



Original article

Predicting impacts of climate change on habitat connectivity of *Kalopanax septemlobus* in South Korea



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ARTICLE INFO

Article history:

Received 24 July 2015

Received in revised form

2 January 2016

Accepted 11 January 2016

Available online 21 January 2016

Keywords:

Castor aralia

Graph theory

Habitat suitability

Maximum entropy modeling

Probability of connectivity

ABSTRACT

Understanding the drivers of habitat distribution patterns and assessing habitat connectivity are crucial for conservation in the face of climate change. In this study, we examined a sparsely distributed tree species, *Kalopanax septemlobus* (Araliaceae), which has been heavily disturbed by human use in temperate forests of South Korea. We used maximum entropy distribution modeling (MaxEnt) to identify the climatic and topographic factors driving the distribution of the species. Then, we constructed habitat models under current and projected climate conditions for the year 2050 and evaluated changes in the extent and connectivity of the *K. septemlobus* habitat. Annual mean temperature and terrain slope were the two most important predictors of species distribution. Our models predicted the range shift of *K. septemlobus* toward higher elevations under medium-low and high emissions scenarios for 2050, with dramatic reductions in suitable habitat (51% and 85%, respectively). In addition, connectivity analysis indicated that climate change is expected to reduce future levels of habitat connectivity. Even under the Representative Construction Pathway (RCP) 4.5 medium-low warming scenario, the projected climate conditions will decrease habitat connectivity by 78%. Overall, suitable habitats for *K. septemlobus* populations will likely become more isolated depending on the severity of global warming. The approach presented here can be used to efficiently assess species and habitat vulnerability to climate change.

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1. Introduction

Climate change is regarded as one of the major drivers of changes in biodiversity and ecosystems, and its possible effects are receiving worldwide attention (Duraiappah et al., 2005; Sala et al., 2000). Indications for impacts of climate change have already been found in many species over a wide taxonomic range (Nussey et al., 2005; Parmesan, 2006; Parmesan and Yohe, 2003). In addition, such impacts may be reinforced by habitat loss and fragmentation, which can lead to species range shifts and a reduction in habitat connectivity (Honnay et al., 2002; Opdam and Wascher, 2004).

Although species may have the capacity to shift their range, long distances between habitats or other barriers may restrict their

movement. Moreover, the ability to move across the landscape depends on species-specific behavior and landscape structure (Bélisle, 2005; Goodwin and Fahrig, 2002). Thus, understanding the range-shifting capacities of species in response to climate change has important conservation implications for the predictions of future extinction risk and distribution changes (Angert et al., 2011). More importantly, because climate change appears to be inevitable, an effective adaptation strategy may involve preserving and restoring landscape connectivity for long-term persistence of ecological processes, such as dispersal and gene flow (Crooks and Sanjayan, 2006; Rosenberg et al., 1997; Templeton et al., 2001).

Landscape connectivity, or the degree to which the landscape facilitates or disturbs movement among resource patches (Taylor et al., 1993), affects dispersal success and colonization rates (With and King, 1999a, 1999b). Such patterns in turn influence the biodiversity, ecosystem function, and resilience of species to climate change (Fahrig, 2003; Gonzalez et al., 2009; Lawler, 2009). Specifically, well-connected landscapes may enable tracking of species' suitable climate and habitat conditions through time and

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thereby may allow ecological and evolutionary processes to be sustained. Increasingly, ecologists have reported that improving connectivity is necessary for biodiversity conservation and is thus one of the most commonly recommended strategies for helping species adapt quickly and survive rapid climate change (Heller and Zavaleta, 2009; Theobald et al., 2012).

Even though global warming has begun to affect the regional climate system (Boo et al., 2004; Jung et al., 2002) and cause range shifts of terrestrial flora in many countries (Allen et al., 2010), it is unknown whether existing biosphere reserves and semi-natural forests may ensure species' long-term persistence. In this study, we use a species distribution modeling tool to model the current and future potential geographic distribution of *Kalopanax septemlobus* (Araliaceae) in South Korea. We then applied a graph-theoretical method to predict the likely impacts of climate change on habitat connectivity. Natural populations of *K. septemlobus* are threatened by climate change and from illegal logging for timber, medicine, and edible products (Chang et al., 2001; Kang, 2003). The objectives of this study are: (1) to identify climatic and topographic factors associated with *K. septemlobus* distribution by using ecological niche modeling (ENM), (2) to predict the current distribution of suitable habitats and project them under future climate scenarios for 2050, and (3) to evaluate changes in habitat distribution patterns and connectivity.

2. Materials and methods

2.1. Study area and focal species

The study area is in the southern half of the Korean Peninsula and the islands of South Korea (Fig. 1), which lie between latitudes 33° and 39°N, and longitudes 124° and 131°E. Its total area is 100,148 km², approximately 64% of which is covered by forests mostly in the north and east regions (KFS, 2012). The area is in a temperate zone with four distinct seasons and is affected by East Asian monsoons. However, global warming has increased the temperature and precipitation levels and widened seasonal and regional weather differences on the Korean Peninsula, changing its climate gradually closer to a subtropical climate (Philander, 2012).

K. septemlobus, commonly known as the prickly castor oil tree, is a hermaphroditic, deciduous tree species in the family Araliaceae. Widely but sparsely distributed through Northeast Asia (Lee and Kang, 2002; Ohashi, 1994), this species blooms in July–August, and various insects act as agents of pollination (Fujimori et al., 2006). Fruits are available in September and October, and seeds are dispersed by birds and squirrels (Iida and Nakashizuka, 1998). It is a multi-purpose tree, important for high quality timber and as a source of food and medicine. However, illegal cutting and over-exploitation due to the increasing demand have led to damage and destruction of its natural habitat (Kang, 2003).

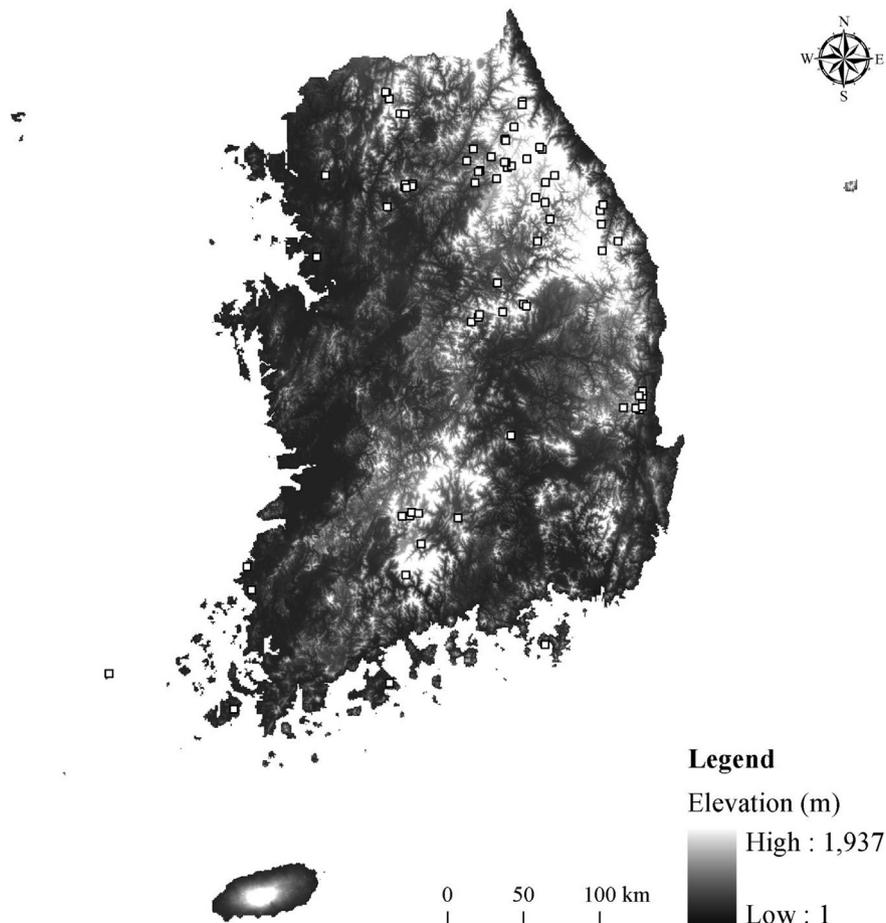


Fig. 1. Digital elevation model of the study area, with the presence locations of *Kalopanax septemlobus* ($n = 72$) indicated as squares.

2.2. Habitat distribution modeling under current and potential future climates

The present potential distribution of *K. septemlobus* was constructed by relating occurrence locations to bio-climatic and topographic variables through a presence-only machine-learning maximum entropy (MaxEnt) distribution modeling (Phillips et al., 2006). We obtained 72 occurrence records of *K. septemlobus* from previously published studies (Kang, 2003; Lee et al., 2000; ME, 2002; Sakaguchi et al., 2012a, 2012b) (Fig. 1). The occurrence locations were separated by a minimum distance of 1 km to avoid spatial autocorrelation biases (Legendre et al., 2002).

Eight environmental variables were chosen according to their potential relevance to the *K. septemlobus* habitat distribution based on previous research (Sakaguchi et al., 2012a, 2010) and other habitat modeling studies (e.g., Khanum et al., 2013; Kumar and Stohlgren, 2009). Four bioclimatic variables, including annual mean temperature, mean diurnal temperature range, precipitation of warmest quarter, and precipitation of coldest quarter, at a 30 arc-second (ca. 1 km) spatial resolution were obtained from the WorldClim database for the current climate of 1950–2000 (Hijmans et al., 2005; <http://www.worldclim.org/bioclim.htm>). For local- and landscape-scale analyses in the study area, the bioclimatic variables were resampled to a 100 m resolution using bilinear interpolation. We also used four topographic variables including slope and aspect, both in degrees; solar radiation; and topographic position index derived from a 100 m digital elevation model. Potential solar radiation was calculated as the sum of direct, diffuse, and reflected radiation for one year based on terrain shading (Kumar et al., 1997). The topographic position index was generated by using ArcView 3.3 with the Topographic Position Index extension version 1.3a (Jennness, 2006). MaxEnt determines the relative contribution of each variable to the model (Phillips et al., 2006). Only variables contributing 1% or more to the model were included in the final model. We tested for multicollinearity by examining Spearman's rank cross-correlations among all of the variables based on 10,000 randomly generated points within the study area. No variables were strongly correlated (i.e., $|r_s| < 0.6$).

We performed MaxEnt modeling by using the default settings, with 1000 iterations. Thirty model replicates were processed; 70% of the locations were randomly selected each time to train the model, and the remaining 30% were used to test the model's predictions. We used ENMtools 1.3 (Warren et al., 2010; Warren and Seifert, 2011) to select the most parsimonious model based on the corrected Akaike's information criterion (AICc) scores (Burnham and Anderson, 2002). Using the 10 percentile training presence logistic threshold (≥ 0.295) (Escalante et al., 2013) from the best-fitting model, habitat patches were defined as contiguous pixels based on an eight-neighbor rule. Patches less than 5 ha, which is considered to be a minimum reserve size for the conservation of biodiversity in fragmented landscapes (Drinnan, 2005), were removed from the analysis.

Future climate projections were obtained from the Korean Climate Change Information Center database (www.climate.go.kr) at 1 km resolution for the year 2050. These were developed on the basis of a model that coupled a regional climate model (HadGEM3-RA) and the Modified Korean (MK) Parameter-elevation Regressions on Independent Slopes Model (PRISM). HadGEM3-RA is based on the version 3 of Hadley Centre Global Environment Model (HadGEM3; Hewitt et al., 2011). The MK-PRISM estimates 1 km enhanced resolution climate grids by using observation data collected from the Automatic Synoptic Observation System (ASOS) and Automatic Weather Observation System (AWOS) in South Korea (Kim et al., 2012).

We focused on two climate change scenarios based on

Representative Concentration Pathways (RCPs) 4.5 and 8.5 (Moss et al., 2010). The RCPs are being used in the IPCC fifth assessment report (AR5) and are measured in terms of atmospheric CO₂-equivalent concentrations rather than direct emissions. Designed to stabilize radiative forcing level at 4.5 W m⁻² in the year 2100 with an approximately 650 ppm CO₂-equivalent, RCP 4.5 is a medium-low emissions scenario, assuming strong mitigation efforts (Thomson et al., 2011). The RCP 8.5 is a high emissions scenario based on a business-as-usual. In RCP 8.5, the radiative forcing level will be expected to reach 8.5 W m⁻² in 2100 with an approximately 1350 ppm CO₂-equivalent (Riahi et al., 2011). Annual mean temperatures over South Korea in 2050 under RCPs 4.5 and 8.5 are expected to increase by 1.9 °C and 3.0 °C, respectively, relative to the current mean of 11.3 °C. RCPs 4.5 and 8.5 represent moderate and strong warming scenarios, respectively, for identifying discriminative patterns and trends in predicted changes to the habitat of *K. septemlobus*.

Future *K. septemlobus* habitats were projected by using the best-fitting MaxEnt model. Future habitat patches (≥ 5 ha) were defined as contiguous pixels with a probability of occurrence ≥ 0.295 by using an eight-neighbor rule.

2.3. Analyzing the extent and connectivity of habitat

For each of the three habitat models, including the current *K. septemlobus* distribution and the two predictions under the RCP scenarios, we calculated the total area of suitable habitats. Then, we estimated the amounts of stable, unsuitable, lost, and gained habitats for each of the two future models. Stable habitat refers to the areas of the current potential range predicted to remain suitable in 2050, and lost habitat refers to areas not predicted to remain suitable in the same period. Gained habitat includes areas that are predicted to be suitable in 2050 that are not currently suitable.

To measure habitat fragmentation, we computed the number of patches (NP), area weighted mean patch size (AWMPS), and largest patch index (LPI), using FRAGSTATS (version 4.2; McGarigal et al., 2012). The LPI is the percentage of total landscape area comprised by the largest patch. The AWMPS is the sum of patch areas across all patches multiplied by the proportional abundance of the patch (i.e., patch area divided by the sum of patch areas). AWMPS is considered more robust than the simple mean patch size when quantifying changes in landscape structure over time (Li and Archer, 1997). We also analyzed altitudinal range shifts of the species by using the mean elevation of current and future suitable habitats.

We estimated the degree of overall connectivity by using a graph-theoretical approach. In ecology, connectivity is often analyzed by graph-theoretical methods with minimal data inputs, which show promise for providing functional and ecologically relevant measures of landscape structure and process (Kang et al., 2012; Minor and Urban, 2007; Urban et al., 2009). A graph is a set of nodes (i.e., discrete patches) connected by links (i.e., movement of organisms) within a landscape-ecological context (Minor and Urban, 2008).

Habitat networks were analyzed as undirected complete graphs. Link weights were determined on the basis of Euclidean edge-to-edge distances between habitat patches. Although long-distance seed dispersal events for *K. septemlobus* are rare (N. Fujimori, unpublished data), we used different threshold distances (100 m–25 km) to consider a range of possible pollen and seed dispersal distances.

To compare current and future levels of overall habitat connectivity, we estimated the Probability of Connectivity (PC) (Saura and Pascual-Hortal, 2007), which is computed as:

$$PC = \frac{\sum_{i=1}^n \sum_{j=1}^n a_i \cdot a_j \cdot p_{ij}^*}{A_L^2} \quad (1)$$

where n is the total number of habitat patches, a_i and a_j are the areas of patches i and j , respectively; and A_L is the total landscape area. p_{ij}^* is defined as the maximum product probability of all possible paths between the patches i and j . The product probability of a path is the product of all the p_{ij} (link weights) included in the path. The p_{ij} values (dispersal probability) were calculated by using a negative exponential function of inter-patch distance (Bunn et al., 2000; Urban and Keitt, 2001), with $p_{ij} = 0.05$ for a threshold distance. When $i = j$, the p_{ij}^* equals 1. PC is defined as the probability that two organisms randomly placed in a landscape will be interconnected by falling into habitat areas within reach of each other given a set of habitat nodes and links between them (Saura and Pascual-Hortal, 2007). This value ranges from 0 to 1 and reaches unity when the landscape is entirely covered by a given habitat type. Further, PC is regarded as a habitat availability index because it integrates topological properties of the habitat network with habitat attributes like habitat patch size (Saura and Pascual-Hortal, 2007). The PC index may be an appropriate metric for studying overall flows of organisms irrespectively of their origin (Bodin and Saura, 2010).

By comparing the PC values of the current and future habitat networks, we predicted the potential impact of climate change on the connectivity of *K. septemlobus* habitats. Based on the present PC values under current climate conditions, we calculated the percent of decrease in PC connectivity caused by shifts in suitable habitat range under RCPs 4.5 and 8.5 for 2050. Graphab 1.2 was used for constructing and evaluating the habitat networks (Foltête et al., 2012).

3. Results

The best model for predicting the *K. septemlobus* occurrence probability had a good fit (AUC-train = 0.89; AUC-test = 0.85). Among the eight variables, the most influential predictor was annual mean temperature, followed by slope. The relative contributions of variables in the model were as follows: (1) annual mean temperature (65.3%); (2) slope (16.8%); (3) precipitation of warmest quarter (5.8%); (4) precipitation of coldest quarter (4.5%); (5) mean diurnal temperature range (2.4%); (6) aspect (2.3%); (7) solar radiation (1.6%); and (8) topographic position index (1.1%). The occurrence probability of *K. septemlobus* decreased with increasing annual mean temperature (Fig. 2a), while it generally increased

with increasing slope (Fig. 2b).

The current suitable habitats, covering 14.2% of the total land area, were mainly found in the protected regions of the Baekdu-daegan, the eastern part of Gyeongbuk province, and the west and central regions of Jeju Island (Fig. 3a). However, more than 50% of current habitat was expected to be rendered unsuitable under RCPs 4.5 and 8.5 (Fig. 3b, c). Particularly in the central and southern regions of South Korea, most patches of suitable habitat were projected to disappear under future climatic conditions (Fig. 3b, c). Under an intermediate scenario, we detected a habitat loss of 57.6% and a habitat gain of 6.3%, resulting in net loss of 51.3% (Table 1). Under a high scenario, we detected a habitat loss of 85.9% and a habitat gain of 0.9%, resulting in net loss of 85.0% (Table 1). Those scenarios also decreased the number of suitable patches in RCPs 4.5 and 8.5 by 51.4% and 83.4%, the size of the largest patch by 62.3% and 96.1%, and the area weighted mean patch size by 69.7% and 97.4%, respectively (Table 2). The mean elevation of future suitable habitats was increased by 88 m and 162 m in RCP 4.5 and RCP 8.5, respectively, from the current mean elevation of 648 m.

The connectivity of the predicted future networks was significantly lower than that of the current network at all threshold distances. In addition, the decreases in connectivity under RCP 8.5 were much higher than that under RCP 4.5 (Fig. 4); more than 99% reduction in connectivity was detected under RCP 8.5 at all threshold distances. Under RCP 4.5 for 2050, the current connectivity level was reduced by almost 77% for the largest dispersal distances and even more for shorter dispersal distances. The average values for the percentage decrease in connectivity over all distances were 78.4% and 99.4% in 2050 under RCPs 4.5 and 8.5, respectively. Moreover, the percentage decreases in network connectivity were consistently higher than decreases in suitable habitat area (i.e., 51.3% and 85.0% for RCPs 4.5 and 8.5, respectively). This result suggests that the loss in habitat area had more deleterious effects on network connectivity.

4. Discussion and conclusions

In this study, we used species distribution modeling coupled with habitat pattern and network analyses to quantify changes in the extent and connectivity of the *K. septemlobus* habitat under current and projected climate conditions for 2050. We found that the distribution of *K. septemlobus* is primarily determined by average annual temperature, indicating that increasing average temperatures due to climate change can be particularly detrimental to the species. As a result, future species distribution models showed that its geographic distribution in South Korea would

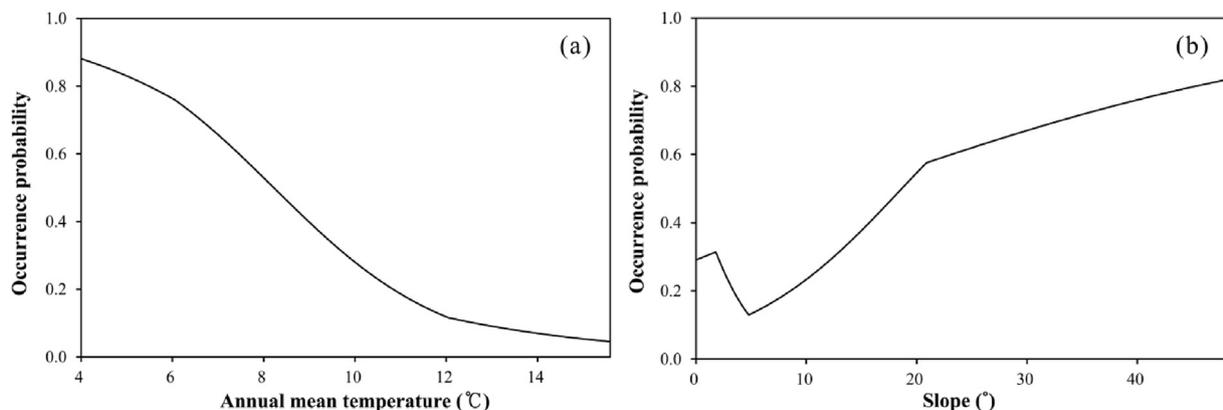


Fig. 2. Response curves of *Kalopanax septemlobus* to gradients of (a) annual mean temperature and (b) slope. Each of the curves represents a MaxEnt model created using only the corresponding variable.

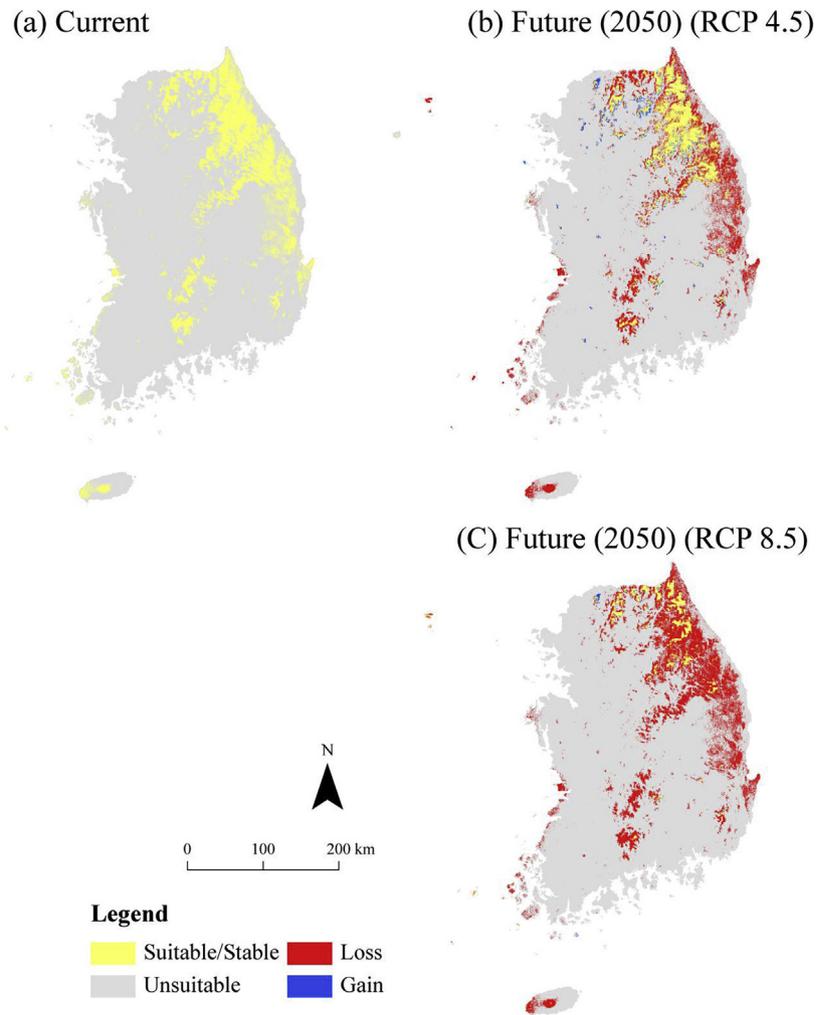


Fig. 3. (a), (b), (c) Predicted current (suitable and unsuitable) and future (suitable/stable, unsuitable, lost, and gained) habitats for *Kalopanax septemlobus*. Future predictions are based on two Representative Concentration Pathway (RCP) scenarios, RCPs 4.5 and 8.5, for the year 2050^a.

Table 1

Current and predicted suitable habitats for *Kalopanax septemlobus* based on two Representative Concentration Pathway (RCP) scenarios, RCPs 4.5 and 8.5, for the year 2050^a.

| | Total habitat | | Stable habitat | | Lost habitat | | Gained habitat | | Net habitat loss | |
|---------|-------------------------|--------|-------------------------|----------|-------------------------|-------|-------------------------|----------|-------------------------|-----|
| | Area (km ²) | | Area (km ²) | (%) | Area (km ²) | (%) | Area (km ²) | (%) | Area (km ²) | (%) |
| Current | 14,299.4 | – | – | – | – | – | – | – | – | – |
| RCP 4.5 | 6961.7 | 6059.5 | 42.4 | 8239.9 | 57.6 | 902.2 | 6.3 | 7337.7 | 51.3 | |
| RCP 8.5 | 2139.2 | 2013.3 | 14.1 | 12,286.1 | 85.9 | 125.9 | 0.9 | 12,160.2 | 85.0 | |

^a Percentages were obtained against the current potential range.

Table 2

Fragmentation metrics for the current and future suitable habitats for *Kalopanax septemlobus* based on two Representative Concentration Pathway (RCP) scenarios, RCPs 4.5 and 8.5, for the year 2050.

| | Number of patches | Area weighted mean patch size (km ²) | Largest patch index |
|---------|-------------------|--|---------------------|
| Current | 10,671 | 4247.8 | 7.7 |
| RCP 4.5 | 5187 | 1288.1 | 2.9 |
| RCP 8.5 | 1769 | 108.9 | 0.3 |

shrink under predicted levels of climate warming. In addition, the resulting changes in the amount of available suitable habitat had a large impact on overall connectivity. If warming continues unabated, most populations of *K. septemlobus* in South Korea will become physically isolated from one another. Therefore, for this

species, a rapid rise of mean temperature will become a severe stress factor. The effects will be particularly extreme if the species lacks capacity to move to other suitable habitat areas and if a lack of gene flow among fragmented populations occurs with the lessened capacity to adapt (Angert et al., 2011; Schloss et al., 2012).

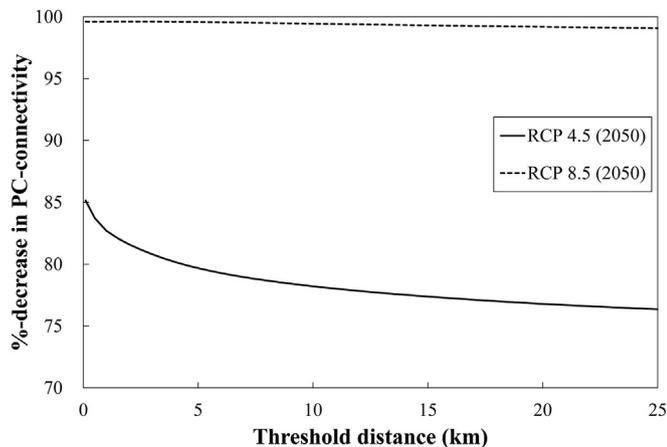


Fig. 4. When compared to current levels of the Probability of Connectivity (PC), percent decrease in PC value resulting from potential shifts in suitable habitats under RCPs 4.5 and 8.5 for 2050 as a function of threshold distance (i.e., dispersal ability).

The MaxEnt model showed that annual mean temperature and slope were the two most important variables predicting habitat suitability for *K. septemlobus*, but variation in the annual mean temperatures explained more than 65% of the total variation in its distribution. This concurs with the results of a previous study suggesting that the ecological niche of this species is constrained mainly by a temperature component among the bioclimatic variables (e.g., Sakaguchi et al., 2010). In regard to slope, some studies reported that *Kalopanax* stands were located in relatively steep- and ridge-slope areas (e.g., Kang and Lee, 1998; Lee et al., 2000), possibly as a result of interspecific competition. Although the growth rate of *K. septemlobus* is high in low-slope valley areas where soil moisture and nutrient are rich, it is known that the species is usually overcome by other competitive tree species and is released to ridge-slope areas (Lee and Kang, 2002).

The predicted current species distribution supported an earlier finding that *K. septemlobus* is widespread both horizontally and vertically in temperate deciduous or coniferous forests of South Korea (Fig. 3a) (Lee and Kang, 2002; Sakaguchi et al., 2012a). However, the model's predictions indicated that this species had a very low probability (<0.25) of occurring in areas with a moderate to high mean annual temperature of 10 °C–16 °C (Fig. 2a). Thus, the species may become increasingly vulnerable to thermal stress associated with climate warming (Allen et al., 2010). Moreover, the model results indicated that persistence of the species may largely depend on its ability to adapt locally to such pressure, which needs further exploration.

With an increase in temperature, the potential range of the species under present climatic conditions would become unsuitable and would shift northwards or to higher elevations (Sakaguchi et al., 2010). The estimated rates of elevational range shift in suitable habitats under the RCPs 4.5 and 8.5 were 17.6 m/decade and 32.4 m/decade, respectively, which are significantly faster than the values previously reported (e.g., Spencer et al., 2010). As a result of range shifts, MaxEnt modeling and habitat pattern analysis predicted the greatest risk of both habitat loss and fragmentation for *K. septemlobus*. The amount of suitable habitat, the number of suitable patches, the size of the largest patch, and the area weighted mean patch size all were projected to decrease by more than 50% by 2050 under the two scenarios, resulting in small populations.

In terms of metapopulation persistence, the ecological network-based index, integrating habitat patch area and connections among patches in a single measure, demonstrated a large reduction in

overall habitat connectivity. Furthermore, the percentage of connectivity loss for each scenario was higher than that expected from the variation in the available suitable habitat area alone or in each habitat pattern metric. This indicates a significant decrease in structural connectivity following habitat loss and fragmentation. Thus, continued warming may create small, isolated populations much more sparsely distributed than those under present condition. Because most seeds of the species are dispersed less than 1 km (N. Fujimori, unpublished), such populations should undergo very limited seed dispersal. In turn, they may be more susceptible to demographic and genetic stochasticity (Gilpin and Soulé, 1986; Goodman, 1987; Shaffer, 1981).

In the case of short distance dispersers such as *K. septemlobus*, the isolation of a potentially suitable habitat located at the center of a species' geographic range raises a concern on the effectiveness of habitat networks because the ability of the species to disperse and colonize newly suitable areas would be restricted (Mazaris et al., 2013). Although climate warming will greatly affect populations inhabiting the southern edge of their distribution ranges (Jueterbock et al., 2014), it can also further weaken the capacity of habitat networks to sustain metapopulations of species with short-range dispersal. For these species, large clusters of functionally connected patches would be broken into several separate clusters if suitable habitats within and surrounding the central parts of the habitat network, currently acting as stepping-stone corridors connecting the large clusters, become smaller and more isolated in response to climate warming. In this sense, the results reported in this study, i.e., the highest reduction in habitat connectivity at lower dispersal distances (Fig. 4), suggest that species with short-range dispersal are more sensitive to habitat connectivity loss under climate change than species with long-range dispersal.

K. septemlobus is a long-lived perennial tree. Long-lived species may persist in fragmented landscapes for long periods during which opportunities for long-distance dispersal of either seed or pollen would increase. Long-lived species also have the potential for rapid adaptation if they have high genetic diversity and large population sizes, whereas short-lived species can evolve rapidly because of their quick generation replacement times. Typical populations of *K. septemlobus* in Korea are small and are known to have very narrow genetic diversity (Sun et al., 2012). Thus, adapting to future climate conditions will be difficult for *K. septemlobus*, particularly if the rate of warming is too rapid. Moreover, considering the dispersal capabilities of *K. septemlobus*, this species will likely be unable to track the projected changes in climate over this century (Sakaguchi et al., 2010).

The complete disappearance of *K. septemlobus* is hardly anticipated, even in areas with decreased habitat suitability by 2050, when considering both the longevity of the species and the competition with other species for limited space (Sakaguchi et al., 2010). For several plant species, climatic responses often lag behind climate change (Bertrand et al., 2011). Although the estimates provided here should not be taken as precise predictions, climate-induced range contraction of *K. septemlobus* is expected to occur throughout the country within the next few decades.

Our results may be conservative because we did not account for the effects of land-use change and elevated CO₂ on *K. septemlobus* habitats. Climate change and agriculture are interrelated processes that threaten biodiversity (MA, 2005). Temperature increases will lead agricultural lands suitable for crops to expand into higher elevational areas. This conversion of natural vegetation to agriculture at high elevations will be an important source of CO₂ emissions. Although elevated CO₂ levels alone may benefit the growth of *K. septemlobus* individuals (Watanabe et al., 2010), *K. septemlobus* will likely experience increases in acute heat stress under elevated CO₂, which can cause large-scale forest mortality events and

subsequent decreases in ecosystem productivity and biodiversity (Ciais et al., 2005; Hamilton III et al., 2008; Thomas et al., 2004). For more accurate future predictions of species distributions, the impacts of the interacting pressures of land use change, elevated CO₂, and climate warming on species should be explored.

K. septemlobus is of ecological and medical importance in Korea. However, over-exploitation combined with climate change will likely lead to its overall population decline, as discussed by Midgley et al. (2003). In addition, it is likely that its remaining range will become disjunct and former metapopulations will become isolated. If a species is not phenotypically plastic, it will be confronted with the high pressure of adapting through evolution or moving through range shifts. And, if a species is unable to do either of these quickly or well, future extinction is likely. It is known that evolutionary responses may be insufficient to keep pace with anthropogenic climate change (Franks et al., 2014). Hence, identifying “climate change refugia”, areas that are suitable under both current and future climates (Franklin et al., 2013), in addition to maintaining or improving connections between the areas to enable range shifts, is important for ensuring species’ long-term persistence. For areas at high risk of habitat loss that are fairly isolated from climate change refugia (i.e., mountain ranges in the southern part of the study area), adaptive strategies such as assisted migration may be implemented (Vitt et al., 2010). Finally, the predictive modeling approach used in this study may also be useful to assess the vulnerability of other threatened species and their habitats to climate change.

Author contributions

W.K. and D.L. designed the study; W.K. and C.-R.P. collected the data; W.K., E.S.M., and C.-R.P. analyzed the data; and W.K. wrote the paper, with substantial contributions from all authors. All authors have read and approved the final manuscript.

Acknowledgments

This study was supported by the Basic Science Research Program through the National Research Foundation of Korea (NRF) funded by the Ministry of Education (No. 2011-0024289).

References

- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manag.* 259, 660–684.
- Angert, A.L., Crozier, L.G., Rissler, L.J., Gilman, S.E., Tewksbury, J.J., Chunco, A.J., 2011. Do species’ traits predict recent shifts at expanding range edges? *Ecol. Lett.* 14, 677–689.
- Bélsisle, M., 2005. Measuring landscape connectivity: the challenge of behavioral landscape ecology. *Ecology* 86, 1988–1995.
- Bertrand, R., Lenoir, J., Piedallu, C., Riofrio-Dillon, G., de Ruffray, P., Vidal, C., Pierrat, J.-C., Gegout, J.-C., 2011. Changes in plant community composition lag behind climate warming in lowland forests. *Nature* 479, 517–520.
- Bodin, Ö., Saura, S., 2010. Ranking individual habitat patches as connectivity providers: integrating network analysis and patch removal experiments. *Ecol. Model.* 221, 2393–2405.
- Boo, K.O., Kwon, W.T., Oh, J.H., Baek, H.J., 2004. Response of global warming on regional climate change over Korea: an experiment with the MM5 model. *Geophys. Res. Lett.* 31, L21206.
- Bunn, A., Urban, D., Keitt, T., 2000. Landscape connectivity: a conservation application of graph theory. *J. Environ. Manag.* 59, 265–278.
- Burnham, K., Anderson, D., 2002. *Model Selection and Multimodel Inference: a Practical Information-theoretic Approach*. Springer, New York.
- Chang, C.S., Kim, H., Kim, Y.S., 2001. Reconsideration of rare and endangered plant species in Korea based on the IUCN red list categories. *Korean J. Plant. Taxon.* 31, 107–142 (in Korean with English abstract).
- Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogee, J., Allard, V., Aubinet, M., Buchmann, N., Bernhofer, C., Carrara, A., Chevallier, F., De Noblet, N., Friend, A.D., Friedlingstein, P., Grunwald, T., Heinesch, B., Keronen, P., Knohl, A., Krinner, G., Loustau, D., Manca, G., Matteucci, G., Miglietta, F., Ourcival, J.M., Papale, D., Pilegaard, K., Rambal, S., Seufert, G., Soussana, J.F., Sanz, M.J., Schulze, E.D., Vesala, T., Valentini, R., 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* 437, 529–533.
- Crooks, K.R., Sanjayan, M.A., 2006. *Connectivity Conservation*. Cambridge University Press, Cambridge.
- Drinnan, I., 2005. The search for fragmentation thresholds in a southern Sydney suburb. *Biol. Conserv.* 124, 339–349.
- Duraipapp, A., Naeem, S., Agardi, T., Ash, N., Cooper, D., Diaz, S., Faith, D., Mace, G., McNeilly, J., Mooney, H., 2005. *Ecosystems and Human Well-being: Biodiversity Synthesis*. World Resources Institute, Washington, DC.
- Escalante, T., Rodriguez-Tapia, G., Linaje, M., Illoldi-Rangel, P., Gonzalez-Lopez, R., 2013. Identification of areas of endemism from species distribution models: threshold selection and Nearctic mammals. *TIP. Rev. Espec. Cienc. Quim Biol.* 16, 5–17.
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.* 34, 487–515.
- Foltête, J.-C., Clauzel, C., Vuidel, G., 2012. A software tool dedicated to the modelling of landscape networks. *Environ. Model. Softw.* 38, 316–327.
- Franklin, J., Davis, F.W., Ikegami, M., Syphard, A.D., Flint, L.E., Flint, A.L., Hannah, L., 2013. Modeling plant species distributions under future climates: how fine scale do climate projections need to be? *Glob. Chang. Biol.* 19, 473–483.
- Franks, S.J., Weber, J.J., Aitken, S.N., 2014. Evolutionary and plastic responses to climate change in terrestrial plant populations. *Evol. Appl.* 7, 123–139.
- Fujimori, N., Samejima, H., Kenta, T., Ichie, T., Shibata, M., Iida, S., Nakashizuka, T., 2006. Reproductive success and distance to conspecific adults in the sparsely distributed tree *Kalopanax pictus*. *J. Plant Res.* 119, 195–203.
- Gilpin, M.E., Soulé, M.E., 1986. Minimum viable populations: processes of species extinction. In: Soulé, M.E. (Ed.), *Conservation Biology: the Science of Scarcity and Diversity*. Sinauer Associates, Sunderland, Massachusetts, pp. 19–34.
- Gonzalez, A., Mouquet, N., Loreau, M., 2009. Biodiversity as spatial insurance: the effects of habitat fragmentation and dispersal on ecosystem functioning. In: Naeem, S., Bunker, D., Hector, A., Loreau, M., Perrings, C. (Eds.), *Biodiversity, Ecosystem Functioning, and Human Wellbeing*. Oxford University Press, New York, pp. 134–146.
- Goodman, D., 1987. How do any species exist? Lessons for conservation biology. *Conserv. Biol.* 1, 59–62.
- Goodwin, B.J., Fahrig, L., 2002. Effect of landscape structure on the movement behaviour of a specialized goldenrod beetle, *Triphaba borealis*. *Can. J. Zool.* 80, 25–34.
- Hamilton III, E.W., Heckathorn, S.A., Joshi, P., Wang, D., Barua, D., 2008. Interactive effects of elevated CO₂ and growth temperature on the tolerance of photosynthesis to acute heat stress in C3 and C4 species. *J. Integr. Plant Biol.* 50, 1375–1387.
- Heller, N.E., Zavaleta, E.S., 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biol. Conserv.* 14–32.
- Hewitt, H., Copsey, D., Culverwell, I., Harris, C., Hill, R., Keen, A., McLaren, A., Hunke, E., 2011. Design and implementation of the infrastructure of HadGEM3: the next-generation Met Office climate modelling system. *Geosci. Model Dev.* 4, 223–253.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25, 1965–1978.
- Honnay, O., Verheyen, K., Butaye, J., Jacquemyn, H., Bossuyt, B., Hermy, M., 2002. Possible effects of habitat fragmentation and climate change on the range of forest plant species. *Ecol. Lett.* 5, 525–530.
- Iida, S., Nakashizuka, T., 1998. Spatial and temporal dispersal of *Kalopanax pictus* seeds in a temperate deciduous forest, central Japan. *Plant Ecol.* 135, 243–248.
- Jenness, J., 2006. *Topographic Position Index (tpi_jen.avx) Extension for ArcView 3.x, v. 1.3a*. Jenness Enterprises. Accessible at the following URL: <http://www.jenness.com/arcview/tpi.htm>.
- Jueterbock, A., Kollias, S., Smolina, I., Fernandes, J.M.O., Coyer, J.A., Olsen, J.L., Hoarau, G., 2014. Thermal stress resistance of the brown alga *Fucus serratus* along the North-Atlantic coast: acclimatization potential to climate change. *Mar. Genom.* 13, 27–36.
- Jung, H.S., Choi, Y., Oh, J.H., Lim, G.H., 2002. Recent trends in temperature and precipitation over South Korea. *Int. J. Climatol.* 22, 1327–1337.
- Kang, H., 2003. *Distribution and Regeneration Strategies of Kalopanax septemlobus in the Natural Deciduous Forest in Gangwon Province, Korea*. Doctoral thesis. Seoul National University, Seoul, p. 138 (in Korean with English abstract).
- Kang, H.S., Lee, D.K., 1998. Site and growth characteristics of *Kalopanax septemlobus* growing at Mt. Joongwang in Pyungchang-gun, Kangwon-do. *J. Korean For. Soc.* 87, 483–492 (in Korean with English abstract).
- Kang, W., Lee, D., Park, C.-R., 2012. Nest distribution of magpies *Pica pica sericea* as related to habitat connectivity in an urban environment. *Landsc. Urban Plan.* 104, 212–219.
- Khanum, R., Mumtaz, A.S., Kumar, S., 2013. Predicting impacts of climate change on medicinal asclepiads of Pakistan using Maxent modeling. *Acta. Oecol.* 49, 23–31.
- Kim, M.-K., Han, M.-S., Jang, D.-H., Baek, S.-G., Lee, W.-S., Kim, Y.-H., Kim, S., 2012. Production technique of observation grid data of 1km resolution. *J. Clim. Res.* 7, 55–68.
- Korea Forest Service (KFS), 2012. *Statistical Yearbook of Forestry*, p. 468 (in Korean).

- Kumar, L., Skidmore, A.K., Knowles, E., 1997. Modelling topographic variation in solar radiation in a GIS environment. *Int. J. Geogr. Inf. Sci.* 11, 475–497.
- Kumar, S., Stohlgren, T.J., 2009. Maxent modeling for predicting suitable habitat for threatened and endangered tree *Canacomyrica monticola* in New Caledonia. *J. Ecol. Nat. Environ.* 1, 94–98.
- Lawler, J.J., 2009. Climate change adaptation strategies for resource management and conservation planning. *Ann. N. Y. Acad. Sci.* 1162, 79–98.
- Lee, C., Choi, Y., Kim, S., Kwon, K., 2000. Site characteristics, and vegetation structure, and dynamics of forest communities growing *Kalopanax septemlobus* (Thunb. ex Murray) Koidz. in Gangwon-do. *Korean J. Plant. Resour.* 13, 227–242 (in Korean with English abstract).
- Lee, D.K., Kang, H.-S., 2002. Distribution of *Kalopanax septemlobus* and its growth in Northeast Asia. *Eurasian J. For. Res.* 5, 85–94.
- Legendre, P., Dale, M.R., Fortin, M.J., Gurevitch, J., Hohn, M., Myers, D., 2002. The consequences of spatial structure for the design and analysis of ecological field surveys. *Ecography* 25, 601–615.
- Li, B.-L., Archer, S., 1997. Weighted mean patch size: a robust index for quantifying landscape structure. *Ecol. Model.* 102, 353–361.
- Mazaris, A.D., Papanikolaou, A.D., Barbet-Massin, M., Kallimanis, A.S., Jiguet, F., Schmeller, D.S., Pantis, J.D., 2013. Evaluating the connectivity of a protected areas' network under the prism of global change: the efficiency of the European Natura 2000 network for four birds of prey. *PLoS One* 8, e59640.
- McGarigal, K., Cushman, S., Ene, E., 2012. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at: the following web site. <http://www.umass.edu/landeco/research/fragstats/fragstats.html>.
- Midgley, G.F., Hannah, L., Millar, D., Thuiller, W., Booth, A., 2003. Developing regional and species-level assessments of climate change impacts on biodiversity in the Cape Floristic Region. *Biol. Conserv.* 112, 87–97.
- Millennium Ecosystem Assessment (MA), 2005. *Ecosystems and Human Well-being*. Island Press.
- Ministry of Environment (ME), 2002. The 2nd National Survey on the Natural Environment (1997–2002) (Korea).
- Minor, E., Urban, D., 2007. Graph theory as a proxy for spatially explicit population models in conservation planning. *Ecol. Appl.* 17, 1771–1782.
- Minor, E.S., Urban, D.L., 2008. A graph-theory framework for evaluating landscape connectivity and conservation planning. *Conserv. Biol.* 22, 297–307.
- Moss, R.H., Edmonds, J.A., Hibbard, K.A., Manning, M.R., Rose, S.K., van Vuuren, D.P., Carter, T.R., Emori, S., Kainuma, M., Kram, T., 2010. The next generation of scenarios for climate change research and assessment. *Nature* 463, 747–756.
- Nussey, D.H., Postma, E., Gienapp, P., Visser, M.E., 2005. Selection on heritable phenotypic plasticity in a wild bird population. *Science* 310, 304–306.
- Ohashi, H., 1994. Nomenclature of *Kalopanax septemlobus* (Thunberg ex Murray) Koidzumi and classification of its infraspecific taxa (Araliaceae). *J. Jpn. Bot.* 69, 28–31.
- Opdam, P., Wascher, D., 2004. Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biol. Conserv.* 117, 285–297.
- Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Syst.* 37, 637–669.
- Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37–42.
- Philander, G., 2012. *Encyclopedia of Global Warming and Climate Change*, second ed. SAGE Publications, Inc, Los Angeles.
- Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. *Ecol. Model.* 190, 231–259.
- Riahi, K., Rao, S., Krey, V., Cho, C., Chirkov, V., Fischer, G., Kindermann, G., Nakicenovic, N., Rafaj, P., 2011. RCP 8.5—A scenario of comparatively high greenhouse gas emissions. *Clim. Change* 109, 33–57.
- Rosenberg, D.K., Noon, B.R., Meslow, E.C., 1997. Biological corridors: form, function, and efficacy. *Bioscience* 47, 677–687.
- Sakaguchi, S., Qiu, Y.-X., Liu, Y.-H., Qi, X.-S., Kim, S.-H., Han, J., Takeuchi, Y., Worth, J.R.P., Yamasaki, M., Sakurai, S., Isagi, Y., 2012a. Climate oscillation during the Quaternary associated with landscape heterogeneity promoted allopatric lineage divergence of a temperate tree *Kalopanax septemlobus* (Araliaceae) in East Asia. *Mol. Ecol.* 21, 3823–3838.
- Sakaguchi, S., Qiu, Y.-X., Liu, Y.-H., Qi, X.-S., Kim, S.-H., Han, J., Takeuchi, Y., Worth, J.R.P., Yamasaki, M., Sakurai, S., Isagi, Y., 2012b. Data from: Climate oscillation during the Quaternary associated with landscape heterogeneity promoted allopatric lineage divergence of a temperate tree *Kalopanax septemlobus* (Araliaceae) in East Asia. Dryad Digital Repository (Accessed 20 Jul 2015). <http://dx.doi.org/10.5061/dryad.91mk9>.
- Sakaguchi, S., Sakurai, S., Yamasaki, M., Isagi, Y., 2010. How did the exposed seafloor function in postglacial northward range expansion of *Kalopanax septemlobus*? Evidence from ecological niche modelling. *Ecol. Res.* 25, 1183–1195.
- Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., 2000. Global biodiversity scenarios for the year 2100. *Science* 287, 1770–1774.
- Saura, S., Pascual-Hortal, L., 2007. A new habitat availability index to integrate connectivity in landscape conservation planning: comparison with existing indices and application to a case study. *Landscape Urban Plan.* 83, 91–103.
- Schloss, C.A., Nuñez, T.A., Lawler, J.J., 2012. Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. *Proc. Natl. Acad. Sci. U. S. A.* 109, 8606–8611.
- Shaffer, M.L., 1981. Minimum population sizes for species conservation. *Bioscience* 31, 131–134.
- Spencer, W., Beier, P., Penrod, K., Winters, K., Paulman, C., Rustigian-Romsos, H., Strittholt, J., Parisi, M., Pettler, A., 2010. California essential Habitat Connectivity Project: a Strategy for Conserving a Connected California. California Department of Transportation, California Department of Fish and Game, and Federal Highways Administration.
- Sun, Y.-L., Lee, H.-B., Kim, N.-Y., Park, W.-G., Hong, S.-K., 2012. Genetic diversity of *Kalopanax pictus* populations in Korea based on the nrDNA ITS sequence. *J. Plant Biotechnol.* 39, 75–80.
- Taylor, P.D., Fahrig, L., Henein, K., Merriam, G., 1993. Connectivity is a vital element of landscape structure. *Oikos* 68, 571–573.
- Templeton, A.R., Robertson, R.J., Brisson, J., Strasburg, J., 2001. Disrupting evolutionary processes: the effect of habitat fragmentation on collared lizards in the Missouri Ozarks. *Proc. Natl. Acad. Sci. U. S. A.* 98, 5426–5432.
- Theobald, D.M., Reed, S.E., Fields, K., Soulé, M., 2012. Connecting natural landscapes using a landscape permeability model to prioritize conservation activities in the United States. *Conserv. Lett.* 5, 123–133.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Townsend Peterson, A., Phillips, O.L., Williams, S.E., 2004. Extinction risk from climate change. *Nature* 427, 145–148.
- Thomson, A.M., Calvin, K.V., Smith, S.J., Kyle, G.P., Volke, A., Patel, P., Delgado-Arias, S., Bond-Lamberty, B., Wise, M.A., Clarke, L.E., 2011. RCP4.5: a pathway for stabilization of radiative forcing by 2100. *Clim. Change* 109, 77–94.
- Urban, D., Keitt, T., 2001. Landscape connectivity: a graph-theoretic perspective. *Ecology* 82, 1205–1218.
- Urban, D., Minor, E., Treml, E., Schick, R., 2009. Graph models of habitat mosaics. *Ecol. Lett.* 12, 260–273.
- Vitt, P., Havens, K., Kramer, A.T., Sollenberger, D., Yates, E., 2010. Assisted migration of plants: changes in latitudes, changes in attitudes. *Biol. Conserv.* 143, 18–27.
- Warren, D.L., Glor, R.E., Turelli, M., 2010. ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography* 33, 607–611.
- Warren, D.L., Seifert, S.N., 2011. Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecol. Appl.* 21, 335–342.
- Watanabe, Y., Satomura, T., Sasa, K., Funada, R.Y.O., Koike, T., 2010. Differential anatomical responses to elevated CO₂ in saplings of four hardwood species. *Plant Cell Environ.* 33, 1101–1111.
- With, K.A., King, A.W., 1999a. Dispersal success on fractal landscapes: a consequence of lacunarity thresholds. *Landscape Ecol.* 14, 73–82.
- With, K.A., King, A.W., 1999b. Extinction thresholds for species in fractal landscapes. *Conserv. Biol.* 13, 314–326.