Postprint: Impacts of Tourism Development on Plant Spillover Effects at Landscape Edges

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Abstract

Landscape modifications caused by human activities can create numerous habitat patches and edge structures, exerting significant influences on plant dispersal. Using plant movement ecology—seed dispersal modes as the classification criterion, we conducted comparative analyses of edge spillover effects for animal-dispersed species, wind-dispersed species, unassisted-dispersal species (including short-distance dispersal species such as gravity-dispersed and ballist-dispersed species), and all species combined, in both recreational and non-recreational zones, as well as in transportation corridors and non-transportation corridors within the Xingkai Lake Nature Reserve. The results showed that edge spillover effects for animal-dispersed species and all species combined in recreational zones were significantly weaker than those in non-recreational zones; whereas wind-dispersed species exhibited substantial spillover in both recreational and non-recreational zones; unassisted-dispersal species showed negligible spillover effects in both experimental areas. In transportation corridors, spillover effects of animal-dispersed species were significantly weaker than those in non-transportation corridors, but wind-dispersed species showed significantly stronger effects; unassisted-dispersal species similarly exhibited only limited spillover in both corridor types, with relatively short distances; no significant difference was found in overall spillover effects. These results indicate that tourism development has impacted plant movement ecology, ultimately leading to alterations in spillover effects.

Full Text

Preamble

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Effects of Tourism Development on Plant Spillover Effects at Landscape Edges

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Abstract

Anthropogenic landscape alteration can create fragmented habitats and alter edge structures, considerably affecting the natural dispersal of plant species. In this study, we conducted a comparative analysis on edge-spillover effects of animal-dispersed, wind-dispersed, unassisted-dispersal (including species dispersed by gravity and ejection), and total species between both recreational/non-recreational zones, and traffic/non-traffic corridors in the Khanka Nature Reserve based on plant individual motion ecology—seed dispersal modes. The results showed that edge-spillover effects of both animal-dispersed and total species were significantly weaker in recreational zones than in non-recreational zones, while wind-dispersed species significantly spilled over in both zones. We only documented a few unassisted-dispersal species spilling over in either zone. The spillover effects of animal-dispersed species were weaker in traffic corridors than in non-traffic corridors; in contrast, the spillover effects of wind-dispersed species in traffic corridors were significantly stronger than in non-traffic corridors. Similar to the recreational and non-recreational zones, a few unassisted-dispersal species spilled over into both experimental corridors and their spillover distances were relatively shorter than those of animal-dispersed and wind-dispersed species. There was no significant difference in total species spillover effects between the two types of corridors. These results indicate that tourism development had a considerable effect on plant motion ecology, leading to changes in spillover effects.

Keywords: plant motion ecology; tourism disturbance; spillover effects; biodiversity conservation

Introduction

Spillover effect is a phenomenon in marine nature reserves where certain adult fish individuals tend to disperse outward beyond reserve boundaries due to increasing population density and spatial resource pressure, thereby increasing population numbers in surrounding areas [1]. In marine nature reserves, this effect is important for fisheries management in areas surrounding protected zones [2-4]. In terrestrial ecosystems, spillover effects have mainly been applied to insect pollination ecological services in agricultural landscapes surrounding forests [5-7], but their application in biodiversity conservation is still rare [8].

As a movement mechanism, spillover effects reflect the ability of species individuals to disperse outward from landscapes, representing the combined result of their movement ecology and external environmental factors [9]. For plant species, spillover effects are related not only to their life history traits and seed morphological structures [10], but also to environmental factors such as the number of dispersal vectors and landscape connectivity [9]. Therefore, external environmental factors have a more pronounced influence on their spillover effects, especially in fragmented landscapes where plant populations typically exist in isolated forms [11].

Building upon the organismal movement ecology framework proposed by Nathan et al. [12], Damschen et al. [9] further proposed a plant individual movement ecology model. This model describes the relationship between plant individual movement ecology and external environmental factors, emphasizing that external environmental factors such as landscape edge structure, wind [13], and birds [13-14] as dispersal vectors affect plant individual movement ecology. To test this model, Brudvig et al. [8] conducted comparative experiments on spillover effects of different groups in the Savannah River basin forest landscape of the southeastern United States, using plant individual movement ecology—seed dispersal modes as classification criteria for animal-dispersed, wind-dispersed, and unassisted-dispersal species. Different landscape edge structures and connectivity effects produced distinctly different impacts on the spillover effects of animal-dispersed species, wind-dispersed species, and gravity-dispersed species, thereby reflecting the influence of external environmental factors on different plant movement ecologies. Animal-dispersed and wind-dispersed species both showed significant spillover at landscape edges with high connectivity, while spillover effects were not obvious at edges with low connectivity; gravity-dispersed species showed no significant response. These results demonstrated the impact of external environmental factors on plant movement ecology [15].

Based on reflections from the above research, if external environmental factors have important impacts on plant movement ecology and ultimately lead to different edge spillover effects, then in tourism landscapes, how will the changes in landscape edge structure caused by tourism development and recreational activities affect the spillover effects of plants with different dispersal modes? Is this impact positive or negative? Can traffic corridors formed by tourism development function as ecological corridors to promote species spillover to edges due to their increased landscape connectivity? Using the plant individual movement ecology framework proposed by Damschen and Brudvig as the theoretical foundation, this study similarly uses plant individual movement ecology—seed dispersal modes as classification criteria to conduct comparative analysis on edge spillover effects of plants with different dispersal modes in tourism landscapes, thereby verifying the potential impacts of tourism development activities on plant spillover effects.

1. Study Area

This study selected the Khanka Lake Nature Reserve on the China-Russia border (45°01 –45°34 N, 131°58 –133°07 E) as the research area. The reserve has high avian diversity and is an important channel for migratory birds in the Asia-Pacific region. According to recent statistics, there are [number] bird species in Khanka Lake, including national first-class protected birds such as Grus japonensis and Ciconia boyciana, and national second-class protected birds. In addition to birds, Khanka Lake also has high diversity of wildlife and plant species, including [number] vertebrate species and national rare and endangered plants including Pinus takahasii Nakai (Khanka pine), Juglans mandshurica Rupr., Phellodendron amurense Rupr., Tilia amurensis Rupr., Fraxinus mandshurica Rupr., and Glycine soja Sieb. Et Zucc.

The climate within the reserve has large temperature variations, with an average annual temperature of 3.1°C; the lowest temperature in January reaches -39°C; the highest in July can reach 36°C; average annual precipitation is 654 mm; average annual wind speed is 4.0 m/s, with 38 days of strong winds annually; the lake freezing period is 147 days, and the ice cover period is 160 days.

The Khanka Lake Nature Reserve includes various landscape types such as forests and lakes. Some landscapes have undergone obvious changes due to long-term human production and living activities, and tourism development in recent years has further led to fragmentation of some landscapes, forming numerous habitat patches. The rapid development of tourism has also substantially increased tourist numbers, providing favorable conditions for spillover effect disturbance experiments.

2. Methods

Field experiments were divided into two parts: one comparing edge spillover effects between recreational and non-recreational zones, and the other comparing edge spillover effects between traffic corridors and non-traffic corridors. The former aimed to verify whether landscape changes and tourist disturbances caused by tourism development had significant impacts on plant spillover effects, while the latter aimed to verify whether traffic corridors function as ecological corridors to facilitate species spillover to landscape edges. The study site was selected at the Fengmingshan scenic area of Khanka Lake Nature Reserve. The survey was conducted during [time period].

The landscape vegetation in this area mainly includes Pinus takahasii Nakai, Corylus heterophylla, Acer mono, Lespedeza bicolor, Spiraea salicifolia, Artemisia lavandulaefolia, Deyeuxia purpurea (large-leaf reed grass), Polygonatum odoratum, Deyeuxia langsdorffii (small-leaf reed grass), Coptis chinensis, Setaria viridis, Juglans mandshurica, Carex ussuriensis, Quercus mongolica, Phellodendron amurense Rupr., and Plantago asiatica.

The survey method for recreational and non-recreational zones involved selecting two sites within the same landscape: a recreational zone with tourism disturbance and a non-recreational zone without tourism disturbance. All vascular plants were surveyed using quadrat methods. To ensure sample independence, the distance between the two experimental sites was approximately 3 km, with similar plant composition and microclimate conditions. The recreational zone had extensive tourist activities and artificial landscapes with frequent tourism disturbance, while the non-recreational zone had no tourism disturbance. Forest edge orientation was consistent (20°). Quadrats were established perpendicular to landscape patch edges. Shrub and herbaceous vegetation cover outside the landscape was approximately 30 m. Each transect was divided into 10 m × 10 m quadrats. Following the methods of López-Barrera et al. [16] and Brudvig et al. [8], we established transects at both experimental sites, using the boundary formed by trees as the landscape edge. Each transect had a total length of 80 m, with 30 m inside the landscape and 50 m outside. Therefore, the length of transects outside the landscape was set as 0–30 m with continuous quadrats, and 30–100 m with intervals. Then all current-year vascular plant seedlings within quadrats were surveyed and counted.

The measurement method for corridor spillover effects was similar to that for recreational zones, i.e., selecting traffic corridors (with many motor vehicles) and non-traffic corridors (narrow open spaces without motor vehicles) for comparative analysis. Both had similar widths. Because traffic corridors have many motor vehicles whose noise may significantly disturb dispersal vectors like birds, the survey distance was extended to 100 m inside the landscape. External quadrats were set continuously, while internal quadrats were set at intervals at distances of 10, 20, 40, 60, and 100 m from the forest edge. Then all current-year vascular plant seedlings within quadrats were surveyed and counted.

3. Species Identification and Classification

We first identified and classified all vascular plant species discovered in the field survey. Species identification primarily referred to the *Flora of Heilongjiang*, *Flora of China*, and comprehensive judgment by reserve experts and existing materials (http://www.plants.csdb.cn/eflora/Default.aspx). All recorded species were then classified based on dispersal mode into animal-dispersed, wind-dispersed, and unassisted-dispersal (here referring mainly to gravity and ejection that only enable short-distance dispersal). This classification was adopted because the vast majority of vascular plants in nature disperse through these methods, while animal and wind dispersal vectors are more obviously affected by external environmental factors. Therefore, this classification method can effectively reflect the impact of environmental factors on species movement ecology. Since some species may have multiple dispersal modes [17], in this research paradigm we only adopted the dispersal mode that had a significant impact on their dispersal distance as the classification standard.

Dispersal mode determination was primarily conducted through existing literature or observation of fruit and seed morphological structures. Animal-dispersed fruits are typically fleshy, with characteristics suitable for animal dispersal, such as bright colors, arils or ridges, or coarse bristles or spines. Wind-dispersed seeds are usually small and numerous, or have fine soft pappus and winged structures suitable for wind dispersal and long-distance airborne transmission. Unassisted-dispersal species typically lack obvious structures for long-distance dispersal, are relatively large in volume, and can only disperse through ejection or gravity. For unidentifiable species, we could refer to fruit and seed characteristics of plants in the same family and genus for comprehensive determination.

4. Data Processing

This study used species richness as the indicator to measure spillover effects. The measurement method employed independent samples t-tests in statistics to compare differences in species spillover effects between recreational and non-recreational zones, and between traffic and non-traffic corridors. The significance level was set at = 0.05. Related figures were completed using Origin 8.5 software.

5. Results Analysis

During the survey period, a total of [number] species were recorded. All species in the non-recreational zone were also recorded in the recreational zone, and there was no significant difference in overall diversity between the two ($P > 0.05$). However, some less abundant species were not recorded in some quadrats of the recreational zone.

Comparison results showed that animal-dispersed, wind-dispersed, and unassisted-dispersal species in recreational and non-recreational zones exhibited significantly different edge spillover effects. In the non-recreational zone, animal-dispersed species showed obvious edge spillover effects, and as distance from the edge increased, the spillover effect…species richness mean reached…higher than inside the landscape ($P < 0.001$). In the -10 to -20 m zone…23.9%…12.7%…-10 m…-30 m…0 to -10 m…-20 to -30 m, species spillover decreased significantly.

Compared with the non-recreational zone, animal-dispersed species in the recreational zone also showed some spillover effects ($t = -15.62885$, $P < 0.001$). Their mean species richness in external space was only 3.5 (0 to -10 m) and 2.2 (-10 to -20 m), both significantly lower than the non-recreational zone (for -20 to -30 m: $t = -5.54028$, $df = 18$, $P < 0.001$; for -10 to -20 m: $t = -7.87839$, $P < 0.001$; for 0 to -10 m: $t = -5.58455$, $df = 18$, $P < 0.001$). The spillover trend was also obviously weaker, with mean species richness of only 1.8 (-20 to -30 m), significantly lower than inside the landscape ($P < 0.04$). At 0-10 m, it was similarly significantly lower than the non-recreational zone at 0-10 m ($t = -1.40933$, $df = 18$, $P = 0.17578$).

[Figure 1: see original paper] Spillover effects at the edges of the recreation zones and the non-recreation zones

Unlike animal-dispersed species, wind-dispersed species produced obvious spillover effects in both recreational and non-recreational zones. In the non-recreational zone, wind-dispersed species richness at 0-10 m reached a mean of [value], 13.5% higher than inside the landscape ($P < 0.05$), and showed obvious decay with increasing distance from the edge. However, in the recreational zone external space, although wind-dispersed species spillover effects were strong, they did not show obvious spatial decay. Wind-dispersed species richness had a mean of [value], 17.6% higher than the non-recreational zone ($P < 0.01$). Wind-dispersed species in both experimental landscapes showed obvious spillover trends at internal edges of 0-10 m, 4.8% higher than internal means ($P > 0.05$).

Unassisted-dispersal species (including gravity-dispersed and ejection-dispersed species that cannot disperse long distances) only had small amounts of spillover in both experimental landscapes. Non-recreational zone unassisted-dispersal species averaged [value] in external space of 0 to -30 m, [value]% higher than inside the landscape ($P < 0.001$). In the recreational zone external space of 0 to -10 m, there was small spillover with mean richness of only [value], and almost no records in -10 to -30 m. Unassisted-dispersal species richness was significantly higher inside than outside at 0-10 m ($t = 22.04541$, $P < 0.001$). Unassisted-dispersal species were similarly scarce inside the landscape, with no records in most quadrats.

Animal-dispersed, wind-dispersed, and unassisted-dispersal groups together determined the overall spillover effects of the two experimental zones. Overall spillover effects differed significantly between the two zones. Due to the negative response of animal-dispersed species, overall spillover effects in the recreational zone were significantly weaker than in the non-recreational zone at distances of 0 to -10 m ($t = -11.28726$, $P < 0.001$) and -10 to -20 m ($t = -3.07562$, $P < 0.04$). At 10-20 m inside the landscape, species richness in the recreational zone was slightly higher than in the non-recreational zone. At 0 to -10 m in the non-recreational zone, overall spillover effects were relatively strong, with mean species richness reaching 19.0, significantly higher than inside the landscape ($P < 0.04$). At 0-10 m inside the landscape, species richness was significantly higher than in the recreational zone.

Comparison results of corridor edge spillover effects showed that animal-dispersed and wind-dispersal species in traffic corridors also exhibited significantly different edge spillover effects from non-traffic corridors. Animal-dispersed species spillover effects were significantly weaker in traffic corridors than in non-traffic corridors, mainly reflected in external space at 0 to -10 m ($t = 4.72746$, $P < 0.03$). Although wind-dispersed species had large spillover in both corridor types with no significant difference detected ($P > 0.05$), wind-dispersed species in traffic corridors produced more significant edge effects than in non-traffic corridors, particularly in the external space of 0 to -10 m from the forest edge (i.e., near the road) ($t = -6.54654$, $P < 0.001$). At -20 to -30 m, wind-dispersed species spillover quantity gradually decreased with increasing distance from the landscape edge.

Inside the landscape at 0-10 m, both traffic and non-traffic corridors had similarly high wind-dispersed species richness, but traffic corridors showed more obvious spillover with mean richness reaching 10.4 at 10-50 m, significantly higher than non-traffic corridors ($P < 0.03$). Unassisted-dispersal species spillover effects were similarly weak in both traffic and non-traffic corridors with no significant difference ($t = 0.85202$, $P > 0.05$). No unassisted-dispersal species were recorded in 0 to -30 m of traffic corridors, while in non-traffic corridors, mean richness was only [value] at 0-10 m, with no significant difference compared to traffic corridors.

Although animal-dispersed and wind-dispersed species showed significantly different spillover effects between the two corridor types, tests of overall spillover effects found no significant difference between them ($t = 1.04876$, $P = 0.40434$). Overall spillover effects were obvious at 0 to -10 m on both sides of the landscape edge, gradually weakening with increasing distance from the edge. At 10 m inside the landscape, species richness was high in both corridor types with no significant difference ($t = -0.2116$, $P > 0.05$).

6. Discussion

Both recreational zones and traffic corridors produced edge spillover effects significantly different from non-recreational zones and non-traffic corridors. Tourism development and landscape changes caused by tourist activities may be the main reasons for these results, but the mechanisms differ.

In our experimental landscapes, spillover effects of animal-dispersed species in both recreational zones and traffic corridors were significantly weaker than in non-recreational zones and non-traffic corridors. Tourism development and tourist activities may have reduced ecological connectivity for some species, hindering seed dispersal by animal vectors [18]. Moreover, extensive artificial recreational facilities built in recreational zone open spaces may have increased landscape contrast, interfering with seed dispersal by small animals such as rodents that help transport large seeds. The directed dispersal hypothesis [19] suggests that animal dispersal vectors help seeds spread to suitable habitats, increasing seedling recruitment success [20-21]. However, in recreational zones, tourism development has led to severe degradation of external habitats at forest edges, such as soil hardening and bacterial proliferation, which may affect the spread of animal-dispersed species to these areas and reduce seedling survival rates.

Changes in landscape edge structure caused by tourism development may also affect species dispersal [22-23]. In our study area, although early human activities had already caused some landscape changes, tourism development in recent years has altered landscape structure more significantly, especially producing large amounts of high-contrast hard edge structures that may increase environmental and functional contrast and abruptness between forest edge interiors and exteriors [23-25], affecting penetration and diffusion of interior species to exteriors [24-25]. The rapid development of local tourism has made tourist activity disturbances increasingly frequent. Field observations found that certain birds with seed dispersal functions were obviously disturbed by tourists during feeding, severely affecting their feeding time and quantity, which may ultimately reduce seed dispersal opportunities in these areas [26]. Large numbers of vehicles entering may also affect animal feeding behavior. Francis et al. found that mechanical noise can significantly affect bird behavior, reducing their seed dispersal [27].

Unlike animal-dispersed species, wind-dispersed species showed strong spillover in both recreational and non-recreational zones, but stronger in recreational zones. The reason may be that tourism development changed forest edge structure, causing obvious changes in wind speed and direction, thereby facilitating small seed dispersal to open habitats [28]. Tourism development-created open habitats also provided more colonization space for exotic seeds, especially increasing invasion opportunities for wind-dispersed species [29]. Since wind-dispersed species seeds are usually very small, they are more likely to attach to tourists and vehicles than other large seeds, so tourist and vehicle entry may also be a reason for increased species in this group.

Wind-dispersed species in traffic corridors produced more significant edge effects than in non-traffic corridors, proving that landscape connectivity promotes wind-dispersed species movement [8]. This may be because increased vehicle numbers and wind speed at road edges facilitate movement and colonization of small seeds within this range. However, wind-dispersed species in traffic corridors at -30 m external space from forest edges (i.e., road edges) also showed obvious effects, possibly due to increased vehicle numbers and road edge wind speed promoting small seed movement and colonization.

Unassisted-dispersal species in this study refer to those with gravity-dispersed and ejection-dispersed modes that cannot achieve long-distance dispersal. Seeds of this group are usually large, lack obvious structures for animal or wind dispersal, and can only disperse within a few meters [9], which may be the fundamental reason for only small amounts of spillover in all experimental zones. This result is also consistent with Brudvig et al. [8]. However, a significant result is that unassisted-dispersal species richness inside recreational zone landscapes was significantly lower than in non-recreational zones at 0-10 m. The reason may be that these species have small individual numbers and are more likely to experience local extinction due to the vortex effect when disturbance factors are present [30]. Tourism development-caused landscape fragmentation can also produce isolation effects on animal pollinators. Most unassisted-dispersal species are animal-pollinated, and fragmentation reduces their pollen transmission, thereby affecting reproduction and renewal of some small local populations [31]. Reduced external pollen quantity due to landscape fragmentation may also increase the possibility of selfing depression in local populations [32], ultimately affecting population renewal [33]. In addition to isolation effects, tourist activities may also affect pollination efficiency of local populations by disturbing insect pollination behavior, leading to reproductive failure, but this inference requires further observation and study.

In this experiment, overall spillover effect is the combined result of animal-dispersed, wind-dispersed, and unassisted-dispersal species spillover. Although no significant difference in overall spillover effects was found between corridor types, the significant differences between animal-dispersed and wind-dispersed groups indicate that tourism development may affect some species even when overall spillover effects are not obviously impacted. This impact comes from different disturbance effects on different species movement ecologies and therefore cannot be reflected by overall diversity but must be identified from movement ecology.

7. Conclusion

This study used seed dispersal modes as classification criteria to investigate plant spillover effects of different dispersal methods in tourism landscapes, reflecting potential impacts of tourism development on plant movement ecology. The study shows that in tourism development practice, it is necessary to maintain landscape integrity and naturalness as much as possible, reduce edge structures, and prevent impacts of tourism activities on ecological processes such as species dispersal. For already fragmented landscapes, various technical and management measures should be used to increase connectivity between patches and permeability of edges to minimize constraints and negative impacts on spillover effects. Tourism development activities in nature reserves should be especially well managed to prevent fragmentation effects and excessive recreational disturbance on species dispersal processes, which is important for biodiversity conservation.

Since this study did not monitor seed rain and seed banks, it somewhat limits in-depth discussion of the relationship between spillover effects and seed dispersal processes in tourism landscapes. Future research should further focus on impacts of tourism development on seed rain and seed banks to provide more direct experimental evidence for tourism disturbance effects on plant dispersal.

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Note: Figure translations are in progress. See original paper for figures.