental stresses and disturbances. Therefore, *P. canadensis* with C-selective type of the CR type is judged to be suitable as a mid- and late-stage restoration tree species rather than an early restoration tree species.

In addition, genera such as *Allium, Artemisia, Corispermum*, and *Potentilla* appeared more than twice in the research sites in this study, but their strategies were different even if they were in the same genus (Fig. 3). Similar to this study, five genera the same as those that appeared in this study appeared in the semi-natural xeric calcareous grasslands in Italy, but the ecological strategies of them appeared differently such as the genus Sanguisorba, which was R/SR in this study but was SC in Italy and the genus Festuca, which was S/SR in this study and appeared to be S, which is the same primary type, in literature (Pierce et al., 2014). Given the foregoing, it is judged that the plants appeared identically or differently even if they were in the same genus, because they can have very diverse ecological strategies by responding sensitively to environmental changes (Critchley, 2000).

The reason why plant CSR ecological strategies are mainly stress-tolerant (S) and ruderal species (R) rather than competitive (C) ecological strategies is predicted to be the fact that since the environment where the study subject plants live is an area where soil moisture is especially poor and various disturbances such as those caused by herbivores or humans frequently occur, strategies with tolerance to moisture and drying are mainly distributed in the environment as such. In deserts, forelands, and alpine meadows where stress environments occur due to frequent disturbances, limited resources, and in particular, the occurrence of seasonal precipitation, species with S-selective and R-selective types, which are two extremes, were mainly distributed similarly to the types of plant CSR ecology strategies that appeared in this study (Caccianiga et al., 2006; Pierce et al., 2007; Zhou et al., 2021), consistently with the results of this study. As such, it is judged that the CSR ecological strategies can be used as an index representing the situation of the region through a comprehensive analysis of the functional characteristics of plant species to evaluate tree species suitable for restoration.

Changes in community CSR ecological strategies and eco-functional diversity following the progress of restoration.

Globally, a total of 4 types of CSR ecological strategies of communities (CS/CSR, SR/CSR, CSR, R/CSR) appeared in the grassland ecosystem, and the type of the ecological strategy of the TTS in Hulunbuir was

CSR (C:S:R = 27:26:47) (Fig. 4). The grasslands that coincided with the research sites in this study were flooded grasslands and savannas, but the ratios of diversity did not completely coincide because the constituent species of these places were mainly C-selective and S-selective types and these types were abundant (Pierce et al., 2017). On the other hand, the grassland where the ratios of diversity of constituent species between R-selective types and S-selective types was similar to those in this study was Montane grassland (R/CSR), but the types of ecological strategies were different from those in the research sites in this study (Pierce et al., 2017). In addition, the ecological strategies of the temperate grasslands (SR/CSR) with the same grassland type were different from those of the Hulunbuir steppe (Pierce et al., 2017). As such, grassland ecosystems show various types of community CSR ecological strategies, and even in the case of the same biomes, the ecological strategies were different from each other. The reasons for the foregoing are judged to be the fact that grassland ecosystems are a type of vegetation that is sensitive to environmental changes (Yang et al., 2019), and among the environmental factors that divide grassland types, especially precipitation is considered to be the cause (Shimoda et al., 2005).

As such, life history strategies of plants are greatly affected by environmental factors such as topographic changes, soil environment development, and increased light intensity, and plants living in one space have similar life history strategies (Brussaard et al., 1996; Li et al., 2017). The types of the CSR ecological strategies of the grassland ecosystem in the research site in this study were largely divided into temperate typical steppe (CSR) and woodland steppe (S/SR) according to the species restored in the damaged grasslands (Fig. 4), and the results as such show that two types of grassland vegetation exist in the field (Fig. 4). The movements of the ecological strategies following the progress of succession restored in the damaged land were R/CR → R/CSR in order of precedence in the restored site where the initially introduced tree species was shrubs similarly to those of temperate typical steppe (CSR). On the other hand, the type of ecological strategies of the place where high trees were introduced was S/SR closely to woodland steppe (Fig. 4). In addition, the introduction of vegetation increased the number of plant CSR ecological strategy types and ecological functional diversity in proportion to the elapsed restoration time (Fig. 5, Fig. 6). In particular, after introducing vegetation into the damaged site, as the site shifted from unrestored site to the restored site and approached the reference ecosystem, the functional diversity of the CSR ecological strategy increased up to three times (Fig. 6). As such, species constituting functional types of plant communities develop while sharing similar or identical ecological strategy attributes (Grime, 2001; Hunt et al., 2004). This trend can also be seen on the triangular diagram. The types of community CSR ecological strategies of the TTS and the WS were CSR and SS/SR, respectively, and the distance between them was 0.4619, indicating that they were completely different. It is judged that the community CSR ecological strategy types were divided into two due to the selection of the species to be restored and the mutual relationship between the constituent species and environmental factors according to the elapse of restoration time.

The research sites that were grouped into grassland ecosystems are those research sites where R-selective shrubs were planted (R-6 year, R-7 year, R-13 year) and CSR-type TTS. As for the movement of the CSR ecological strategies here, the CSR ecological strategies moved from NR to approach TTS

(Fig. 4). The results as such coincided with the trend for the distance to the TTS on the arrangement of community ecological strategies to be larger in the case of R-7 year (0.1247) and R-13 year (0.1440) than in the case of NR (0.3107) and R-6 year (0.3407) (Fig. 4). In addition, the results coincided with the result in which after the introduction of vegetation to the damaged land, the ecological and functional diversity in the unrestored land increased by two times at the maximum as the restoration time elapsed (Fig. 6).

Meanwhile, the types of CSR ecological strategies of NR and R-6 year were R/CR types that were intensively distributed toward the R-selective type, and the distance between the two regions was 0.0459 (Fig. 4). It is judged that although the CSR ecological strategy of most of the constituent species of these two vegetations were R-selective of annual species, similar community CSR ecological strategies appeared between the two regions because *C. fruticosum*, a slow-growing perennial plant, was dominant. In addition, it is judged that plant species diversity is low and plant community development is slow in this area because this area is a temporary habitat where disturbances occur and has environmental conditions where it is difficult for plants to live. The distance between R-7 year and R-13 year, which are R/CSR types, was 0.0690, and the reason why similar types appeared (Fig. 4) is judged to be the fact that as *C. microphylla* or *C. fruticosum* became dominant, this area became to have similar ecological strategies. In addition, the distance between R-6 year and R-7 year was shown to be 0.2173, indicating large differences in community CSR ecological strategies appeared from 6 years after restoration (Fig. 4). The reason is judged to be the fact that because the R-13 year and R-7 year restored sites were dispersed to the R and S strategies, unlike the NR and R-6 year, which were arranged near the R strategy, and the distance between the communities was shorter in the case of NR and R than in the case of NR and R-6 year so that this site was close to TTS, which is the reference site(Fig. 4).

In addition, in the case of the research sites grouped into the grassland ecosystem, *C. microphylla* and *C. fruticosum* were mainly planted as initial restoration tree species. These two species were mainly dominant in the research sites in this study and were observed every year during the study period. The reason why they grew well is the strategy to increase adaptability and survival rate through symbiosis with nitrogen-fixing bacteria. It is judged that since species with the strategies as such were used as restoration species in devastated areas, they could continue to help the introduction and settlement of various plant species or species with similar strategies. Therefore, it is judged that these research sites are moving toward temperate typical steppes with the most stable ecological strategy because the richness of constituent species developed evenly as time passed after restoration.

The woodland grasslands were divided into restored sites where trees were planted (S/SR) and woodland steppes (S/SR), and the distance between them was 0.0783 (Fig. 4). The reason for the foregoing is judged to be the fact that they were grouped into similar types because they belong to the same dominant species (*P. sylvestris* var. *mongolica*) group. Therefore, it is judged that the restoration site of R-10 year is advancing toward the restoration goal as it is approaching WS. However, in R-10 year, the abundance of *C.. microphylla* Lam was somewhat high, and since the coverage in the lower layer and the supply of excessive resources could rather reduce the species richness (Li et al., 2017), it seems that the foregoing should be periodically monitored and observed along with the growth status of the constituent species. In addition, since S type plants grow slowly, and their leaves are decomposed slowly even under favorable conditions due to various characteristics, they can affect the circulation of substances, which is important in the ecosystem (Hunt et al., 2004). Therefore, it is judged that the strategy should be improved to make dispersed combinations of the research sites groups into woodland steppe and other types so that they would not be concentrated only on S type.

The development of increased eco-functional diversity through the introduction of vegetation into the damaged site in this study is expected to have the largest effects on the development of the eco-functional groups of plants growing in the same microenvironment according to the elapsed time of restoration, change from floating sand dunes to fixed sand dunes, improvement of soil holding capacity, and increases in soil nutrients, etc. In fact, the change in the topography of Horqin sandy land in Hulunbuir, which was a grassland in the past, led to changes in dominant species and decreases in plant species diversity and eventually, *C. microphylla* and *Setaria viridis*, which were tree species at the early stage when the decline of vegetation did not progress very much, were replaced by *C. microphylla* and *Setaria viridis*oon when the decline of vegetation progressed severely so that Horqin sandy land soon became wastelands (Squires et al., 2009). When considered in the aspect of recovery of the vegetation in the restored sites in this study, *Artemisia halodendrom* (SR), an annual herb, appeared in R-7 year and R-10 year restoration sites, which are semi-fixed dunes, *C. hyssopifolium* (R/CR), an annual herb, was found in R-6 year, R-7 year and R-10 year, *C. microphylla*(S/SR), a perennial shrub, was found in R-7 year, R-10 year and R-13 year, and *A. cristatum*(S/SC), a perennial herb, was found only in R-13 year (SI. 3). Also, in R-13 year, sand dunes were changed into fixed dunes so that the topography and soil were restored. The results as such indicate that changes in plant life cycle strategies are related to environmental changes, since changes in plant species composition according to restoration time in the research site in this study can be seen as the opposite direction to Horqin's vegetation reduction.

Changes in Plant Species Diversity according to the Progress of Restoration

Plant species diversity was the lowest in NR and the highest in TTS, and among restored sites, plant species diversity was the highest in R-13 year with the longest restoration time. Therefore, in the case of R-13 year with the longest restoration time among all restoration sites, the level of plant species diversity was similar to that of grasslands (Fig. 7). With an average of 10 taxa or more, the restoration sites had larger numbers of species than the unrestored sites, and the plant diversity in the areas where more than 10 years had passed since restoration increased more than twice compared to areas where 6 to 7 years had passed since restoration. The phenomenon of increases in the appearance of Hulunbuir native species seems to clearly show the result of restoration(Zhang, 1998). Identically to this study, the introduction of vegetation into damaged lands increased plant species diversity in restored areas compared to wastelands degraded areas thereby proving that the effect of vegetation restoration was clear (Lv et al., 2008; Quan et al., 2015; Yao et al.., 2018). In addition, plant species diversity in other Hulunbuir dry and semi-arid grasslands and woodland steppes increased with wetting, and was 7 times higher in wet mesic grassland than in damaged lands (Amartuvshin et al., 2022). Similarly, in this study, when drylands were considered as NR and semi-arid grasslands and forest grasslands were considered as restoration sites and reference ecosystems, respectively, plant species diversity was shown to be 3 times higher at the oldest restored site than NR, and 5 times higher at the reference ecosystem (TTS, WS) than NR (SI. 1). In view of this, this study demonstrated the restoration effect of the introduction of vegetation as the introduction of vegetation increased plant species diversity.

Also, in Inner Mongolia, stock farming plays an important role in the rural economy, and natives are particularly interested in plants that can be used as food sources for animals that are directly related to their lives (Angerer et al., 2008). In Hulunbuir, most of the poaceae and legumes, including *Leymus*, which are rich in nutrients in underground stems, are used as food sources for animals (Zhu et al., 2013; Zhu et al., 2019). In the research sites in this study, pants that can be used as food sources were shown to be *Leymus chinensis, Agropyron cristatum, Calamagrostis epigeios, Cleistogenes squarrosa, Corethrodendron fruticosum, Stipa sareptana* var. *krylovii* (Flora of China, 2023). Among the plants used for vegetation restoration, *C. microphylla* and *C. fruticosum* were actually detected in the feces of livestock living in the research site in this study (Kim et al., 2021), indicating that they are used as food sources for animals. Given the foregoing, it can be seen that the introduction of native tree species and useful resource vegetation to damaged grasslands increases plant species diversity so that many species can be used as food sources. Therefore, it can be seen that the damaged grasslands is becoming an environment where wild animals can live and it is predicted that as plants are gradually diversified, the diversity of the fauna will increase. In addition, the increase in food sources for livestock through vegetation restoration is judged to be of great significance because it not only has a great impact on the restoration effect by continuously inducing active participation in restoration and enhancing restoration awareness, but also is directly related to the lives of local residents.

Conclusion

This study is the first attempt to identify the movements of the CSR ecological strategies and the increase in eco-functional diversity in Hulunbuir grasslands in Asia through analysis of CSR ecological strategies. The introduction of trees in the damaged grasslands increased the diversity of eco-functional groups, and led to the transition to temperate typical grasslands in case the life form of the initially introduced plants was shrubs, and to forest grasslands in the reference site in case the life form of the initially introduced plants was trees + shrubs. As such, the development of the diversity of CSR ecological strategies in proportion to the passage of time in the restored site means that the vegetation restoration of the damaged site has been successfully achieved, and this succession series may vary depending on the life form of the introduced woody plants. Therefore, in the restoration of damaged lands in the steppe, it is judged that restoration plants should be selected and introduced by considering the final goal of restoration (grass steppe, woodland steppe) first.

For the successful ecological restoration of damaged grasslands in the field, above all, the participation of local residents in Hulunbuir and the promotion of positive awareness of the restoration project played a great role. In particular, this is because the food source for livestock desired by local residents has increased through the restoration project.

When considering these points, it is thought desirable to set the temperate typical steppe (TSS), where plants for animal feeding, which are more importantly used as a food source for livestock as the final goal of restoration rather than the woodland steppe (WS). To this end, planting shrubs such as *C. microphylla* and *C. fruticosum* as initial restoration species introduced will lead to herbaceous steppes more quickly. In addition, in order to prevent damage to introduced vegetation caused by sand movement here, the installation of fences using reeds or straw can be said to be an important consideration for successful ecological restoration.

Declarations

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Author's contributions

Eui-Joo Kim performed the experiments, analyzed data, and wrote the manuscript text. Seung-Hyuk Lee performed the experiments, collected, and analyzed data, and wrote a first draft version of this manuscript. Ji-Won Park analyzed data and prepared figures 1(left), 6-7. Jeong-Min Lee reviewed the manuscript text, and prepared figures 5, supplementary. Yoon-Seo Kim prepared figure 1(right)-3, and Se-Hee Kim prepared figure 4-5 and wrote the references according to the style. Sung-Bae Joo performed the experiments, collected data, and reviewed the manuscript. Keong-Mi Cho prepared supplementary material. Young Han You designed and performed the experiments and analyzed data and reviewed the manuscript and proofreading. The authors read and approved the final manuscript.

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Figures

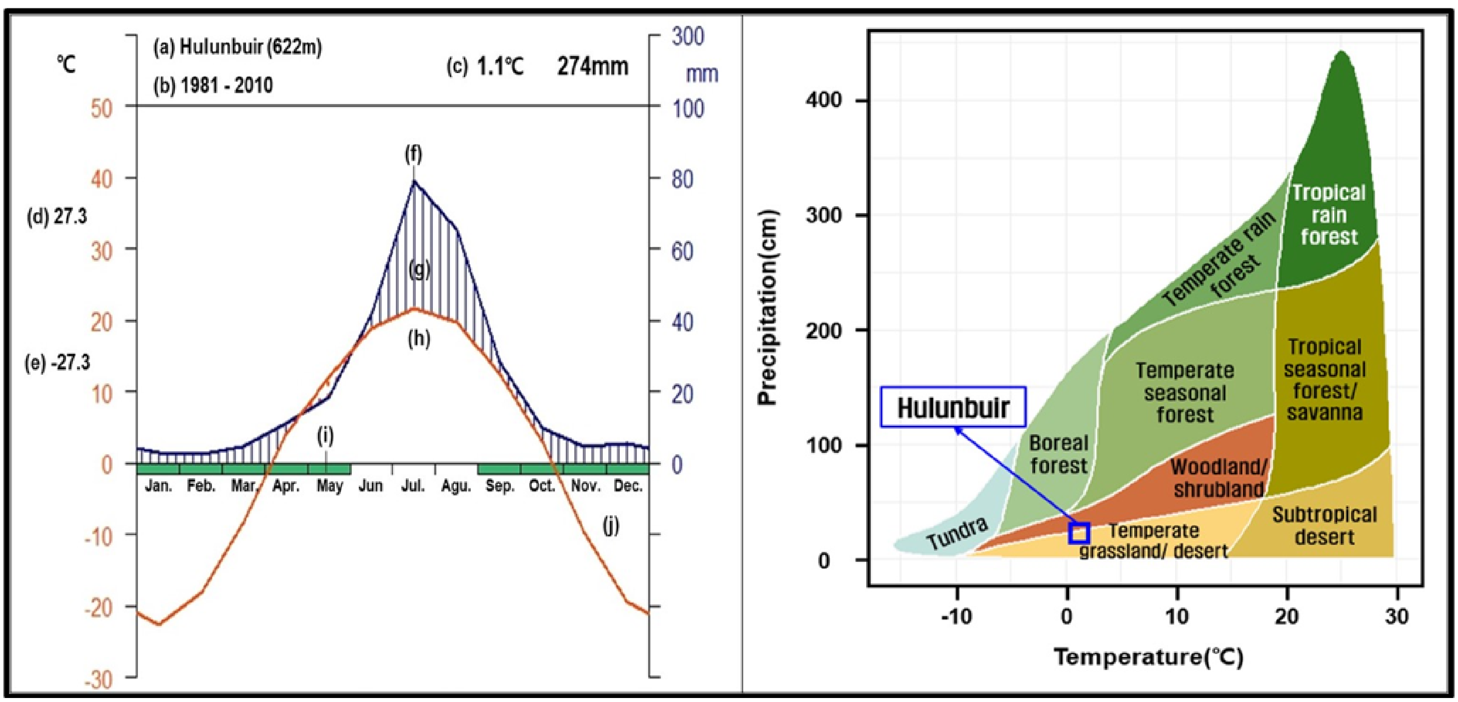

Figure 1

Climate diagram from 1981 to 2010 (left) and Whittaker's biome classification (right) in Hulunbuir. (a): location name and altitude, (b): the period of observation, (c): mean temperature and annual mean precipitation, (d): maximum temperature of warmest month, (e): minimum temperature of coldest month, (f): mean monthly temperature, (g): humid period, (h): mean monthly precipitation, (i): a month in which the average daily minimum temperature is 0°C or lower, (j): the dry season in left figure. In right figure, the blue dot means the corresponding biome in Hulunbuir

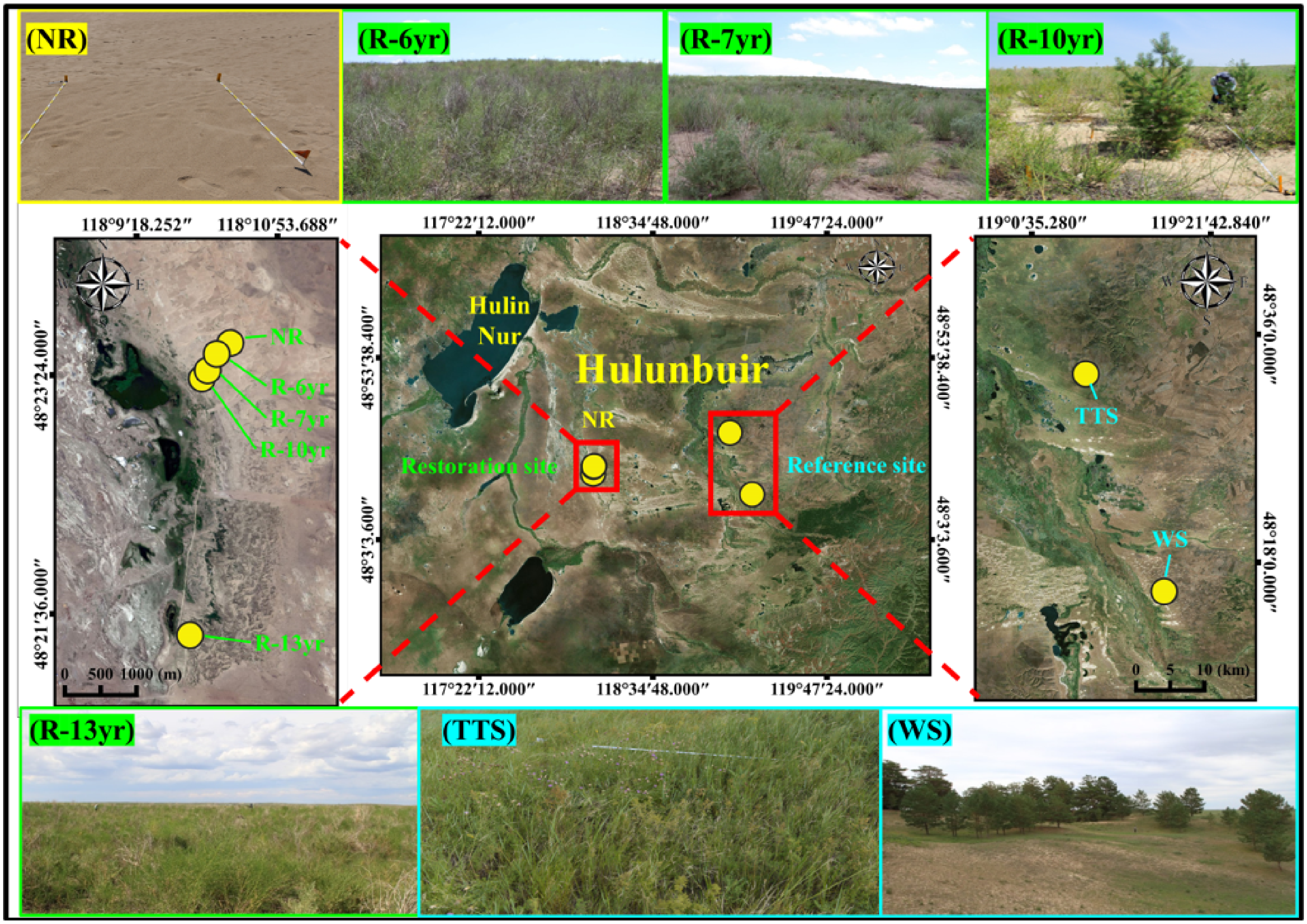

Figure 2

A total of four photos at the top of the figure are landscape photos (from right to left) of restored sites (R-6yr, R-7yr, R-10yr) including the unrestored site (NR), respectively. And in the center photo, the leftmost one explains the location of the unrestored site and the restoration point, the one located in the center shows the location of all research stations in the Hulunbuir area, and the one on the rightmost shows the location of the reference ecosystem. And, from the right to the left at the bottom, a total of three pictures shows the restored area (R-10yr), temperate typical steppe (TTS), and forest meadow (WS). The red solid line emphasizes the location of the research site, and the dotted line is the direction line for the enlarged photo of the location of the research site. Abbreviation explanation: R-number_yr means Restoration-restoration elapsed time year, TTS means temperate typical steppe, WS means woodland steppe, NR means Non restoration

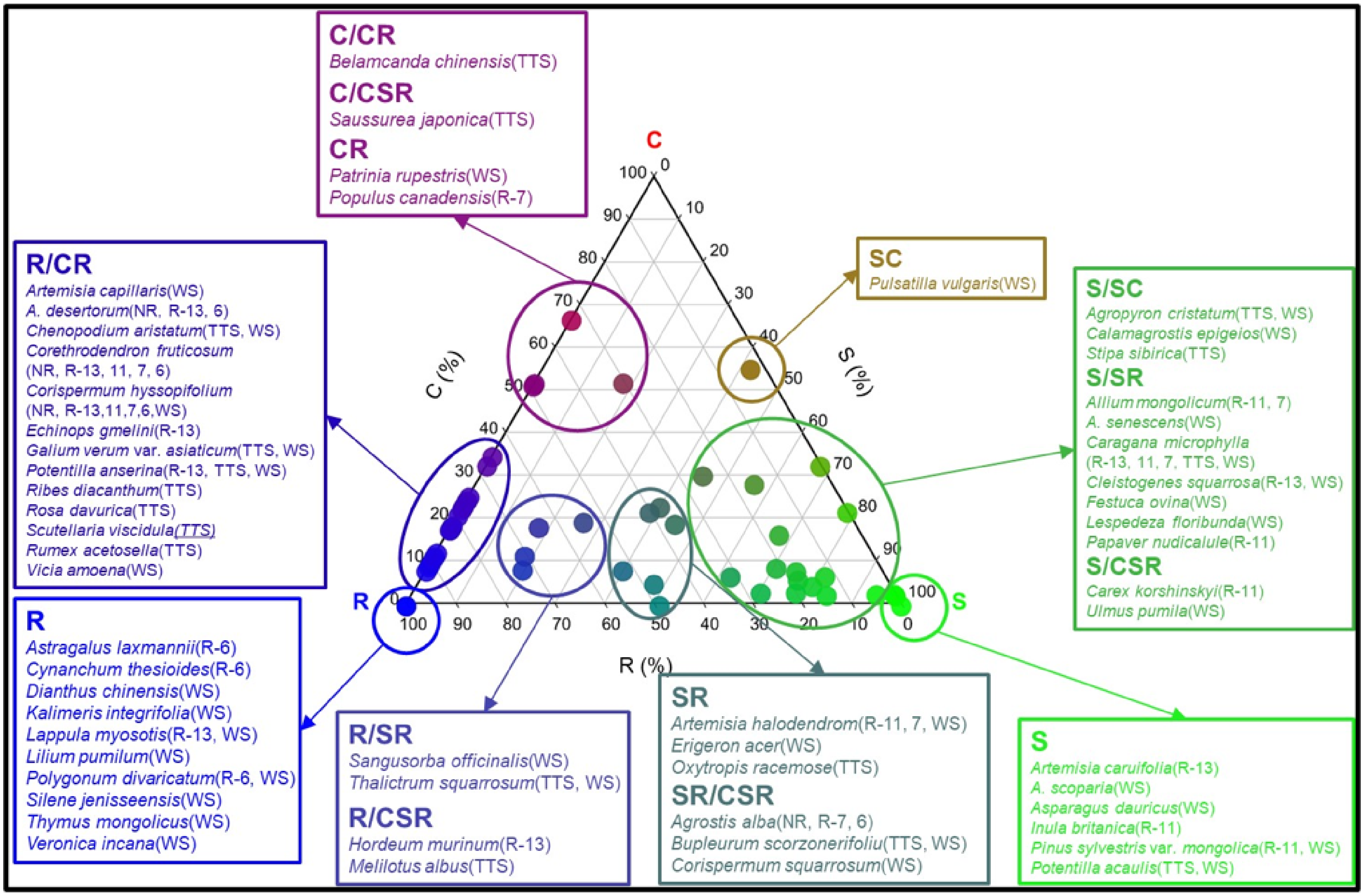

Figure 3

Ternary plot showing relative proportion (%) of C-, S- and R- selection for 56 taxa measured from research site in Hulunbuir. Species corresponding to the CSR strategy class proposed by Grime (2001) are marked with the species name in the box. Ticks on the axes indicate the matching gridlines inside the triangle. In trigonometry, the classification of C-S-R types is expressed in the colors of Red (C-selected), Green (S-selected), and Blue (R-selected), and the color of the point is the RGB value provided by the CSR analysis tool 'StrateFy'. Abbreviation explanation: R-number. means Restoration-restoration elapsed year, TTS means temperate typical steppe, WS means woodland steppe, NR means Non restoration

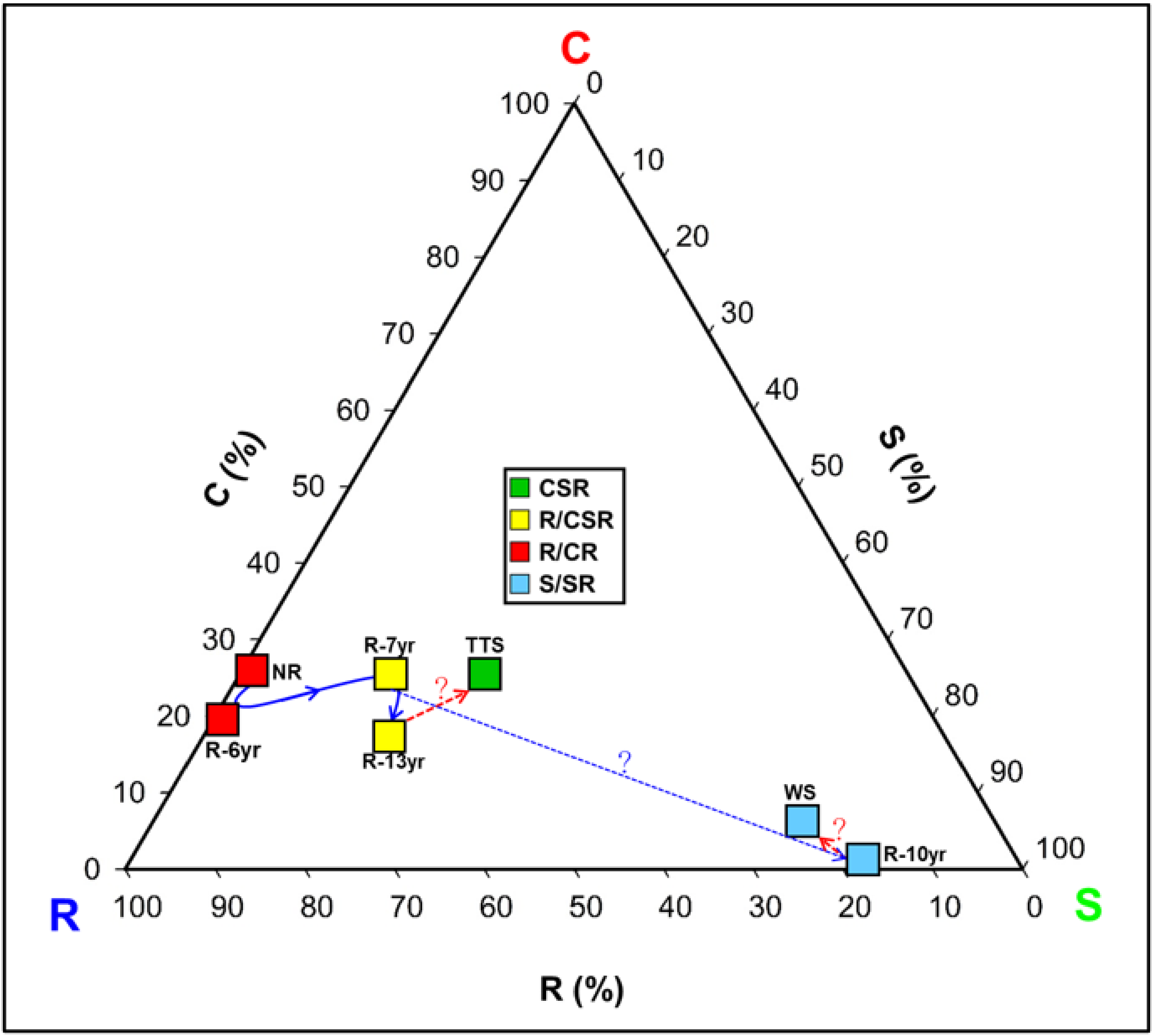

Figure 4

Trinomial plot showing the relative percentages of C-, S-, and R-selection for communities at the study site at Hulunbuir. The dots on the triangle diagram are arranged in relative proportions of each institute's community CSR ecological strategy, and the color of the circle represents the community CSR ecological strategy, as shown in the legend at the top left. Blue solid arrows indicate the direction from dry land to restored land and reference ecosystems. The arrows on the blue dotted line indicate the projections of transitions in the order of restoration elapsed time. The red dot and question mark markers represent subliminal predictions moving forward to the reference ecosystem. The scales of the axes of the triangular degree indicate the coincident grid lines inside the triangle. Classification of C-S-R types in trigonometry is indicated by the colors red (C-choices), green (S-choices), and blue (R-choices). Abbreviation Explanation: R-Number means Restoration - elapsed years of restoration, TTS means temperate typical steppe, WS means forest steppe, and NR means no restoration

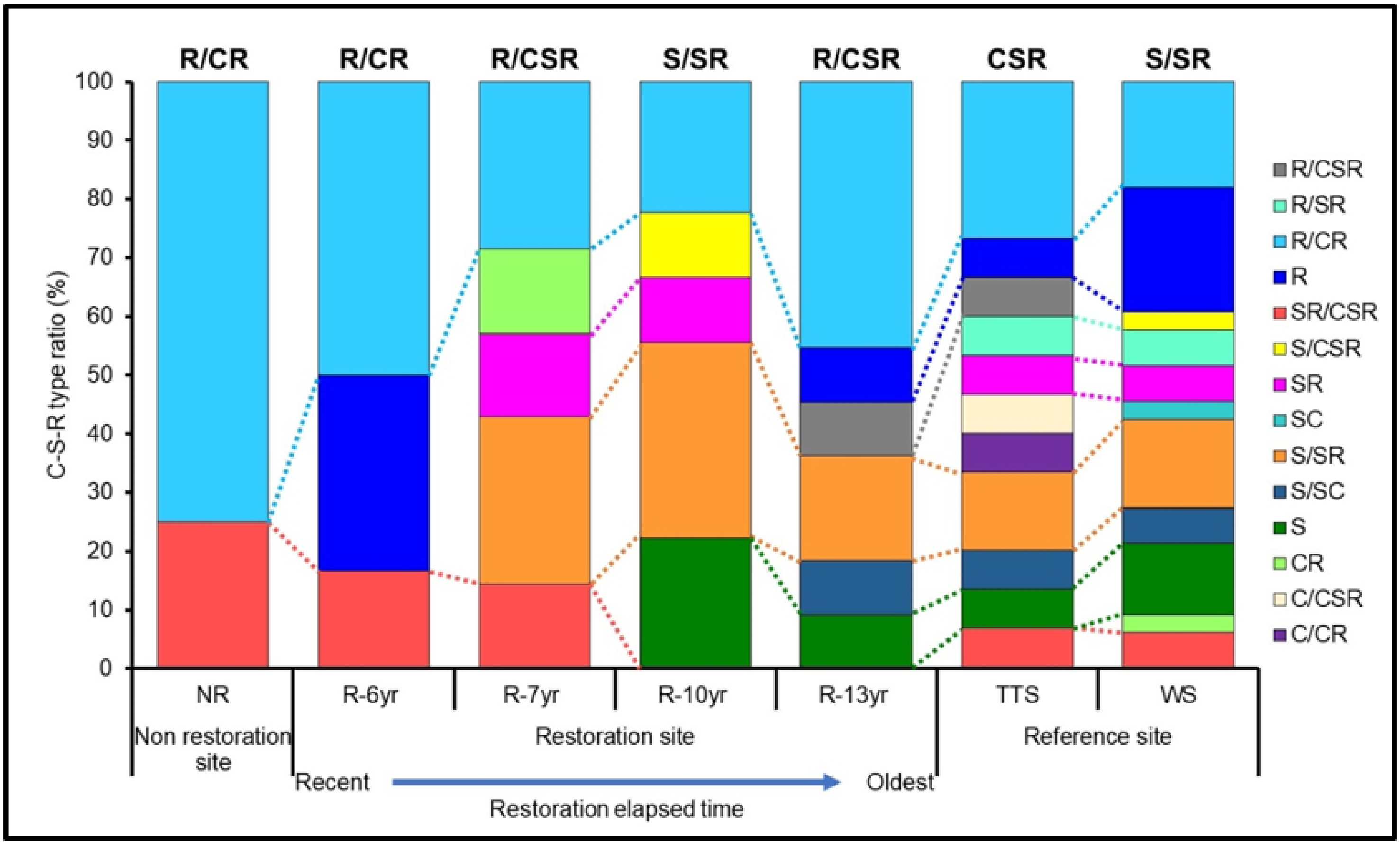

Figure 5

Ratio of types of C-S-R ecological strategies occupied from research site in Hulunbuir among a total of 19 CSR strategy class proposed by Grime (2001). The black letters above the bar graph indicate the study site's community CSR ecological strategy. Abbreviation explanation: R-number_yr means Restoration-restoration elapsed time year, TTS means temperate typical steppe, WS means woodland steppe, NR means Non restoration

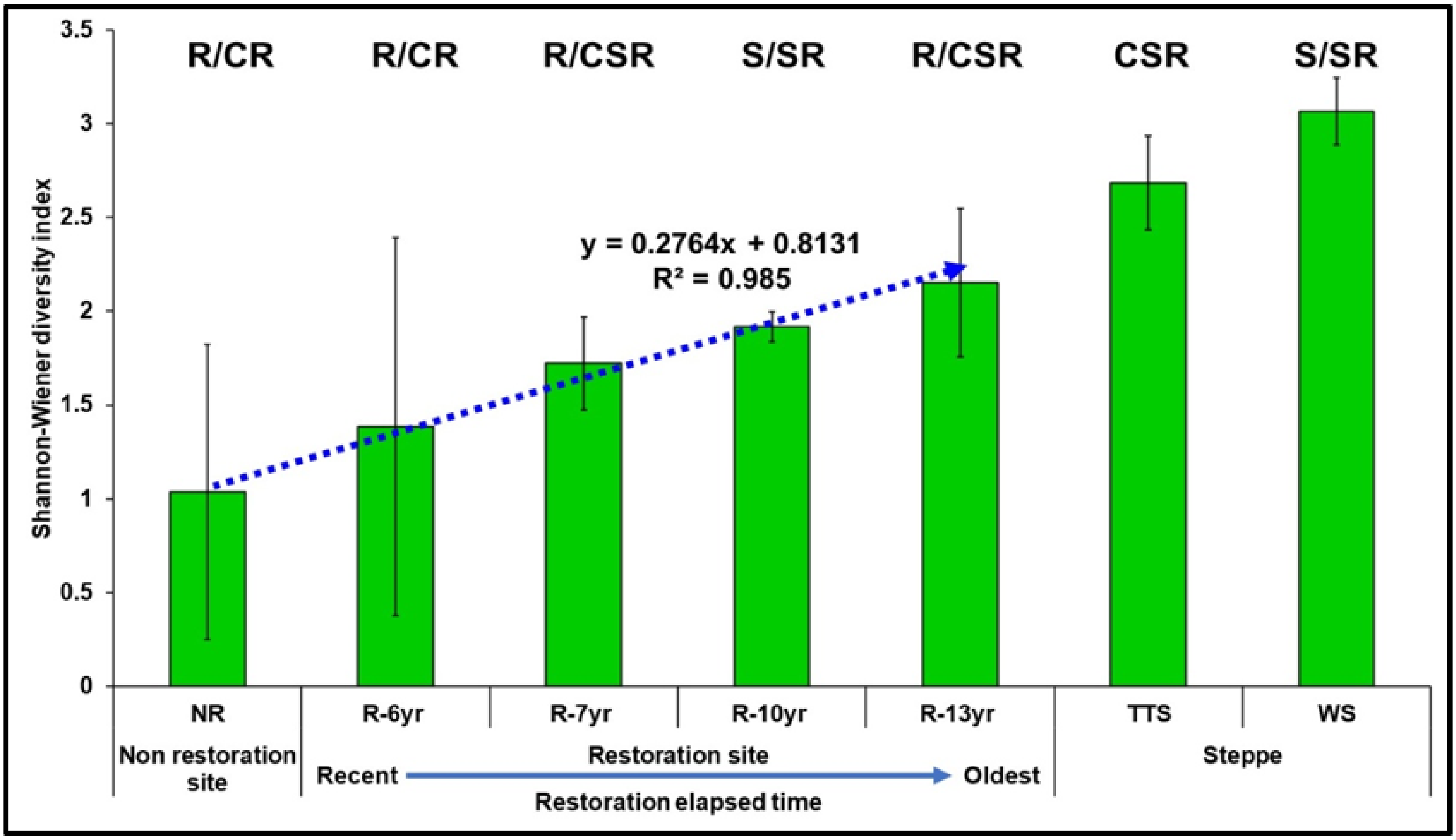

Figure 6

Comparison of Shannon-wiener diversity of community CSR ecological strategy by research site in Hulunbuir. Error bars represent the standard deviation. Bars means the Shannon-wiener diversity of composition ratio of community CSR per study site. The blue dotted line above the bars of the unrestored and restored area means the regression line (R^2 = 98.5%). NR: site of non-restoration, R-arabic numeral yr.: site of year time after restoration. Abbreviation explanation: R-number. means Restoration-restoration elapsed year, TTS means temperate typical steppe, WS means woodland steppe, NR means Non restoration

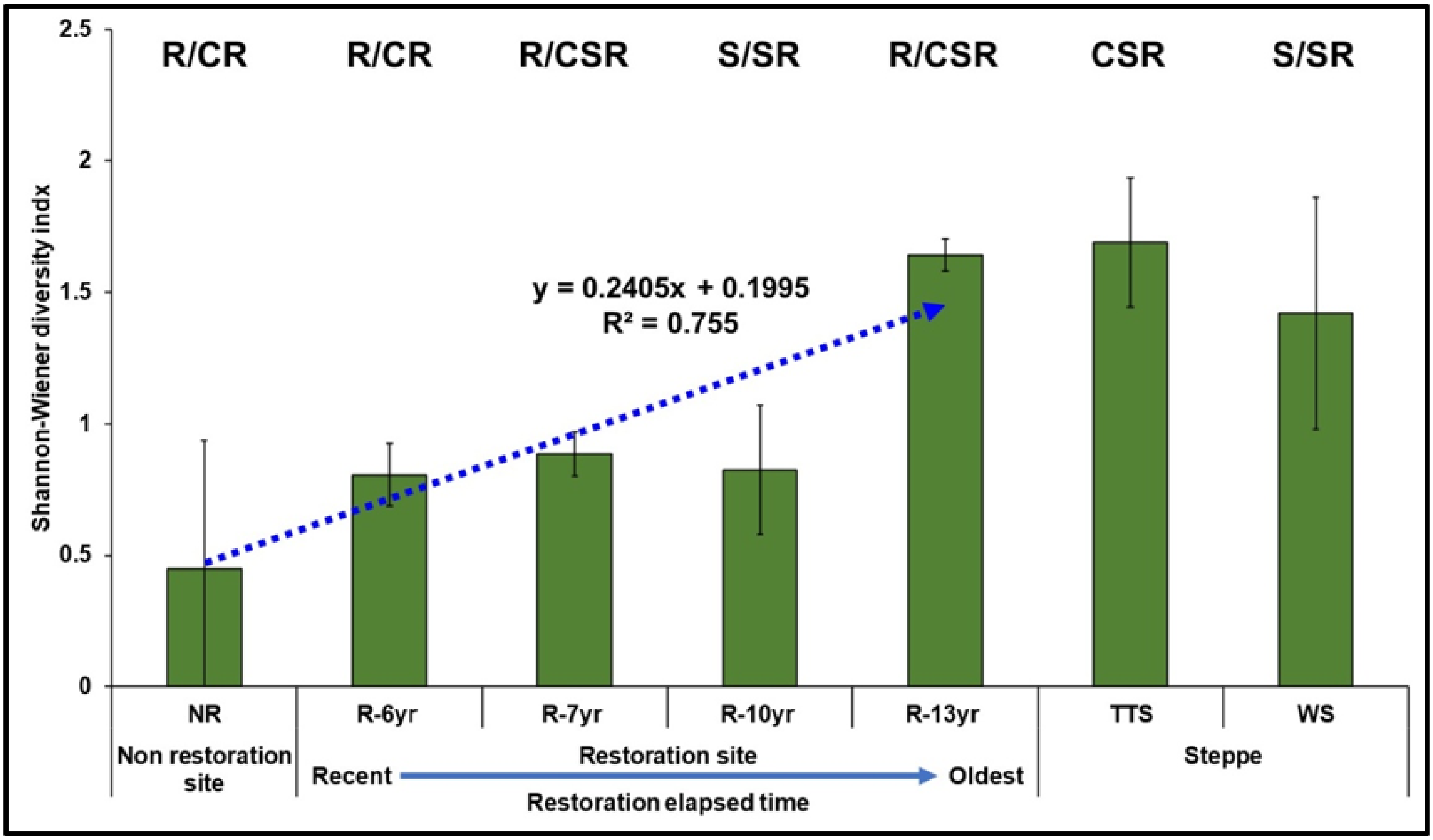

Figure 7

Comparison of Shannon-wiener diversity of plant species ecological strategy by research site in Hulunbuir. Error bars represent the standard deviation. Bars means the Shannon-wiener diversity of composition ratio of community CSR per study site. The blue dotted line above the bars of the unrestored and restored area means the regression line (R^2 = 75.5%). Abbreviation explanation: R-number. means Restoration-restoration elapsed year, TTS means temperate typical steppe, WS means woodland steppe, NR means Non restoration

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Supplementarydata.pdf