

Changes in Species Diversity and Spatiotemporally Fluctuation across Human-modified Ecosystems

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The changes of plant communities at Angol valley and Baetgol valley in Geoje-do were studied. Both α -diversity and γ -diversity decreased with the sizes and degrees of habitat fragmentations. The mean number of winner species decreased with habitat fragmentation. All *Quercus* species, including *Quercus acutissima*, significantly declined in importance, while the many introduced species, including *Trifolium pretense*, all increased in importance. As the proportional change in adult survival rate increased, the absolute value of the bias in the elasticity prediction also increased from 2003 to 2011 at undisturbed forests. However, the bias was low for decreases in disturbed populations. Moran's *I* values showed overall decreases for habitat fragmentation and for the periods of habitat conversion. Eventually, plant communities, due to urbanization in Goeje-do, might have led to decreased chances of common species when the environment was disturbed.

Key words : Plant communities, α -diversity, γ -diversity, common species, urbanization

Introduction

The Geoje-do is located in the south of main land of Korea and at the western part of the North Pacific Ocean. However the island was connected with bridges and a submarine tunnel recently. The Angol valley and Baetgol valley near Aju-dong in Goeje-do were placed typically forests with mostly genus *Pinus* and genus *Quercus* under the protection for a long time. However, many forests of these areas were disturbed by construction of tunnel, roads, and many apartments. Many forests of Geoje-do have suffered the rapid ongoing urbanization. Thus, it was expected to be useful experimental conditions because it has done a turning point from undistributed and isolated sites to human disturbed sites during several years.

Assessing the state of biodiversity at different points in space and time are necessary for efficient biodiversity conservation in an important forest region. Information for monitoring biodiversity is required to establish a link between the state of biodiversity and human pressures, to propose scenarios based on forecasted evolutions of pressures and society responses and, in turn, to contribute to the development of adequate policies [1].

Although the rare species and protected areas are usually targeted, conservation biology and ecological monitoring are also concerned with common species and the 'unreserved matrix' in which they live [14]. Quantitatively, common species play a key role in ecosystems and the most abundant species even contribute disproportionately to spatial patterns of species richness [15]. Variation in the abundance of a few common species may therefore have important consequences on ecosystems across large geographical areas, because common species are also typically widespread. Yet, declines in the abundance of common species often remain undetected due to their wide distribution. Widespread species can experience numerous local extinctions but still be observed at larger scales [19]. Cases where data is available are rare, but changing abundances of common species are documented in several taxonomic groups [2,6,9,26], suggesting that even these species suffer substantial declines in response to human disturbance, such as habitat modification and destruction, overexploitation or climate change. The consequences of human disturbance on species abundance are generally not random; some species tend to decline consistently ('loser' species), whereas others ('winner' species) benefit from disturbance [30]. This wide-spread phenomenon results in biotic homogenization (BH), i.e. a temporal increase in community similarity [22], which can be measured as a similarity of gene pools (genetic BH), taxonomic identi-

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ties (taxonomic BH) or functional traits (functional BH) of species across biota [4]. To identify mechanisms underlying BH, one can examine the characteristics of winner versus loser species. This was done in several groups, showing that declining species can be characterized in terms of dispersal mode, sensitivity to herbivory or growth form in plants [3]. In addition, the approach comparing the attribute of loser versus winner species should be combined with a study of the relationship between BH and the intensity of disturbance for a proper elucidation of the origin of BH. These two approaches have rarely been combined to examine functional BH [7], especially in plants, although functional BH of plant communities has obvious consequences for ecosystem functioning.

Here, we focused on habitat specialization, a proxy for niche width, because a widespread pattern of BH in plant communities is that loser species are generally habitat-specialist species [7,26], thus leading to functional BH. Using data from a common plant monitoring survey at Angol valley and Baetgol valley in the Geoje-do, as well as GIS-derived indices of landscape disturbance in space (habitat fragmentation) and time (habitat conversion), we specifically addressed the following questions: (i) Does landscape disturbance influence the average specialization of plant communities, with more generalist communities in more disturbed landscapes? (ii) Is this change in community composition associated with taxonomic homogenization of plant communities?

Materials and Methods

Study area and human disturbance indices

We have chosen plant communities at Angol valley and Baetgol valley in Geoje-do to study a landscape disturbance in spatiotemporally fluctuating environments. We will assume that the fitness of individuals in each habitat is a linear function of population density in that habitat and has a stochastic element that may or may not be correlated with the other habitat. To quantify habitat fragmentation at Angol valley and Baetgol valley, we used the land use pattern from 2003 to 2011. At the start of each year, the adults will select habitat according to the expected fitness rewards in each habitat.

We classified habitats of Angol valley and Baetgol valley according to the European CORINE Land Cover habitat classification and subsequently aggregated them into three cate-

gories: forests (St. A), agricultural landscapes (St. B), and urban areas (St. C) (Fig. 1). St. A has been conserved forest. However, St. B and St. C have gradually been disturbed recently. In each survey square, we calculated edge density as a measure of landscape fragmentation, i.e. the sum of all polygon perimeters within a square (excluding the square perimeter), divided by square area.

Spatial partition of taxonomic diversity

We investigated the effect of human disturbance on the spatial distribution of total diversity in a given square (γ -diversity) using multiplicative partitioning of diversity within plots (α -diversity) and between plots (β -diversity). Following the recommendations of Jost [16], we measured taxonomic diversity using the 'true diversity' Shannon index, $\exp[-\sum p_i \ln p_i]$, where p_i is the abundance of species i . We preferred this index to species richness because accounting for species abundance is crucial to the study of community similarity [18]. We then used the vegan R package [23] to partition γ -taxonomic diversity in each square into within-plot and between-plot diversity for each 1-km² square. We performed this partitioning on the whole data set, but also on the subset of plots sharing the same habitat within a square. This allowed us to examine β -diversity within habitat types without the inflating effect of habitat differences within squares.

We subsequently tested the effect of landscape disturbance indicators on mean α -, β -, and γ -taxonomic diversity, using simple linear models in which α -, β - or γ -taxonomic diversity was a function of habitat fragmentation, the periods of habitat conversion and an interaction between these two variables. All residuals were normally distributed.

Species attributes

To analyze whether winner species differed in their ecological attributes from loser species, tests were set up to investigate different species traits. All species were assigned into categories for each traits and G-test or Wilcoxon rank test revealed, whether certain species traits were more common among winner species than loser species or vice versa. The investigated traits and predictions, about how they should be distributed among winner and loser species according to hypothesized vegetation change, are described in the following. Species are distributed according to their ecological optima with respect to basic requirements such as

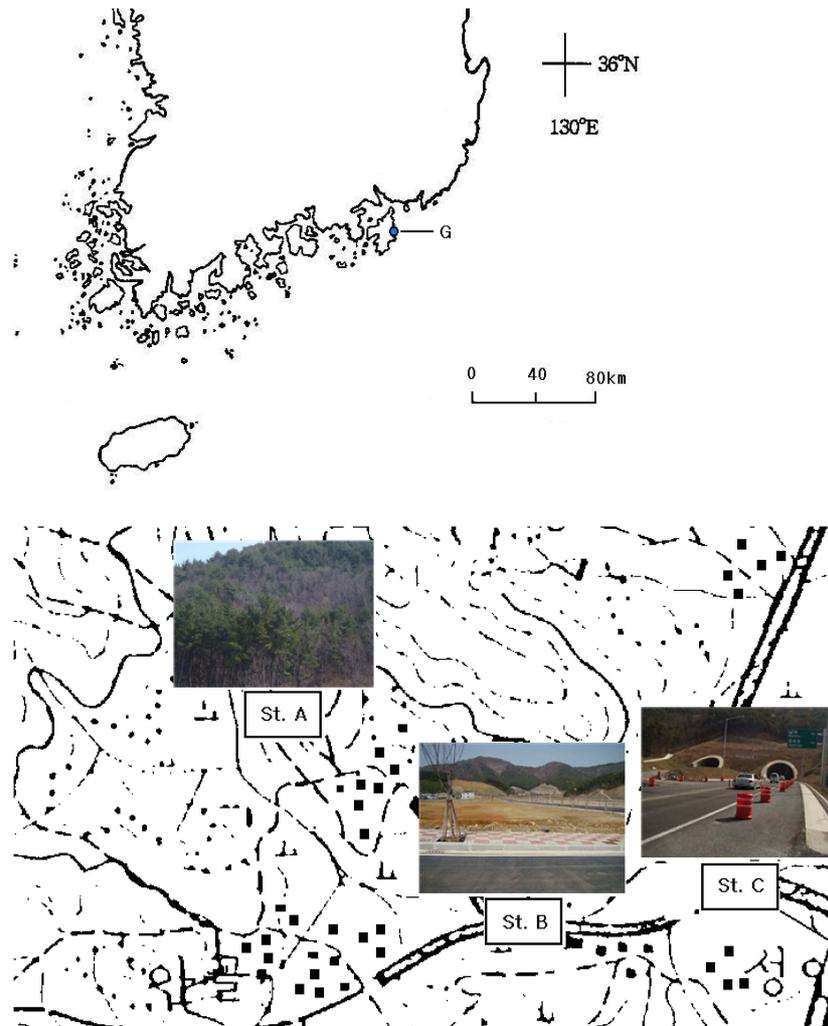


Fig. 1. The plant monitoring scheme (G) in Geoje province. Photos of the study areas, where forest (St. A), urban areas (St. B), and road construction (St. C).

light and nutrients, and this can be characterized with indicator values such as those described by Ellenberg *et al.* [13]. When comparing the Ellenberg values of winner and loser species, any difference would be expected to be in accordance with predictions about vegetation change. Hence follows, that winner species were expected to have higher values than loser species for the continentality, moisture, and nitrogen indices and lower values for the light, soil reaction and temperature indices.

Conversion of surrounding habitats

To measure of landscape stability for each square, we considered a rate of change in land-use among the three habitat categories, calculated as the total number of polygon changes (i.e. habitat conversion) during the last nine years,

divided by the total number of polygons in a square. This yielded an index of habitat conversion, ranging between 0, when all polygons within a square had remained in the same habitat class, and 1, when all polygons within a square were modified at least once in nine years.

We performed all calculations using the Geographical Information System ArcView 3.2 (Economic and Social Research Institute (ESRI) [11] with the Patch Analyst extension [12] and R 2.10.1 (R Development Core Team) [24]. We checked that habitat fragmentation and conversion were uncorrelated. We also ruled out a possible effect of geographical clustering by checking the absence of spatial autocorrelation in square fragmentation and surrounding habitat conversion using the global Moran's *I* statistic in the *spdep* R package.

Moran's *I* statistic for class *k* was calculated as follows:

$$I(k) = \frac{n \sum_i \sum_{j(i \neq j)} W_{ij} Z_i Z_j}{S \sum_i Z_i^2}$$

Where Z_i is $p_i - \bar{p}$ (\bar{p} is the average of p_i); W_{ij} is 1 if the distance between the *i*th and *j*th plants is classified into class *k*; otherwise, W_{ij} is 0; *n* is the number of all samples and *S* is the sum of W_{ij} ($\sum_i \sum_{j(i \neq j)} W_{ij}$) in class *k*. Under the randomization hypothesis, *I* (*k*) has the expected value $u_1 = -1/(n-1)$ for all *k*. Its variance, u_2 , has been given, for example, in Sokal and Oden [28,29]. Thus, if an allele is randomly distributed for class *k*, the normalized *I* (*k*) for the standard normal deviation (SND) for the plant genotype, $g(k) = \{I(k) - u_1\} / u_2^{1/2}$, asymptotically has a standard normal distribution [5]. Hence, SND *g* (*k*) values exceeding 1.96, 2.58, and 3.27 are significant at the probability levels of 0.05, 0.01, and 0.001, respectively.

Results

Both α -diversity within squares and γ -diversity decreased with habitat fragmentation and surrounding habitat conversion (Table 1, Fig. 2). The effects of both landscape variables were of comparable magnitude and independent of each other (non-significant interaction, Table 1). The resulting β -diversity was unrelated to landscape disturbance variables when all habitat types within a square were considered (Table 1, Fig. 2). However, β -diversity within habitat types (i.e. the differentiation between plots of a same habitat) tended to decrease with increasing habitat fragmentation, but not with increasing habitat conversion.

The mean number of winner species decreased with habitat fragmentation (Table 2). The relationship between mean community specialization and surrounding habitat conversion, however, depended on habitat type (significant in-

teraction between habitat type and habitat conversion. There was a significant negative relationship between community specialization and surrounding habitat conversion in forest sites.

In addition, the canopies of these forests are undergoing systematic shifts in composition and structure. All *Quercus* species including *Quercus acutissima* significantly declined in importance while many introduced species including *Trifolium pretense* all increased (Table 2). Evergreen including *Pinus densiflora* declined faster than oak group (59% vs. 21%). Note that across all oak species, these declines in importance are driven by dramatic declines in density rather than declines in average tree basal area, which has actually increased as the stem size distribution has shifted from an approximation of the reverse *j* shaped curve often seen in expanding population to the hump shaped distribution expected in mature populations (Fig. 3). This observed shift is entirely consistent with that expected for a population in decline. A stepwise linear regression of apparent native species invasions initially based on all predictor variables retained only mean patch size, starting successional index and road density, contributing 39.1%, 7.7% and 2.8% respectively for a combined adjusted r^2 of 48.6%, $P < 0.0001$). At the species level, we observed no significant relationship between individual species specialization Θ and species response to landscape disturbance, when considering the 23 most common species (linear model on 21 d.f.: $t = -1.08$, $P = 0.27$ for habitat fragmentation; $t = -0.36$, $P = 0.51$ for surrounding habitat conversion; $R^2 = -0.23$).

We detected substantial bias when using elasticity values to predict the proposal change in population growth rate following a given proportional change in a vital rate (Fig. 4). As the proportional change in adult survival rate increased, the absolute value of the bias in the elasticity

Table 1. Effects of landscape fragmentation and habitat conversion on Shannon taxonomic diversity indices in plant communities across spatial scales. α -, β - and γ -diversity refer to true Shannon diversity within 10-m² plots, between plots and at the 1-km² square level, respectively. The direction of significant relationships is indicated in parentheses after the P-value.

Community	d.f.	α -diversity		β -diversity		γ -diversity	
		F	P	F	P	F	P
Disturbance variables							
Fragmentation	1	6.58	0.07(+)	0.21	0.57	5.22	0.05(+)
Conversion	1	5.39	0.09(+)	2.88	0.14	9.50	0.01(+)
Interaction	1	2.61	0.11	0.03	0.76	1.07	0.42
Residuals	27						
Multiple R-squared		0.43		0.10		0.33	

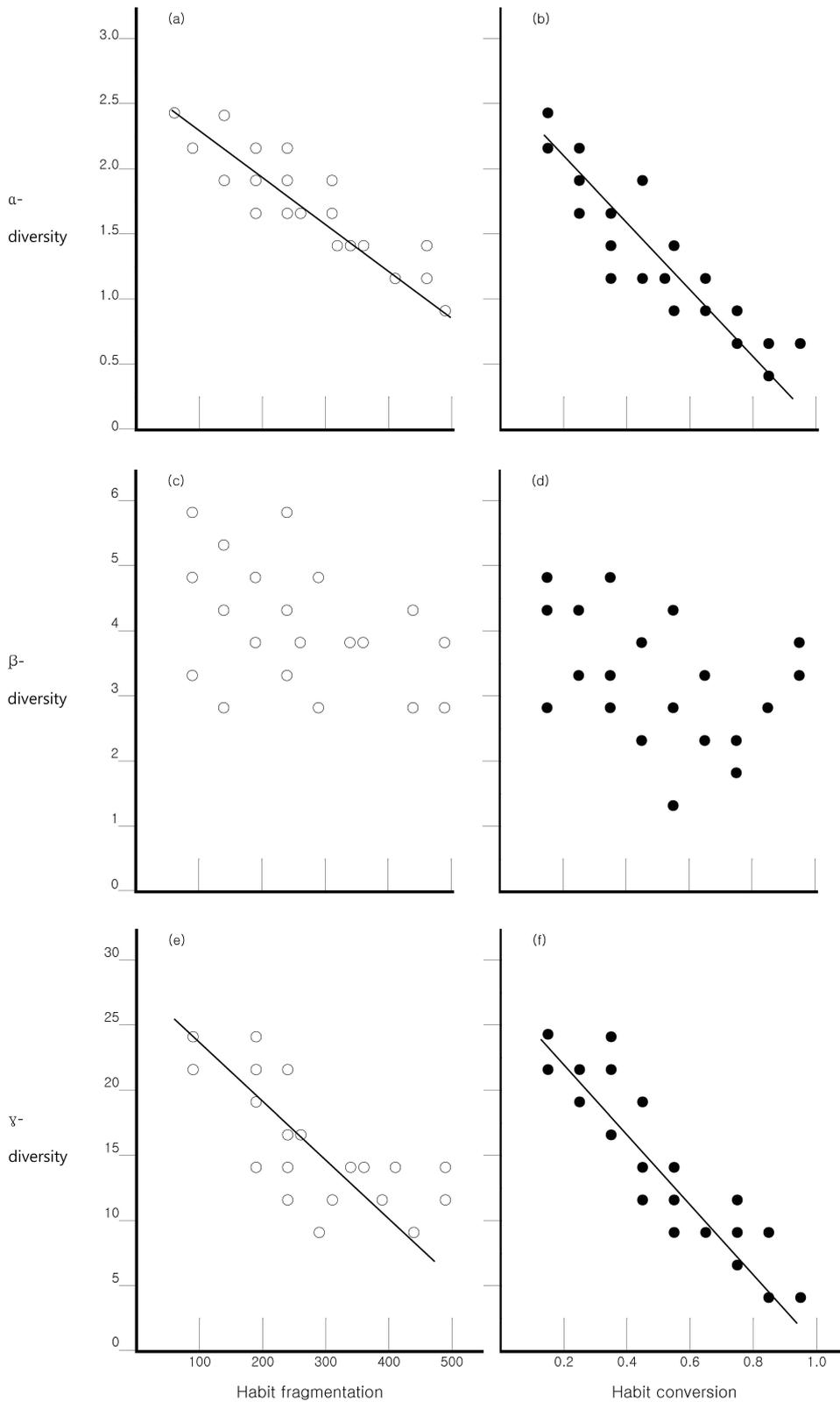


Fig. 2. Relationship between different levels of plant taxonomic diversity and spatial (a, c, e) or temporal (b, d, f) landscape disturbance. (a, b) α -diversity is the average Shannon diversity within 10-m² plots; (c, d) β -diversity is the average Shannon diversity between plots; (e, f) γ -diversity is the total Shannon diversity at the 1-km²-square level. P-values indicate the statistical significance of the effects of landscape disturbance variables, obtained from a linear model.

Table 2. Species abundance before disturbance and plant types after disturbance at Angol valley and Baetgol valley

Species	Distribution on 2003		Distribution on 2011	
	Common	Rare	Winner	Loser
<i>Pinus densiflora</i> Siebold et Zucc.	○			○
<i>Alnus firma</i> S. et Z.	○			○
<i>Carpinus laxiflora</i> BL.	○			○
<i>Quercus acutissima</i> Carruth.	○			○
<i>Quercus variabilis</i> BL.	○			○
<i>Quercus dentate</i> Thunb.	○			○
<i>Quercus aliena</i> BL.	○			○
<i>Rubus crataegifolius</i> Bunge	○			○
<i>Prunus sargentii</i> Rehder	○			○
<i>Humulus japonicus</i> Sieb. Zucc.	○			○
<i>Boehmeria spivata</i> Thunb.	○			○
<i>Boehmeria tricuspis</i> Makino	○			○
<i>Glycine soja</i> S. et Z.		○		○
<i>Lespedeza cuneata</i> G. Don	○			○
<i>Rhus sylvestris</i> S. et Z.	○			○
<i>Ampelopsis brevipedunculata</i> var. <i>geterophylla</i> Hara		○		○
<i>Pyrola japonica</i> Klenze		○		○
<i>Rhododendron mucronulatum</i> Turcz.	○			○
<i>Rhododendron yedoense</i> var. <i>poukhanense</i> (Lev.) Nakai	○			○
<i>Ligustrum obtusifolium</i> S. et Z.	○			○
<i>Lonicera japonica</i> Thunb.	○			○
<i>Hemerocallis fulva</i> L.		○		○
<i>Miscanthus sinensis</i> var. <i>purpurascens</i> (Andersson) Rendle	○		○	
<i>Setaria viridis</i> (L.) Beauv.		○	○	
<i>Carex humilis</i> Leyss	○		○	
<i>Smilax sieboldii</i> Miq.		○	○	
<i>Rumex crispus</i> L.		○	○	
<i>Chenopodium album</i> var. <i>centrorubrum</i> Makino		○	○	
<i>Capsella bursa-pastoris</i> (L.) Medicus		○	○	
<i>Trifolium pratense</i> L.		○	○	
<i>Trifolium repens</i> L.	○		○	
<i>Plantago asiatica</i> L.		○	○	
<i>Artemisia Montana</i> Pampan	○		○	
<i>Artemisia princeps</i> var. <i>orientalis</i> (Pampan.) Hara	○		○	
<i>Cirsium japonicum</i> var. <i>ussuriense</i> Kitamura		○	○	
<i>Taraxacum officinale</i> Weber		○	○	

Notes: Explanation of common, rare, winner, and loser was shown in text.

prediction also increased from 2003 to 2011 at undisturbed forests. However, the bias low for decreases in disturbed populations.

Moran's *I* values were overall decreases for habitat fragmentation and) for the periods of habitat conversion (Table 3). The significant positive values were shown a spatial correlation within same plot. Whereas, negative values were indicated that neighboring plants within same plot did not have shown similar BH. Some plots of St. B and St. C were explanted for urbanization on 2003 ~ 2011. Thus they were treated blanks in Table 3.

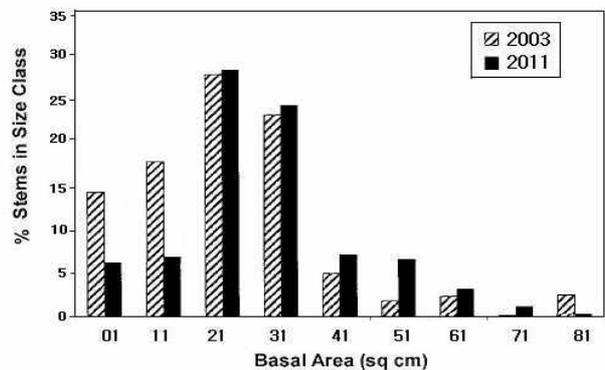


Fig. 3. Changes in size class distribution of stems of *Quercus* species.

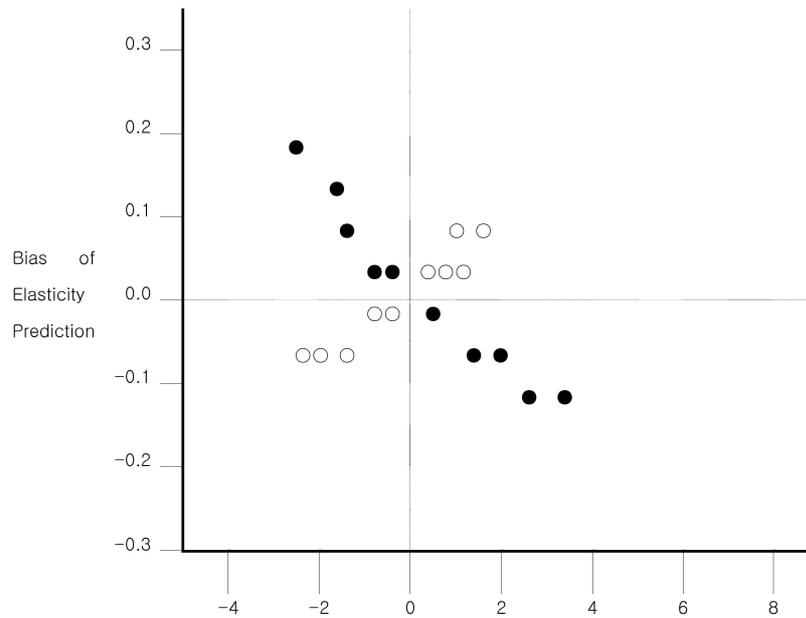


Fig. 4. The relationship between the bias produced by the predicted proposal change in population growth rate relative to the observed proportional change in population growth rate (Y-axis) and the proportional change made to each vital rate (X-axis). ○: Unfragmented forest understory communities, ●: Fragmented forest understory communities,: References lines.

Table 3. Spatial autocorrelation coefficients (Moran’s *I*) among ten distance classes for three regions

Area	I	II	III	IV	V	VI	VII	VIII	IX	X
Before urbanization										
St-A	0.444***	0.397**	0.346*	0.275**	0.144	0.116	-0.019	-0.095	-0.117	-0.162**
St-B	0.391**	0.333	0.274**	0.256*	0.155	0.102	-0.106	-0.124	-0.159	-0.241
St-C	0.465***	0.353***	0.319**	0.252*	0.124	0.020	0.007	-0.0123	-0.188	-0.205
After urbanization										
St-A	0.442***	0.394**	0.341*	0.276**	0.142	0.114	-0.023	-0.094	-0.115	-0.169**
St-B	0.387**	0.287*	0.156	0.106	0.001	-0.017	-	-	-	-
St-C	0.433***	0.347***	0.315**	0.200	-0.002	-	-	-	-	-

*: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

St. A, St. B, and St. C are same as those of Fig. 1. -: Fragmentation plots.

Discussion

Several ecological studies have documented taxonomic or functional BH in a variety of taxa [7,17,20] but the underlying mechanisms are not fully understood. Although it is generally admitted that BH results from human activities, the relative effects of, for instance, species addition or expansion versus species extirpation remain unclear and may be scale dependent [21]. Most studies were conducted at large spatial scales (up to continental levels), where the expansion of introduced species seems to be a widespread cause of BH [27]. Fewer studies have investigated BH at a finer scale (landscape to regional level for plants), where it

may be driven mostly by declines of native species [18,21,25].

Gaston and Fuller [15] reported that common species play a key role in ecosystems and the most abundant species even contribute disproportionately to spatial patterns of species richness. *Pinus thunbergii* and *Quercus aliena* were dominant on most plots of both regions. But, the *P. densiflora* forest of region A is distributed well in the middle plots exposures compared with the opposite ones. *Q. aliena*, *Q. mongolica*, and *Carpinus laxiflora* largely occupied the middle and lower exposures of region B. *P. thunbergii*, *Q. aliena*, and *Rhododendron mucronulatum* were common species in study areas. Declines in the abundance of common species were observed at larger scales. The reasons were suggested that these species suffer

substantial declines in response to human disturbance, such as habitat modification and destruction during past ten years or more. Especially, *P. thunbergii*, *Q. aliena*, and *R. mucronulatum* tend to decline consistently ('loser' species), whereas *Chenopodium album* var. *centrorubrum*, *Miscanthus sinensis* var. *purpurascens*, *Rumex crispus*, and *Taraxacum officinale* ('winner' species) benefit from disturbance. This wide-spread phenomenon results in biotic homogenization (BH), i.e. a temporal increase in community similarity [22]. A similarity of gene pools (genetic BH), taxonomic identities (taxonomic BH) or functional traits (functional BH) of species across biota were measured most 10-m² plots (Table 1). Taxon richness is a major component of biological diversity and an important ecosystem characteristic [3,10]. Many plots were shown with the dramatically decrease of biodiversity or abundance across areas. Shannon-Weaver index of diversity also decreased among the areas with the areas St. B and St. C having lower value than the values of undisturbed forests (St. A). The reasons were considered the decreases or loss of common species and former winner species across human-modified ecosystems at both areas.

Environmental heterogeneity is usually cited as playing a critical role in determining the spatial structure of plant but colonization patterns and stochastic events affecting establishment and mortality are also important. Eventually, plant communities according to urbanization in Goeje-do might have led to decreased chances of common species when the environment was disturbed.

We suggest that plant density and species diversity in the communities in Goeje may be driven by the same ecological factor. High constant human disturbances are thought to decrease environmental tolerance, neighboring densities, and subsequently a higher number of functional guilds in the understory. Common species were also very important to conserve biodiversity as mentioned in the introduction because they have done the major roles of functional BH including water supply to young rare plants and young shrubs in the forests.

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초록 : 도시화로 인한 생태계에서 종 다양성의 변화와 공간시기적 변동

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거제도 안골 골짜기와 뱃골 골짜기에서 식물 군락의 변화를 조사하였다. 알파-다양도와 감마-다양도는 서식지 단절의 크기와 정도에 따라 감소하였다. 우세종의 평균 종수도 서식지 단절에 따라 감소하였다. 상수리나무를 비롯한 참나무과 종들은 붉은토끼풀 같은 도입된 귀화식물의 증가에 따라 주요도가 감소하였다. 교란이 일어나지 않은 숲에서 성체 생존율의 뭉이 증가함에 따라 탄력 예상치의 절대적 비는 2003년부터 2011년까지 증가하였다. 그러나 교란 집단에서는 비가 낮았다. Moran의 I값은 전반적으로 서식지 단절지역과 서식지전환 시기에서는 감소하였다. 결국 거제도에서 도시화에 따른 식물 군락은 환경이 교란되었을 때 보편종의 감소를 유발하였다.