Dispersal potential mediates effects of local and landscape factors on plant species richness in *maeulsoop* forests of Korea

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Abstract

Questions: At what spatial scales do plant species with different dispersal potentials respond to landscape characteristics? Do seed rain data support these scale-dependent responses? Does the relative importance of local factors and surrounding landscape characteristics vary according to species dispersal potential?

Location: Agricultural landscape, Jinan County, Korea.

Methods: Forest plant species from 15 traditional Korean village forests, *maeulsoops,* were recorded and categorized into short-distance dispersal (SDD) and long-distance dispersal (LDD) species based on dispersal mode. Seed rain samples were collected every 2 wk for 4 mo and identified at the genus level. Local factors (anthropogenic influence and *maeulsoop* area) were assessed through field surveys and satellite imagery. Landscape characteristics surrounding *maeulsoops* (forest cover diversity, composition and fragmentation) were assessed at multiple spatial scales using Shannon-Wiener index and PCA. The best regression model at each scale was identified by model selection based on AICc, and the effect of each explanatory variable on species richness was quantified with hierarchical partitioning.

Results: A total of 107 forest plant species (39 SDD and 68 LDD) were recorded, and a total of 25 bird-dispersed genera were identified in seed rain samples. Species richness in plant records and genus richness in seed samples were strongly affected by anthropogenic influence and *maeulsoop* area, respectively. SDD species richness was significantly and positively influenced by total forest cover at small scales of around 150 m. In contrast, LDD species richness was significantly influenced by deciduous forest cover at large scales (1500–3500 m). At these larger scales, the relative importance of landscape characteristics for species richness was higher for LDD than for SDD. These results for LDD species were most notably supported by genus richness in seed rain data.

Conclusions: The most important findings of the study highlight that (1) plant species responses to forest cover are scale-dependent; and (2) dispersal potential mediates the effects of local and landscape factors on plant species richness. The results suggest that conservation strategies for native forest species in *maeulsoops* should not only focus on habitat-specific characteristics but also consider species-specific interactions with surrounding landscapes.

Introduction

Semi-natural woodlands are important in maintaining biodiversity in agricultural landscapes. Due to their potential roles as refuges or corridors for plants and animals, woodlands such as hedgerows, remnant forests and groves, which are threatened by landscape fragmentation, are receiving increasing attention in landscape ecology (Le Coeur et al. 2002; Marshall & Moonen 2002; De Sanctis et al. 2010; Gonzalez-Varo 2010; Wulf & Kolk 2014). In

contrast to the traditional conservation planning for these habitats, which focuses on the enhancement of local characteristics such as habitat quality and habitat area (Honnay et al. 1999; Petit et al. 2004), landscape ecologists emphasize the importance of plant species-specific interactions with landscape structures (De Blois et al. 2002; Simmering et al. 2006). Plant species are expected to show different responses to landscape fragmentation according to their dispersal potential (Verheyen et al. 2003; Roy & De Blois 2006; Aparicio et al. 2008). However, it is still unclear to what extent local and landscape characteristics differentially influence the distribution of plant species according to their dispersal potential, and at what spatial scales the relative influences of landscape effects are at maximum. At the same time, it would be worthwhile to compare the spatial scales at which maximum responses of species richness in the woodlands and in seed rains to landscape variables appear in agricultural landscape according to species dispersal potential. This comparison of spatial scales of response, at the two levels of dispersed seeds and established plants, gives us a better understanding of the underlying ecological process related to the mechanism of seed dispersal and establishment in woodlands. An increased knowledge regarding these ecological processes is essential for improving and guiding conservation strategies for these threatened semi-natural habitats.

In this study, we examined the effects of local and landscape characteristics on the richness of native forest plant species with different dispersal potentials and bird-dispersed genera in seed rain samples in Korean traditional village forests, *maeulsoops*. At least several 100 yr ago, *maeulsoops* were established mostly to complement village landscapes based on indigenous practices for protecting villages from floods and strong winds (Whang & Lee 2006; Lee et al. 2007; Koh et al. 2010). *Maeulsoops* have recently received considerable attention from a biological perspective as important woodland habitats for plants and animals in Korea's fragmented agricultural landscapes (Kim & Lim 2006; Park et al. 2006). In the past few decades, however, these habitats have been destroyed by agricultural expansions, road construction and regional demands for park space (Lee et al. 2007). The main conservation planning for the threatened *maeulsoops* has been similar to traditional conservation strategies, concentrating on enhancing habitat quality by reducing human disturbance, and on increasing habitat area by planting trees at the boundary of the habitat (Kang et al. 2004; Park et al. 2004; Kim & Lim 2006). Although these conservation strategies help to sustain the biodiversity of *maeulsoops*, they do not consider how landscape characteristics influence their biodiversity. This perspective is urgently needed because *maeulsoops* expand or connect mountain forests that play an important role in maintaining biodi-

versity in Korea (Price 2003; Cho et al. 2008; Kwon et al. 2008; Kang et al. 2012).

Understanding the different responses of species richness to local and landscape characteristics according to their different dispersal potentials is essential for increasing our knowledge about species distribution (Dupré & Ehrlén 2002; Deckers et al. 2004b; Kolb & Diekmann 2005; Vandewalle et al. 2010). Dispersal potential is associated with seed dispersal modes because diaspores with morphological adaptations for animal and wind dispersal, or containing food bodies for ant-mediated dispersal, often achieve longer-distance dispersal than diaspores lacking such adaptations (Willson 1993). The spatial pattern of seed dispersal determines species recruitment (Nathan & Muller-Landau 2000), colonization (Verheyen et al. 2003; Bossuyt et al. 2004; Roy & De Blois 2006), migration (Takahashi & Kamitani 2004) and thereby composition (Aparicio et al. 2008). These consequences of seed dispersal are modulated by local characteristics such as habitat area, human disturbance and landscape composition and connectivity (Petit et al. 2004; Honnay et al. 2005; Reitalu et al. 2012). However, few studies focus on the influences of those local and landscape factors on species composition according to their different dispersal potential (Deckers et al. 2004a; Kolb & Diekmann 2004). In addition, little attention has been paid to identifying the spatial scale at which the response of species richness to landscape characteristics is maximized according to their different dispersal potentials.

To assess the effects of local and landscape characteristics on the richness of plant species and seed genera with different dispersal potentials at multiple spatial scales, we classified species into two categories of dispersal ability (short- and long-distance dispersal) based on their dispersal mode, and used multi-scale analysis for detecting scale-dependent landscape characteristics. For the local habitat characteristics, which are independent of spatial scales, we focused on anthropogenic influence and *maeulsoop* area. For scale-dependent landscape characteristics, we focused on forest composition and diversity in landscapes surrounding *maeulsoops* at different spatial scales. In particular, we address three questions in this study: (1) at what spatial scales do plant species with different dispersal potentials respond to landscape characteristics; (2) do seed rain data support a scale-dependent response; and (3) does the relative importance of local factors and surrounding landscape characteristics vary according to species dispersal potential?

Methods

Study area

The study region was located in Jinan County, South Korea (Fig. 1a), which has a temperate monsoon climate
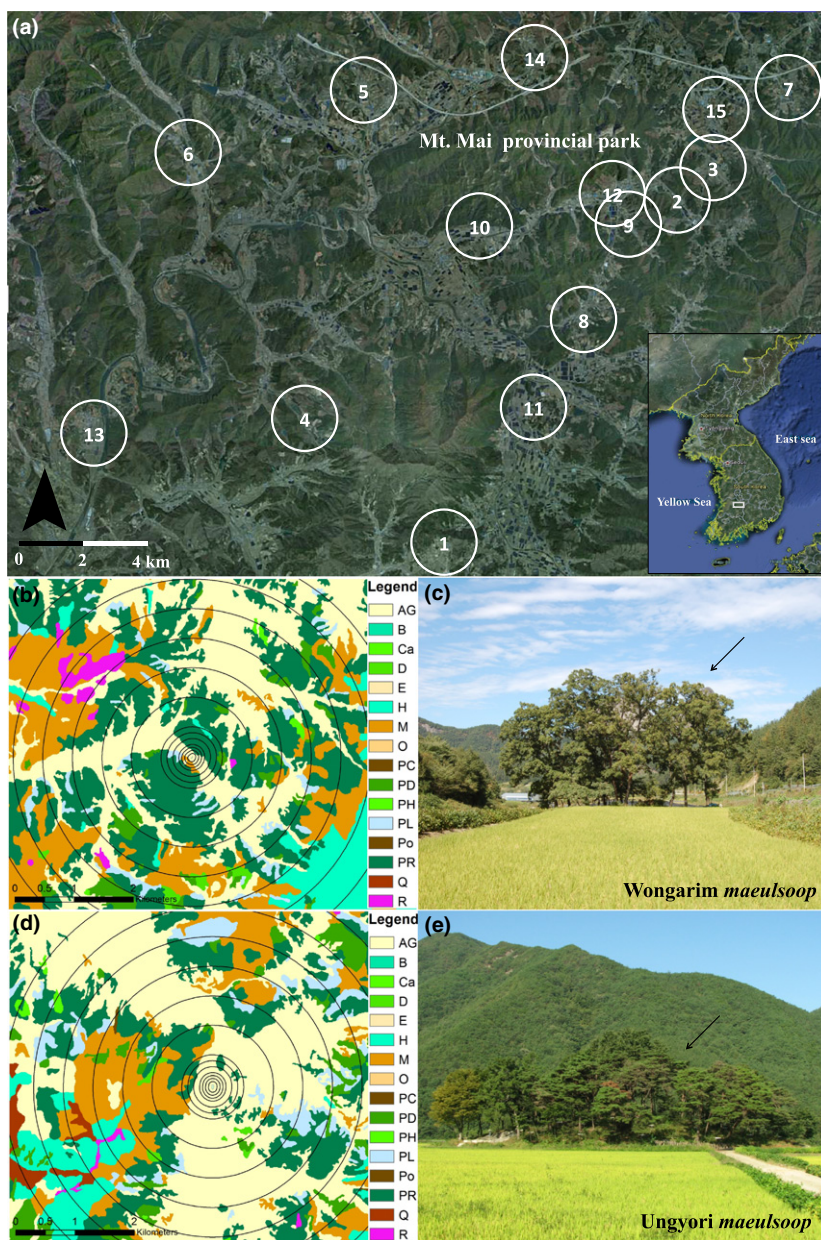
Fig. 1. Study region and study sites in Jinan-County, Korea: (**a**) Distribution of 15 individual study sites and their 1-km landscape sector on Google Earth satellite image accessed on 28 Jan 2006 (for detailed information of study sites refer to Appendix S1); (**b**) multiple landscape sectors for Wongarim *maeulsoop* (site 2 in **a**) overlayed on a forest cover type map (for detailed information on forest type refer to Appendix S2); (**c**) photograph of Wongarim *maeulsoop* adjacent forest mountain (captured by D. L. on 27 Sep 2008); (**d**) multiple landscape sectors for Ungyori *maeulsoop* (site 11 in a); (**e**) photograph of Ungyori *maeulsoop* isolated forest mountain (captured by I. K. on 19 Sep 2009).

with an annual rainfall range of 1300–1700 mm. The altitude of Jinan County is 200–400 m a.s.l. and the average annual temperature is about 11.8 °C (−1.8 °C in January and 26 °C in August). This landscape is dominated by forest (81.3%) and crop fields (10.5%). The dominant vegetation types are deciduous (*Quercus acutissima*, *Q. variabilis*, *Q. serrata*, *Q. dentata* and *Q. mongolica*), coniferous (*Pinus*

densiflora, *Pinus rigida*, *Larix kaempferi*) and mixed (Korea Forest Service 2008; Oh et al. 2010) forest. Approximately 80 *maeulsoop* forests still exist in the agricultural fields of Jinan County. We selected 15 *maeulsoops* that consisted of several dominant deciduous (*Zelkova seratta*, *Celtis sinensis* and *Carpinus tschonoskii*) and/or coniferous (*Pinus densiflora*) tree species. The selected *maeulsoops* covered all levels of

maeulsoop size and the range of surrounding landscape characteristics in the study areas. Therefore, the selected 15 *maeulsoops* ranged from an isolated, large, old tree to groves of ca. 0.6 ha in area, and they lie in landscapes representing a gradient from low (28%) to high (68%) proportions of mountain forest at 1-km radius.

Plant sampling

Vascular plants for the 15 selected *maeulsoops* were investigated in three sampling periods, August 2009, May 2009 and September 2010. In each period, we allocated the sampling time proportional to the area and heterogeneity of a given *maeulsoop* site. The average sampling time for a *maeulsoop* of medium size (0.2 ha) and heterogeneity was 3 h per sampling visit. At each sampling visit, we randomly walked through the *maeulsoop* patches, identifying all native forest plant species. Of the native species, annual and biannual herbs that usually live in non-forest areas were excluded from the sampling to focus on the dispersal from forest to *maeulsoops*. Additionally, in each *maeulsoop*, all trees and herbs that were planted and managed by villagers were excluded. The remaining recorded forest plant species in each *maeulsoop* were classified into short- and long-distance dispersal (SDD and LDD, respectively) species. Botanical literature and seed databases (Lee 2006; Liu et al. 2008; Lee et al. 2009) were used for determining the seed dispersal ability. Because of the small size and the relatively simple plant communities of *maeulsoop*, we are confident that our field survey included almost all native forest species in each *maeulsoop* during the sampling periods. We used the recorded species richness of SDD and LDD plants as dependent variables (hereafter, SDD_{rich} and LDD_{rich}) for further analyses.

Seed sampling

Using seed traps, we collected seed rain samples for end-ozoochorous (LDD) species. We did not collect data for SDD species (e.g. ballistic, barochorous and myrmecochorous) because their seeds are dispersed mostly near ground level and are, therefore, difficult to collect in seed traps. During 5 June–23 July and 31 August–27 October 2010, seeds of bird-dispersed genera were trapped in seed rain samples using fine mesh (<0.1 mm) on PVC pipe frames (70 × 70 cm, ca. 0.5 m^2) at around 80 cm from the ground (similar to Harvey's (2000) seed trap). A total of 159 seed traps were placed in the 15 selected *maeulsoops*. The number of seed traps in each *maeulsoop* was approximately determined by the size and length of the *maeulsoop* (0.63 ± 0.30 traps/100 m^2 *maeulsoop*). The surface area of traps in each *maeulsoop* covered a fairly small proportion, 0.31% ± 0.15%, of the *maeulsoop* area. During the sam-

pling period, seed rain samples were collected every 2 wk, resulting in a total of seven sampling events for the 14 wk in each *maeulsoop*. In the laboratory, seed trap contents were sieved to separate litter and insect excreta from the seeds. All seeds with a diameter >1 mm were collected and identified to genus level. Seeds were identified from pictures in *Seeds of wild plants of Korea* (Lee et al. 2009). We used the second-order Jacknife estimator (Xu et al. 2012) to estimate genus richness in seed rain samples in each *maeulsoop* (hereafter, $Seed_{rich}$). The estimate of LDD genus richness in seed rains (sample size: sampling time × the number of seed traps) was performed using the 'specpool' function of the R package 'vegan' (R Foundation for Statistical Computing, Vienna, AT).

Local variables

Assessment of the level of anthropogenic influence of *maeulsoops* ($Anth_{level}$) was based on five aspects: area–perimeter ratio of the *maeulsoop* patch for considering potential edge effects, paved road intensity, mowing frequency, soil disturbance frequency within 5 yr, and size and usage frequency of public facilities (e.g. pavilion and storage for villagers) in a *maeulsoop*. To assess these aspects, we used digitized maps, visited fields and asked village residents. Each category was evaluated on a three-level intensity score, from 0 (low), 1 (medium) and 2 (high intensity). Because we assumed that all aspects equally influenced the plant community in *maeulsoops*, we summed the scores of all five factors for each *maeulsoop*. Then we reclassified the summed scores for each *maeulsoop* on an anthropogenic influence scale ($Anth_{level}$) with three levels (low, medium and high): five *maeulsoops* with summed scores of 2–3 were categorized as low level ($Anth_{low}$), four *maeulsoops* with summed scores of 4–5) were categorized as medium level ($Anth_{medium}$) and six *maeulsoops* with summed scores of 6–7 were characterized as high ($Anth_{high}$; Appendix S1).

For each selected *maeulsoop*, the area of *maeulsoops* ($Patch_{size}$) was calculated by digitizing the boundary of *maeulsoops* on a captured Google Earth satellite image on 28 Jan 2006 (http://earth.google.com). Digitizing and geometric correction for *maeulsoop* patches were performed using Arc GIS 9.2 (ESRI, Redlands, CA, US). The mean (±SD) area of the $Patch_{size}$ was 0.22 ± 0.18 ha and the median was 0.13 ha.

Landscape variables

A digital forestry map (1:15 000 map, surveyed in 2009 by Korean Forest Research Institute; hereafter forest map) was employed to analyse landscape variables such as forest cover diversity and composition in landscape surrounding

maeulsoops. The forest map includes 16 forest cover types and the three non-forest types of agricultural land, graveyard and open water areas (Appendix S2). The dominant forest cover types in the study areas were *Pinus rigida* plantations, mixed forest and deciduous forest. We calculated the proportion of forest cover types within 13 different landscape buffer sectors (50, 100, 150, 200, 300, 400, 500, 1000, 1500, 2000, 2500, 3000 and 3500 m radius) surrounding *maeulsoops* (Fig. 1b, c). Using these proportions, we calculated the Shannon-Wiener Index ($H's = -\Sigma[p_i \times \log_{10}(p_i)]$, where p_i is the proportion of each forest cover) for forest cover diversity. Forest cover diversity in the surrounding landscape (F_{div}) increased with landscape buffer distance. Within the 150-m landscape buffer, the F_{div} values ranged from 0 to 0.45, but within the 3000 m landscape buffer, the values ranged from 0.55 to 0.80.

To represent forest composition and fragmentation, we reduced the dimension of landscape characteristics using PCA on the proportion of forest cover types and the proportion of agricultural areas at each landscape buffer sector. Prior to the PCA, we combined the 16 forest cover types into four forest covers (coniferous, deciduous, mixed and other; Appendix S2). The PCA was applied to five variables, which were the proportions (percentage data) of agricultural areas and of the four forest covers in the landscape surrounding *maeulsoops*; the five variables were not standardized prior to the PCA.

The first two principal component axes (PC1 and PC2) explaining between 75% and 99% of the variability were extracted ('rda' function in the R package 'vegan'). Within all the selected spatial scales, PC1 had a positive loading for most forest cover groups, which indicates *maeulsoop* sites within forest-rich landscapes, and a negative loading on agricultural area (Fig. 2a). Therefore, this PC1 value can also be interpreted as the intensity of forest fragmentation.

Within small spatial scales, positive PC2 values indicate *maeulsoop* sites within mixed forest-rich landscapes, while negative PC2 values indicate sites located in coniferous forest-rich landscapes (Fig. 2a). Within large spatial scales, highly positive PC2 values suggest that the landscape is dominated by deciduous rather than by mixed forest (Fig. 2b, c). Therefore, increasing PC2 values indicate that a landscape is occupied more by mixed or deciduous forest cover than by coniferous forest cover. Finally, PC1 and PC2 can be interpreted as the amount of total forest cover (or the intensity of forest fragmentation) and the ratio between mixed or deciduous forest and coniferous forest cover, respectively. Axes PC1 and PC2 were determined as landscape variables with the Shannon-Wiener diversity index of forest cover (F_{div}).

Statistical analyses

To evaluate the effects of local and landscape variables on SDD_{rich}, LDD_{rich} and $Seed_{rich}$, we applied model selection procedures and hierarchical partitioning analysis at each landscape buffer scale. To avoid problems of collinearity (Dormann et al. 2012), we first identified predictors showing high pair-wise correlation (Spearman rank correlation for pairs with $Anth_{level}$ $|\rho| > 0.7$ or Pearson's correlation for all other pairs, $|r| > 0.7$) and retained only the predictor with high predictive power in single predictor models. We conducted this screening for all possible pairs of predictors between local and landscape variables (Appendix S3). Across all spatial scales, there were no high correlations between $Anth_{level}$ and other local and landscape variables (i.e. $Patch_{size}$, F_{div}, PC1 and PC2; $|\rho| \leq 0.70$) and between $Patch_{size}$ and landscape variables (i.e. F_{div}, PC1 and PC2; $|r| \leq 0.56$). Therefore, we retained all local variables ($Anth_{level}$ and $Patch_{size}$). However, F_{div} values were highly correlated
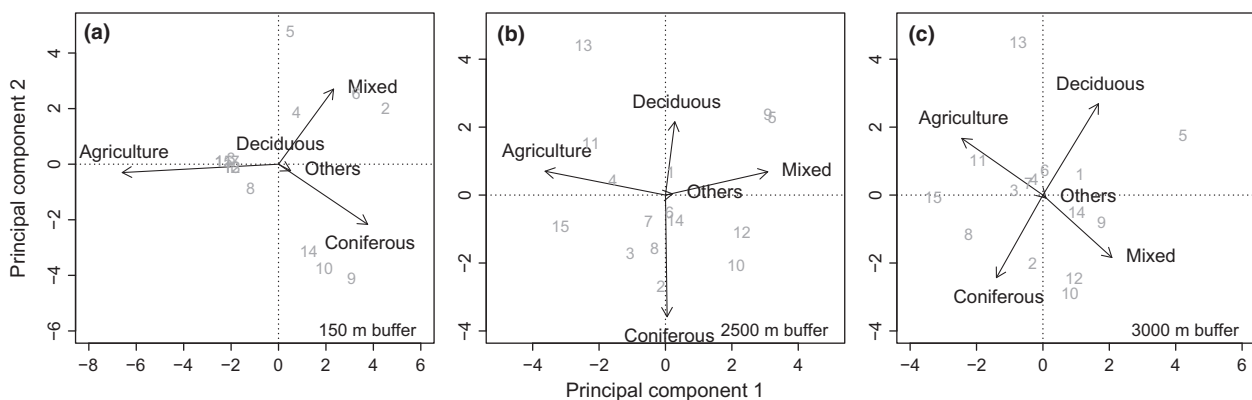
Fig. 2. First two principal components of a PCA ordination of landscape elements surrounding *maeulsoop* patches within a (**a**) 150-m buffer, (**b**) 2500-m buffer and (**c**) 3000-m buffer. Plot (**a**) is similar for all spatial scales between 50 m and 1500 m. Plot (**b**) is similar for the spatial scales of 2000 m and 2500 m. Plot (**c**) is similar for the spatial scales of 3000 m and 3500 m. Numbers in plots indicate the *maeulsoop* site number shown in Fig. 1a.

with PC1 at a small scale ($r = 0.75$ at 150 m) and with PC2 at large scales ($r = 0.79$ at 1000 m and $r = 0.71$ at 3500 m). This indicates that forest cover diversity (F_{div}) increases with total forest cover (PC1) at small scales and increases with mixed or deciduous forest cover (PC2) at large scales. Because of the high correlation between forest cover diversity and PC values, only PC1 and PC2 were selected as landscape variables for linear regression models.

We tested all possible model combinations of the screened predictors (i.e. $Anth_{level}$, $Patch_{size}$, PC1 and PC2), including an intercept only model for three different response variables (i.e. SDD_{rich}, LDD_{rich} and $Seed_{rich}$). We transformed some of the response and explanatory variables to meet the assumption of normally distributed residuals in multiple linear regression models. Specifically SDD_{rich} and LDD_{rich} were square-root-transformed, and $Patch_{size}$ was transformed by $\log(x + 1)$. For the model fitting with $Seed_{rich}$, we considered $\log$ (sampling times $\times$ number of seed traps) for each site as an offset to account for the differences in sampling effort between sites.

For each model combination, we calculated the adjusted AIC for a small sample size, AICc (Burnham & Anderson 2002). This value was used to calculate the AICc difference (ΔAICc) between the AICc of each model and the minimum AICc of the most highly ranked model. At each spatial scale, we present the models with ΔAICc <2 as being strongly supported by the collected data, and the significance of each variable by performing an analysis of covariance. We report significance values that are unadjusted for the selection of the most predictive spatial scale, as is customary in studies of this kind (Garcia & Chacoff 2007; Schmidt et al. 2008; Rusch et al. 2011; Koh et al. 2013). We note that selection of the most predictive scale is not a simple case of multiple testing. Rather, the choice of the most predictive scale can be viewed as a hierarchical parameter estimation problem, where the other model parameters are estimated conditional of the parameter representing the spatial scale. Instead of such an integrated hierarchical analysis that could be most readily implemented using a Bayesian approach, we performed the customary approach of a simple search over a grid of predetermined spatial scales, with separate models estimated at each spatial scale.

We present model weights, w, based on Δ(AICc) and relative likelihoods, which quantify the relative support of models given the data (Burnham & Anderson 2002). Based on AICc and model weight values, we selected the best model at each spatial scale for the three different response variables. AICc and model weight values were obtained using the R package 'MuMIn'. When $Anth_{level}$ had an overall significant influence on the response variable, we performed Tukey's HSD multiple comparison test to com-

pare mean values of all possible pairs of the three levels of $Anth_{level}$ using the R package 'multcomp' (Hothorn et al. 2008). If the best model had more than two predictors, we assessed the relative importance of the selected predictors using hierarchical partitioning (Mac Nally 2000) using the R package 'hier.part'. Lastly, spatial autocorrelation in the residuals of the regression models was tested with Moran's I using the R package 'spdep' (Dormann et al. 2007). All statistical analyses were performed using R version 2.14.0.

Results

Species and genus richness in plant records and seed samples

In the 15 *maeulsoops*, we recorded a total of 107 native forest plant species. Of these, 39 species were classified as SDD (Appendix S4) and 67 species were classified as LDD plant species (Appendix S5). The mean ($\pm$SD) number of SDD_{rich} and LDD_{rich} per *maeulsoop* was 5.1 ± 2.8 and 17.4 ± 9.1, respectively.

We collected a total of 2675 seeds in 25 genera, mainly dispersed by birds. *Morus* ($n = 960$, 35.8%) was the most abundant genus, followed by *Rubus* ($n = 668$, 25.0%), *Aralia* ($n = 340$, 12.7%) and *Prunus* ($n = 166$, 6.2%). For eight genera the number of collected seeds ranged between ten and 100, and for 12 genera the number of collected seeds was below ten (Appendix S6). Based on these seed rain samples, we estimated 13.6 ± 5.8 as the richness of seeds at the genus level ($Seed_{rich}$) for the sites (Appendix S7).

Model comparison at different landscape scales

The four retained local and landscape predictors ($Anth_{level}$, $Patch_{size}$, PC1 and PC2) were used to compare all possible regression model combinations (i.e. 16 linear models including the intercept only model) for predicting SDD_{rich}, LDD_{rich} and $Seed_{rich}$. For SDD_{rich} and LDD_{rich}, $Anth_{level}$ was the only predictor that was selected in the best models at all spatial scales (Fig. 3a). At small spatial scales around 150 m, the $Anth_{level}$ + PC1 model was the best model for predicting SDD species richness ($Anth_{level}$: $F_{2,11} = 19.75$, $P < 0.001$ and PC1: $F_{1,11} = 5.69$, $P = 0.036$; note that these P-values are unadjusted for the selection of the most predictive spatial scale; see section on Statistical analyses for more information). In particular, the coefficients of PC1 in the models at 150 and 200 m were significant, and the highest adjusted r^2 appeared at 150 m. For LDD species richness, the $Anth_{level}$ + PC2 model was the best model at large spatial scales between 500 and 3500 m (Fig. 3a). The coefficient of PC2 in this model was significant at 1500–3500 m. The highest adjusted r^2 of the $Anth_{level}$ + PC2 model was found at the 3000 m scale ($Anth_{level}$: $F_{2,11} = 31.46$, $P < 0.001$ and PC2: $F_{1,11} = 26.02$,

P =0.0003). For both SDD and LDD plant species richness, Tukey's HSD multiple comparison test for mean values of three levels of $Anth_{level}$ showed significant differences between high and low ($P < 0.001$) as well as high and medium levels ($P < 0.001$), but there was no difference between low and medium levels ($P = 0.80$ for SDD_{rich}, $P = 0.78$ for LDD_{rich}; Fig. 3b, c).

In contrast to the best models of SDD_{rich} and LDD_{rich}, $Anth_{level}$ was not selected in the best models of $Seed_{rich}$ for any spatial scales. Instead, only $Patch_{size}$ was selected in the best models of $Seed_{rich}$ at all spatial scales. The $Patch_{size}$ + PC1 model was selected as the best model for predicting $Seed_{rich}$ at 150, 200, 500 and between 1500 and 3000 m (Fig. 3a). The adjusted r^2 of the $Patch_{size}$ + PC1 model was highest at 2500 m ($Patch_{size}$: $P = 0.007$ and PC1:

$P = 0.043$), and the coefficient of PC1 was only significant at the 2500 m spatial scale (Fig. 3d, Table 1). Interestingly, however, two different peaks appeared at relatively small scales, 100 and 500 m, respectively. There was no significant spatial autocorrelation in the residuals of the selected best models of all spatial scales for SDD_{rich} (Moran's I = –0.005, $P = 0.06$), LDD_{rich} (Moran's I = –0.071, $P = 0.50$) and $Seed_{rich}$ (Morn's I = –0.059, $P = 0.11$).

Hierarchical partitioning

The hierarchical partitioning analysis revealed the relative importance of local and landscape variables in the selected best models (Table 1). Local variables ($Anth_{level}$ and $Patch_{size}$) showed an overall higher importance than
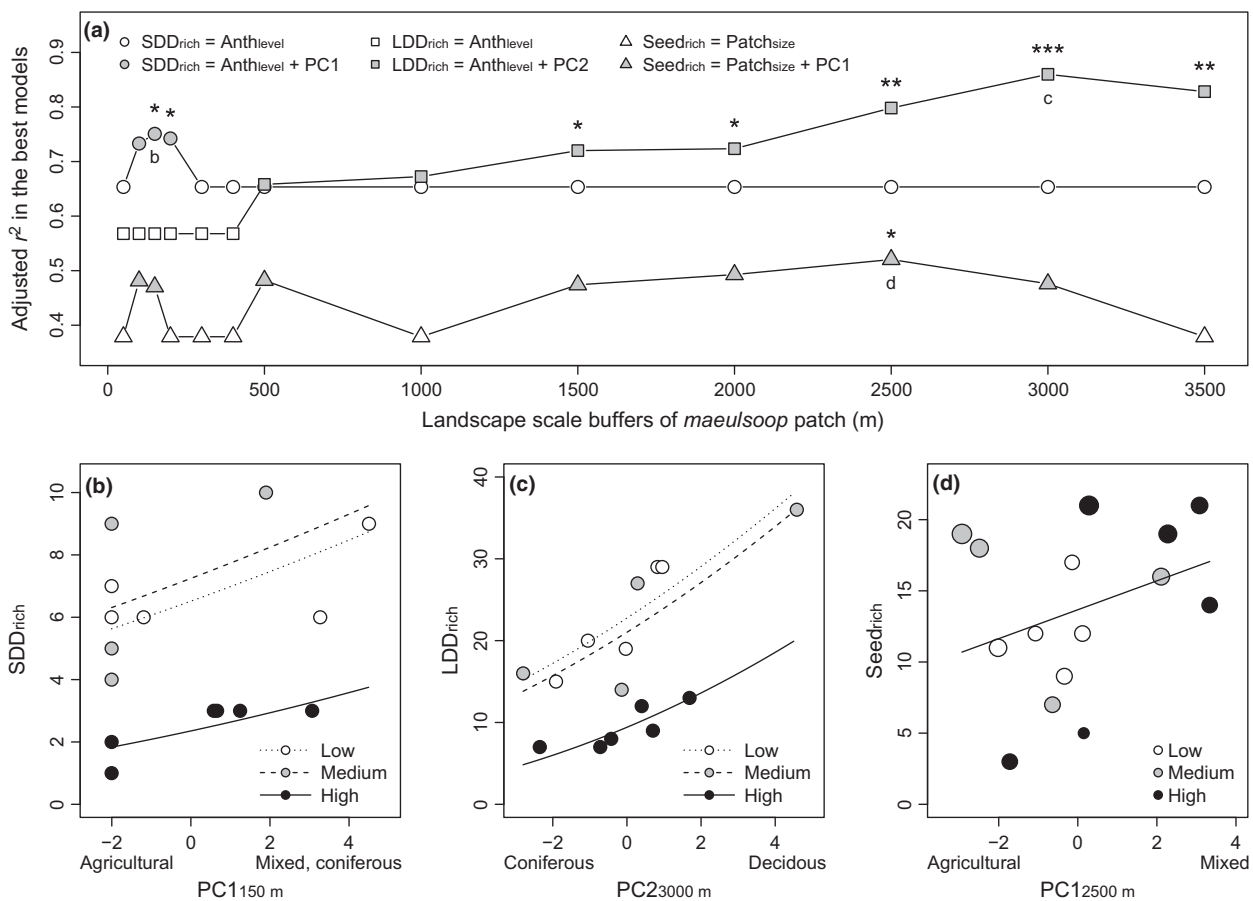
Fig. 3. Scale-dependent responses of species richness of SDD plants (SDD_{rich}), LDD plants (LDD_{rich}) and genus richness in seed rain samples ($Seed_{rich}$) to local and landscape characteristics. (**a**) Adjusted r^2 of the best models at different spatial scales; (**b**) the relationship between PC1 and SDD_{rich} in the best model at 150 m; (**c**) the relationship between PC2 and LDD_{rich} in the best model at 3000 m; (**d**) the relationship between PC1 and seed genus richness in the best model at 2500 m. In plot (**a**), the selected best model of each species or genus richness is presented as a function of local (anthropogenic influence level [$Anth_{level}$] and *maeulsoop* [$Patch_{size}$] area and landscape variables (PC1 and PC2). Stars indicate the unadjusted significance level of landscape variables in the selected models: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. Small letters, b, c and d, indicate the highest adjusted r^2 for SDD species richness, LDD species richness and genus richness in seed samples, respectively. In plots (**b**–**d**), classes low, medium and high indicate the levels of anthropogenic influence. In plots (**b**) and (**c**), model predictions were back-transformed (using code from Martin et al. 2013). In plot (**d**), point size is proportional to $Patch_{size}$; only one line is shown as $Anth_{level}$ is not included in the model.

Table 1. Summary of model selection statistics for evaluating short-distance dispersal species richness (SDD$_{species}$), long-distance dispersal species richness (LDD$_{species}$) and estimated genus richness in seed rain samples (Seed$_{genus}$) using anthropogenic influence (Anth$_{level}$), patch area of *maeulsoop* (Patch$_{size}$), PC1 and PC2. At the selected landscape scales, the regression models showed the best fits (model with minimum AICc value) for each response variable.

Response	Scale (m)	Model	−Log-lik	AICc	ΔAICc	w_i	Adj. r^2	Hierarchical Partitioning
SDD$_{species}$	150	(Anth$_{level}$)*** + PC1*	1.61	19.89	0.00	0.69	0.75	Anth$_{level}$ = 88%, PC1 = 12%
		(Anth$_{level}$)***	4.74	21.47	1.58	0.31	0.65	
LDD$_{species}$	3000	(Anth$_{level}$)*** + PC2***	5.29	27.30	0.00	1.00	0.86	Anth$_{level}$ = 67%, PC2 = 33%
Seed$_{genus}$	2500	Patch$_{size}$** + PC1*	40.42	92.84	0.00	0.68	0.52	Patch$_{size}$ = 70%, PC1 = 30%
		Patch$_{size}$*	43.10	94.36	1.52	0.32	0.38	

The first model listed for each response variable represents the minimum AICc model. Only models with a ΔAICc of 2 or less at the spatial scale of the minimum AICc model are included as competing models. Log-link and Adj. r^2 indicate log-likelihood and adjusted r^2, respectively. Variables in parentheses indicate a negative relationship. Stars indicate significance levels unadjusted for the selection of the most predictive spatial scale (*$P < 0.05$, **$P < 0.01$ and ***$P < 0.001$).

landscape variables (PC1 and PC2) in the selected best models of SDD$_{rich}$, LDD$_{rich}$ and Seed$_{rich}$. However, the relative importance of local variables was reduced in the best models of LDD$_{rich}$, and Seed$_{rich}$, compared to the best model of SDD$_{rich}$. The relative importance of landscape variables was approximately three times higher in the best model of LDD$_{rich}$ and Seed$_{rich}$ than in the best model of SDD species richness.

Discussion

The present study shows a scale-dependent response of the species richness of SDD and LDD and genus richness in seed rain samples to local and landscape variables. Although these species richness values were highly influenced by local factors such as anthropogenic influence and patch size, the results indicate that species richness responded to landscape structures at different spatial scales according to their dispersal potential. SDD species richness was significantly affected by the amount of forest cover within a small-scale landscape sector. However, LDD species richness was significantly affected by the amount of deciduous forest cover within a large-scale landscape sector. Our most important finding was that the large spatial scale at which LDD species richness responded to landscape characteristics was supported by the genus richness in seed rain sample data, which responded to forest cover at similar spatial scales. The landscape variables were more important for LDD species richness and genus richness in seed rain samples than for SDD species richness.

For *maeulsoop* forests, the intensity of anthropogenic influence was a major determinant of plant species richness, and patch size was a major determinant of genus richness in seed rain samples. The high intensity of human impact led to loss of SDD and LDD species richness. Several factors might contribute to this. For example, high frequencies of soil disturbance, paved vehicle roads penetrating forests, narrow forest patch shapes and human use

of facilities are likely to result in worse *maeulsoop* soil conditions (Kang et al. 2004). Therefore, these anthropogenic influences were likely to interrupt re-colonization of plant species and seed recruitment in *maeulsoops* but not to affect genus richness in seed rain samples. This hypothesis is supported by the fact that anthropogenic influence was not selected as a factor in the best model predicting the seed rain genus richness in our study (Table 1). For the genus richness in seed rain samples, patch size, instead of anthropogenic influence, was maintained in the selected best model. Patch size seems to be related to the amount of forage resources and, consequently, it may also be related to the abundance of frugivorous birds influencing the amount of seed dispersal (Garcia & Ortiz-Pulido 2004).

Interestingly, we found no difference in plant species richness of SDD and LDD between low and medium levels of anthropogenic influence. One reason could be that the chosen class limits do not correspond to differences in disturbance levels as perceived by the plant communities. For example, the road intensity around a *maeulsoop*, one of the five factors assessing anthropogenic influence in this study, did not differ strongly between the low (no adjacent road) and medium (an adjacent road) levels compared to the high level (a road penetrating a *maeulsoop*). However, we assumed that all five factors contributed equally to anthropogenic influence levels and did not examine the relative importance of different factors of anthropogenic influence. Alternatively, the two classes could be too broad and encompass different parts of a hump-shaped relationship between diversity and disturbance corresponding with the Intermediate Disturbance Hypothesis (IDH; Connell 1978). This could be further investigated using a continuous index or proxy of anthropogenic disturbance for *maeulsoops*. Therefore, further studies with a focus on estimating the relative influence of different factors of anthropogenic influence or testing the IDH on *maeulsoops* by developing a

quantitative disturbance variable integrating several important factors are warranted. This would allow for development of more targeted conservation strategies for *maeulsoops*.

Our study revealed that the optimal spatial scales for SDD and LDD plant species richness and genus richness in seed rain samples corresponded to their potential dispersal distances. Additionally, the spatial scales of surrounding landscape characteristics for SDD (150 m) and LDD (3000 m) species and seed rain (2500 m) were within reasonable spatial ranges. Jackson & Fahrig (2012) showed that species responded to a spatial extent of the landscape that was four to nine times their median dispersal distance. Therefore, when we applied this estimate to the median seed dispersal distance of species with SDD modes (ca. 20 m) and LDD modes (ca. 400 m) reported by Vittoz & Engler (2007), the expected spatial extent ranges were 80–180 m for SDD species and 1600–3600 m for LDD species. The distance around 100 m is often defined as a dispersal distance for SDD species (Nathan & Muller-Landau 2000; Jordano et al. 2007). The spatial scale revealed as relevant for SDD species in our study is also in line with another study of hedgerows adjacent to forests, showing that the richness of herbaceous forest plant species increased when forest cover increased within a 100-m distance from the forest edges (Wehling & Diekmann 2009). Furthermore, the significant response of LDD species richness to large-scale landscapes is supported by Pejchar et al. (2008), who showed a correlation between the abundance of seed rain by birds and a 'wetness index' reflecting soil and canopy moisture increased with spatial scale. However, they did not indicate the optimal spatial landscape scale. This best spatial scale for LDD species richness is remarkably supported by the seed rain data where genus richness responded to landscape structure at similar spatial scales (Fig. 2). The other two peaks that appeared at small landscape scales (100 and 500 m) for genus richness in seed rain samples might be a result of the seeds being dispersed by relatively small birds foraging in the *maeulsoop* patches (Park et al. 2006). From fecal samples collected on the installed seed traps in our *maeulsoop* sites, Joo & Park (2012) identified seven bird species including a small-sized bird (e.g. *Passer montanus*) and a medium-sized bird (e.g. *Cyanopica cyanus*) that were potential dispersers of seeds. According to the seed dispersal study of *Prunus mahaleb* (Jordano et al. 2007), short-distance-dispersed seeds (<250 m) were mostly transported via small-sized birds, while long-distance-dispersed seeds (>1500 m) were mediated mostly through medium-sized birds and mammals. Another study also demonstrated that body size could be an important factor for determining the spatial scales of surrounding landscapes at which organisms such as insects moved (Holland et al. 2005).

Our findings not only show that species respond differently to surrounding landscapes at particular spatial scales related to their dispersal potential, but also indicate that species respond differently to forest fragmentation and forest diversity according to their dispersal potential. The response of SDD species to the amount of forest cover at relatively small-scale landscapes means that they are more vulnerable to adjacent forest fragmentation than that of LDD species (Fig 2a, b). This finding is in line with the study of Montoya et al. (2008), who reported that animal-dispersed tree species were less vulnerable to forest loss than wind-dispersed species because plant–animal interactions alleviated the effect of forest destruction on the collapse of forest plant communities. The response of LDD species and genus richness in seed samples to the amount of deciduous and mixed forest covers may be evidence that these forests are the seed source areas of LDD species. Because deciduous and mixed forest covers were highly correlated with forest diversity (Appendix S3), *maeulsoops* may play a role in maintaining plant species diversity in fragmented agricultural landscapes. Furthermore, even *maeulsoops* that are represented by just one isolated, large old tree may facilitate seed dispersal in fragmented agricultural landscapes, as indicated by Herrera & Garcia (2009). From this perspective, the connectivity between isolated *maeulsoops* and scattered deciduous and mixed forest covers is recommended as a topic for further studies (Harvey 2000). Graph-theoretical connectivity models incorporating seed-dispersing animal behaviour may be one possible approach for investigating the potential role of *maeulsoops* as stepping-stones for seed dispersal (Minor & Gardner 2011).

The hierarchical partitioning analysis for the species richness of SDD and LDD, and the genus richness in seed rain samples identified the relative importance of local and landscape variables and highlighted that the relative importance varied with species dispersal potential. The relative importance of local and landscape variables for LDD and species collected in seed rain samples (ca. 70% and 30%, respectively) partially coincides with the result obtained in agricultural landscapes of Germany. Kolb & Diekmann (2004) showed that the independent relative importance of habitat quality (topography, water content and soil nutrients) and landscape structure (habitat area, isolation and continuity) on predicting forest plant species was approximately 70% and 30%, respectively. However, our findings emphasized that landscape structure was relatively more important for LDD than for SDD species. This result can be attributed to the interaction between landscape and seed dispersal mediating animal behaviour (Levey et al. 2005). The different sensitivities according to dispersal potential is also consistent with the studies of Metzger (2000) and Jesus et al. (2012), which have shown that zoochorous species react more sensitively to landscape

structure such as forest fragmentation than barochorous species. Deckers et al. (2004b) also demonstrated that zoochorous species were more largely influenced by hedgerow structure and landscape fragmentation than anemochorous species. Therefore, our findings suggest that *maeulsoop* conservation should focus on landscape aspects concerning different species dispersal potentials as well as on disturbance aspects to enhance plant species richness. For *maeulsoops* adjacent to forest patches, a strategy towards keeping this proximity is needed because *maeulsoops* can provide refuges for SDD plant species based on the relevant spatial scale, ca. 150 m. For isolated *maeulsoops*, we may need to focus on determining *maeulsoop* conservation priorities based on their location associated with forest fragmentation and connectivity in Korean agricultural landscapes based on the spatial scale revealed as relevant for LDD species, around 2500 m.

Conclusions

Our results not only show that anthropogenic influence and patch size were the most important factors in determining plant species richness of *maeulsoops,* but also highlighted surrounding landscape structures as relevant factors. Most importantly, our study demonstrated that different response scales of species richness to landscape factors followed their dispersal potential. This suggests that SDD species were vulnerable to adjacent forest fragmentation, but LDD species survived in isolated forest patches within certain large-scale ranges. Along with revealing relevant spatial scales for species richness according to their dispersal potential, this study emphasizes that dispersal potential mediates the effects of local and landscape factors on species richness. The relative importance of landscape characteristics for the species richness of LDD plants and genus richness of dispersed seeds was higher than that for SDD species richness. Therefore, we suggest that decisions about *maeulsoop* management need to focus on landscape factors as well as local factors.

Acknowledgements

References

Aparicio, A., Albaladejo, R.G., Olalla-Tarraga, M.A., Carrillo, L.F. & Rodriguez, M.A. 2008. Dispersal potentials determine responses of woody plant species richness to environmental factors in fragmented Mediterranean landscapes. *Forest Ecology and Management* 255: 2894–2906.

Bossuyt, B., Honnay, O. & Hermy, M. 2004. Scale-dependent frequency distributions of plant species in dune slacks: dispersal and niche limitation. *Journal of Vegetation Science* 15: 323–330.

Burnham, K.P. & Anderson, D.R. 2002. *Model selection and multimodel inference: a practical information-theoretic approach.* Springer, New York, NY, US.

Cho, K.H., Hong, S.K. & Cho, D.S. 2008. Ecological role of mountain ridges in and around Gwangneung royal tomb forest in central Korea. *Journal of Plant Biology* 51: 387–394.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs – high diversity of trees and corals is maintained only in a non-equilibrium state. *Science* 199: 1302–1310.

De Blois, S., Domon, G. & Bouchard, A. 2002. Landscape issues in plant ecology. *Ecography* 25: 244–256.

De Sanctis, M., Alfò, M., Attorre, F., Francesconi, F. & Bruno, F. 2010. Effects of habitat configuration and quality on species richness and distribution in fragmented forest patches near Rome. *Journal of Vegetation Science* 21: 55–65.

Deckers, B., Hermy, M. & Muys, B. 2004a. Factors affecting plant species composition of hedgerows: relative importance and hierarchy. *Acta Oecologica-International Journal of Ecology* 26: 23–37.

Deckers, B., Verheyen, K., Hermy, M. & Muys, B. 2004b. Differential environmental response of plant functional types in hedgerow habitats. *Basic and Applied Ecology* 5: 551–566.

Dormann, C.F., McPherson, J.M., Araujo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., (...) & Wilson, R. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30: 609–628.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., (...) & Lautenbach, S. 2012. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 35: 1–20.

Dupré, C. & Ehrlén, J. 2002. Habitat configuration, species traits and plant distributions. *Journal of Ecology* 90: 796–805.

Garcia, D. & Chacoff, N.P. 2007. Scale-dependent effects of habitat fragmentation on hawthorn pollination, frugivory, and seed predation. *Conservation Biology* 21: 400–411.

Garcia, D. & Ortiz-Pulido, R. 2004. Patterns of resource tracking by avian frugivores at multiple spatial scales: two case studies on discordance among scales. *Ecography* 27: 187–196.

Gonzalez-Varo, J.P. 2010. Fragmentation, habitat composition and the dispersal/predation balance in interactions between the Mediterranean myrtle and avian frugivores. *Ecography* 33: 185–197.

Harvey, C.A. 2000. Windbreaks enhance seed dispersal into agricultural landscapes in Monteverde, Costa Rica. *Ecological Applications* 10: 155–173.

Herrera, J.M. & Garcia, D. 2009. The role of remnant trees in seed dispersal through the matrix: being alone is not always so sad. *Biological Conservation* 142: 149–158.

Holland, J.D., Fahrig, L. & Cappuccino, N. 2005. Body size affects the spatial scale of habitat–beetle interactions. *Oikos* 110: 101–108.

Honnay, O., Hermy, M. & Coppin, P. 1999. Impact of habitat quality on forest plant species colonization. *Forest Ecology and Management* 115: 157–170.

Honnay, O., Jacquemyn, H., Bossuyt, B. & Hermy, M. 2005. Forest fragmentation effects on patch occupancy and population viability of herbaceous plant species. *New Phytologist* 166: 723–736.

Hothorn, T., Bretz, F., Westfall, P. & Heiberger, R.M. 2008. multcomp: simultaneous inference for general linear hypotheses. R package version, 1.2-19. http://CRAN.R-project.org/package=multcomp.

Jackson, H.B. & Fahrig, L. 2012. What size is a biologically relevant landscape? *Landscape Ecology* 27: 929–941.

Jesus, F.M., Pivello, V.R., Meirelles, S.T., Franco, G.A.D.C. & Metzger, J.P. 2012. The importance of landscape structure for seed dispersal in rain forest fragments. *Journal of Vegetation Science* 23: 1126–1136.

Joo, S. & Park, S. 2012. Identification of bird species and their prey using DNA barcode on feces from Korean traditional village groves and forests (*maeulsoop*). *Animal Cells and Systems* 16: 488–497.

Jordano, P., Garcia, C., Godoy, J.A. & Garcia-Castano, J.L. 2007. Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences of United States of America* 104: 3278–3282.

Kang, H.-K., Bang, K.-J., Lee, S.-J. & Kim, H.-B. 2004. Management guidelines of village groves through an analysis of growth environments. *Journal of Korean Institute of Traditional Landscape Architecture* 22: 63–74.

Kang, W., Koh, I., Park, C.-R. & Lee, D. 2012. An analysis of changes in forest fragmentation and morphology in surrounding landscapes of *maeulsoops* and Jinan-gun. *Korean Journal of Environment and Ecology* 26: 941–951.

Kim, J.-W. & Lim, J.-C. 2006. A phytosociological review of the forests (*maeulsoop*). *Keimyung Korean Studies Journal* 33: 81–114 [in Korean.].

Koh, I., Kim, S. & Lee, D. 2010. Effects of *bibosoop* plantation on wind speed, humidity, and evaporation in a traditional agricultural landscape of Korea: field measurements and modeling. *Agriculture, Ecosystems & Environment* 135: 294–303.

Koh, I., Rowe, H.I. & Holland, J.D. 2013. Graph and circuit theory connectivity models of conservation biological control agents. *Ecological Applications* 23: 1554–1573.

Kolb, A. & Diekmann, M. 2004. Effects of environment, habitat configuration and forest continuity on the distribution of forest plant species. *Journal of Vegetation Science* 15: 199–208.

Kolb, A. & Diekmann, M. 2005. Effects of life-history traits on responses of plant species to forest fragmentation. *Conservation Biology* 19: 929–938.

Korea Forest Service. 2008. The 4th Forest Type Map.

Kwon, J.-O., Oh, J.-H., Lee, J.-Y., Park, C.-R. & Choi, M.-S. 2008. Locations and topographical character of the *maeulsoop* in the southwestern and the eastern region. *Journal of the Korean Association of Geographic Information Studies* 11: 85–93 [in Korean.].

Le Coeur, D., Baudry, J., Burel, F. & Thenail, C. 2002. Why and how we should study field boundary biodiversity in an agrarian landscape context. *Agriculture, Ecosystems & Environment* 89: 23–40.

Lee, C.-B. 2006. *Coloured flora of Korea*. Hyangmunsa, Seoul, KR.

Lee, D., Koh, I. & Park, C.-Y. 2007. *Ecosystem services of traditional village groves in Korea*. Seoul National University, Seoul, KR.

Lee, J., Kim, J.-H., Lee, S.M., Park, S.-H., Ali, M.A., Kim, J., Lee, C. & Kim, G. 2009. *Seeds of wild plants of Korea*. The Wild Plant Seed Bank of Korea, Seoul, KR.

Levey, D.J., Bolker, B.M., Tewksbury, J.J., Sargent, S. & Haddad, N.M. 2005. Effects of landscape corridors on seed dispersal by birds. *Science* 309: 146–148.

Liu, K., Eastwood, R.J., Flynn, S., Turner, R.M. & Stuppy, W.H. 2008. Seed information database (release 7.1, May 2008) In: http://www.kew.org/data/sid.

Mac Nally, R. 2000. Regression and model-building in conservation biology, biogeography and ecology: the distinction between and reconciliation of 'predictive' and 'explanatory' models. *Biodiversity and Conservation* 9: 655–671.

Marshall, E.J.R. & Moonen, A.C. 2002. Field margins in northern Europe: their functions and interactions with agriculture. *Agriculture, Ecosystems & Environment* 89: 5–21.

Martin, E.A., Reineking, B., Seo, B. & Steffan-Dewenter, I. 2013. Natural enemy interactions constrain pest control in complex agricultural landscapes. *Proceedings of the National Academy of Sciences of the United States of America* 110: 5534–5539.

Metzger, J.P. 2000. Tree functional group richness and landscape structure in a Brazilian tropical fragmented landscape. *Ecological Applications* 10: 1147–1161.

Minor, E.S. & Gardner, R.H. 2011. Landscape connectivity and seed dispersal characteristics inform the best management strategy for exotic plants. *Ecological Applications* 21: 739–749.

Montoya, D., Zavala, M.A., Rodriguez, M.A. & Purves, D.W. 2008. Animal versus wind dispersal and the robustness of tree species to deforestation. *Science* 320: 1502–1504.

Nathan, R. & Muller-Landau, H.C. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution* 15: 278–285.

Oh, H.K., Han, Y.H., Park, K.U., Beon, M.S. & Kang, B.S. 2010. Study on the vegetation of Seongjubong, Jinan. *Journal of Agriculture & Life Sciences* 41: 56–68.

Park, J.-C., Kim, B.-S., Yun, S.-H. & Park, S.-M. 2004. A study on the restoration of Neunggil village forests in Jinan. *Journal of Korean Society of Rural Planning* 10: 27–32.

Park, C.-R., Shin, J.-H. & Lee, D. 2006. Bibosoop: a unique Korean bibotope for cavity nesting birds. *Journal of Ecology and Field Biology* 29: 75–84.

Pejchar, L., Pringle, R.M., Ranganathan, J., Zook, J.R., Duran, G., Oviedo, F. & Daily, G.C. 2008. Birds as agents of seed dispersal in a human-dominated landscape in southern Costa Rica. *Biological Conservation* 141: 536–544.

Petit, S., Griffiths, L., Smart, S.S., Smith, G.M., Stuart, R.C. & Wright, S.M. 2004. Effects of area and isolation of woodland patches on herbaceous plant species richness across Great Britain. *Landscape Ecology* 19: 463–471.

Price, M.F. 2003. Why mountain forests are important. *Forestry Chronicle* 79: 219–222.

Reitalu, T., Purschke, O., Johansson, L.J., Hall, K., Sykes, M.T. & Prentice, H.C. 2012. Responses of grassland species richness to local and landscape factors depend on spatial scale and habitat specialization. *Journal of Vegetation Science* 23: 41–51.

Roy, V. & De Blois, S. 2006. Using functional traits to assess the role of hedgerow corridors as environmental filters for forest herbs. *Biological Conservation* 130: 592–603.

Rusch, A., Valantin-Morison, M., Sarthou, J.-P. & Roger-Estrade, J. 2011. Multi-scale effects of landscape complexity and crop management on pollen beetle parasitism rate. *Landscape Ecology* 26: 473–486.

Schmidt, M.H., Thies, C., Nentwig, W. & Tscharntke, T. 2008. Contrasting responses of arable spiders to the landscape matrix at different spatial scales. *Journal of Biogeography* 35: 157–166.

Simmering, D., Waldhardt, R. & Otte, A. 2006. Quantifying determinants contributing to plant species richness in mosaic landscapes: a single- and multi-patch perspective. *Landscape Ecology* 21: 1233–1251.

Takahashi, K. & Kamitani, T. 2004. Effect of dispersal capacity on forest plant migration at a landscape scale. *Journal of Ecology* 92: 778–785.

Vandewalle, M., de Bello, F., Berg, M.P., Bolger, T., Doledec, S., Dubs, F., Feld, C.K., Harrington, R., Harrison, P.A., (…) & Woodcock, B.A. 2010. Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. *Biodiversity and Conservation* 19: 2921–2947.

Verheyen, K., Honnay, O., Motzkin, G., Hermy, M. & Foster, D.R. 2003. Response of forest plant species to land-use change: a life-history trait-based approach. *Journal of Ecology* 91: 563–577.

Vittoz, P. & Engler, R. 2007. Seed dispersal distances: a typology based on dispersal modes and plant traits. *Botanica Helvetica* 117: 109–124.

Wehling, S. & Diekmann, M. 2009. Importance of hedgerows as habitat corridors for forest plants in agricultural landscapes. *Biological Conservation* 142: 2522–2530.

Whang, B. & Lee, M. 2006. Landscape ecology planning principles in Korean Feng-Shui, Bi-bo woodlands and ponds. *Landscape and Ecological Engineering* 2: 147–162.

Willson, M.F. 1993. Dispersal mode, seed shadows, and colonization patterns. *Vegetation*, 108: 261–280.

Wulf, M. & Kolk, J. 2014. Plant species richness of very small forests related to patch configuration, quality, heterogeneity and history. *Journal of Vegetation Science* 25: 1267–1277.

Xu, H., Liu, S., Li, Y., Zang, R. & He, F. 2012. Assessing non-parametric and area-based methods for estimating regional species richness. *Journal of Vegetation Science* 23: 1006–1012.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. The three levels of anthropogenic influence for the 15 *maeulsoops*.

Appendix S2. Forest types in digital forestry map and reclassification for PCA.

Appendix S3. Pair-wise correlations among local and landscape variables at different spatial scales.

Appendix S4. Recorded forest plant species that were classified into short-distance dispersal species based on their dispersal mode.

Appendix S5. Recorded forest plant species that were classified into long-distance dispersal species based on their dispersal mode.

Appendix S6. Species identification in seed rain samples collected in the 15 *maeulsoops* during the sampling periods, and photograph of installed seed traps in *maeulsoops*.

Appendix S7. Seed rain genera accumulation curves and Jack2 estimation curves for the 15 *maeulsoops*.