Report

The Circe Principle Explains How Resource-Rich Land Can Waylay Pollinators in Fragmented Landscapes

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Summary

Global declines in pollinators, associated with land-use change [1–6] and fragmentation [7–10], constitute a serious threat to crop production and biodiversity [11]. Models investigating impacts of habitat fragmentation on pollen flow have categorized landscapes simply in terms of habitat and non-habitat. We show that pollen flow depends strongly on types of land use between habitat fragments. We used paternity analysis of seeds and a combination of circuit and general linear models to analyze pollen flow for the endangered tree *Gomortega keule* (Gomortegaceae) [12] in the fragmented Central Chile Biodiversity Hotspot [13]. Pollination probability was highest over pine plantation, moderate over low-intensity agriculture and native forest, and lowest over clearfells. Changing the proportions of the land uses over one kilometer altered pollination probability up to 7-fold. We explain our results by the novel "Circe principle." In contrast to models where land uses similar to native habitat promote pollinator movement, pollinators may actually be waylaid in resource-rich areas between habitat patches. Moreover, pollinators may move with higher probability between habitat patches separated by some resource-poor land uses. Pollination research in fragmented landscapes requires explicit recognition of the nature of the nonhabitat matrix, rather than applying simple binary landscape models.

Results

We used paternity assignment of seeds of *Gomortega keule* (detailed in [14]) to map effective movement of mainly syrphid fly pollinators [15] between all possible paternal and maternal tree pairs in the study area. We found an extensive network of pollinator movement in this highly fragmented land-use mosaic. Our results showed movement over distances up to 6 km, outside of the native forest, between habitat patches, from small sites and single trees to large sites as well as in the other direction ([14], in contrast to [16]). However pollination was not detected over many of the possible tree-to-tree connections (Figure 1).

The empirical pollinator movement data was overlaid on a map of the study area classified into four readily identifiable predominant land-use types: agriculture (subsistence farms under low-intensity management), timber plantations (Monterey pine, *Pinus radiata*), clearfells (recently felled pine plantations), and native forest (broadleaf and primarily evergreen forest dominated by wind-pollinated Southern beech, *Nothofagus glauca* and *N. obliqua*; flowering trees, including *Aextoxicon punctatum, Persea lingue*, and *Gevuina avellana*; and limited understory vegetation [17]) (Figure 1). The influence of land-use type on the probability of pollination between pairs of trees was estimated in both a general linear model and a circuit model.

General Linear Model

A general linear model (GLM) was used to predict pollination probability between pairs of trees (Equation 1) (R v. 2.11.1 [18]). The fitted probabilities of this GLM were linearly related to the observed values (in binned distances), with a correlation coefficient of 0.88.

$$\text{logit}[P] = b_0 + b_1 S_M + b_2 S_F + b_3 \log(D_{tot}) + b_4 R_A + b_5 R_P + b_6 R_C + b_7 C_{tot}$$

(Equation 1)

$[P]$ is the probability of pollination success; b_x are coefficients; S_M and S_F are the diameter at 1.3 m height of the mother and father trees, respectively; D_{tot} is the total distance (+1 m) between trees; R_A, R_P, and R_C are the fractions of the total distance made up by agriculture, plantations, and clearfells, respectively; and C_{tot} is the number of fragments between the pairs, a measure of landscape complexity (see Table 1).

Of the four land-use types tested in this GLM, fraction of total distance occupied by plantation showed the highest pollination probability, and the lowest pollination probability was through clearfell areas. Agricultural areas showed a pollination probability not significantly different from that of native forest (Table 1). This is in contrast to some studies of insect-pollinated trees that have found that pollinators fly farther across open habitats (e.g., [19]) and suggests that there may be behavioral differences between those study organisms and *G. keule*'s pollinators. The probability of pollination over each of the land-use types may be compared in a pairwise fashion using the coefficients of the GLM (Table 2). Pine plantation and clearfell showed the greatest differentiation, with travel over 1 km of plantation 26.8 times more likely than travel over 1 km of clearfell.

The GLM was also used to model pollination probabilities in alternative hypothetical landscape scenarios. Figure 2 shows all possible scenarios in which the area between a maternal and paternal tree pair contains all four land-use types, each present as a single contiguous patch in units of 10% of the landscape. A clear pattern is visible wherein the greater the proportion of clearfell area in the landscape, the lower the logit estimate of pollination probability. Conversely, the greater the proportion of plantation and native forest in the landscape, the greater the logit estimate of pollination probability. Moderate estimates of pollination probability are achieved with near equal proportions of the four land-use types. Once the logit estimate of the pollination probability for a given scenario is calculated, it is possible to directly compare the likelihood of

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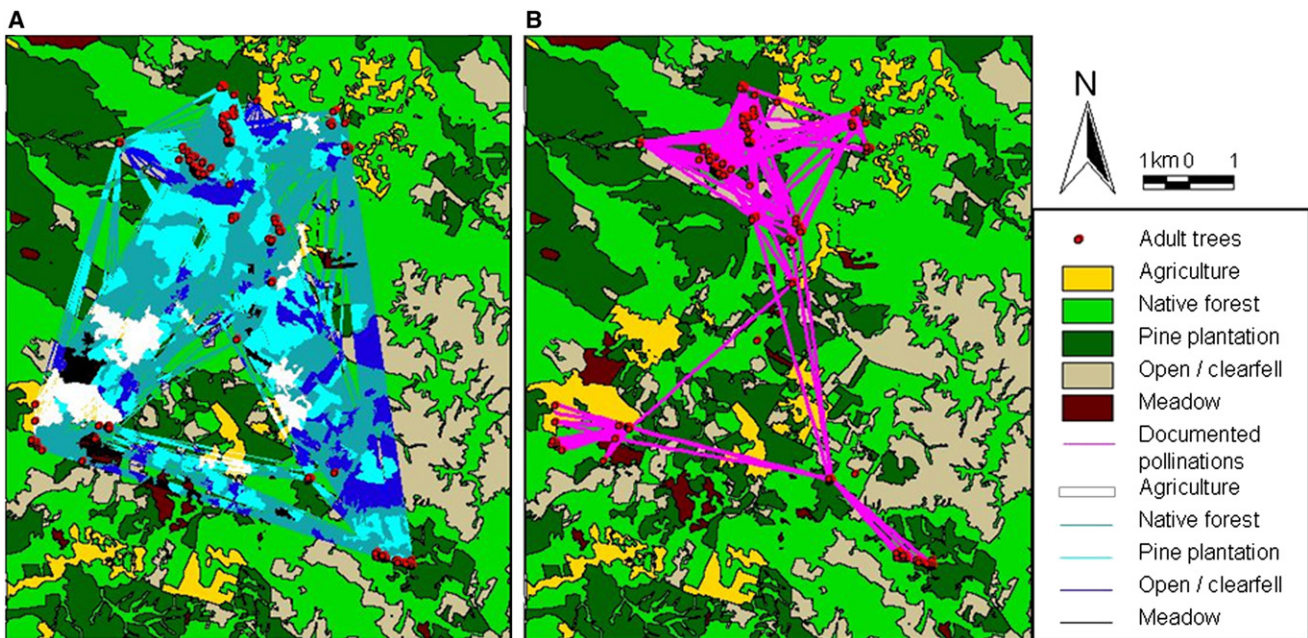*Correspondence: david.boshier@plants.ox.ac.uk

Figure 1. Map of Land-Use Types and Pollen Movement in the Study Area in Maule, Chile

(A) Location of the 443 adult *Gomortega keule* trees (red dots) and all possible connections between the trees subdivided into the land-use types that they cross (blue, white, and black lines).

(B) Location of the 443 adult *G. keule* trees (red dots) and lines representing all documented pollination events (pink lines).

pollinator travel in alternative landscape scenarios. For example, the landscape scenario at the bottom of Figure 2 contains 0.7 km of clearfell and 0.1 km each of native forest, plantation, and agriculture. The landscape scenario at the top of the graph contains 0.7 km of plantation and 0.1 km each of native forest, agriculture, and clearfell. Calculation of the odds ratio shows that pollination is 7.156 times more likely in the landscape at the top of the graph than in the landscape at the bottom of the graph (Equation 2).

$$\begin{aligned} \text{logit (pollination line)} &= \text{intercept} + (\text{proportion of distance} \\ &\quad \text{over native forest} \times 1.00) + (\text{proportion of distance over} \\ &\quad \text{agriculture} \times 0.89) + (\text{proportion of distance over plantation} \\ &\quad \times 1.2) + (\text{proportion of distance over clearfell} \times -2.08) \\ &\quad + (\log(\text{total distance}) \times -0.46) + (4 \times -0.063)^* \\ &\quad + (25 \times 0.03)^\S + (25 \times 0.01) \end{aligned}$$

*Where one patch of each land-use type is crossed
§Where the diameter of both the seed and pollen trees is 25 cm

logit (landscape with 0.7 km of plantation and 0.1 km each of native forest, agriculture, and clearfell) = −3.541
logit (landscape with 0.7 km of clearfell and 0.1 km each of native forest, plantation, and agriculture) = −5.509
log(odd ratio) = logit (landscape a) − logit (landscape b) = 1.968
odds ratio = 7.156

(Equation 2)

Circuit Model

Electrical circuit, or resistor network, models are increasingly used to investigate flows of organisms and genes across landscapes [20]. Circuit models benefit from mathematical homology with diffusion and random walks, with variables that are readily interpretable from a biological perspective. However, these models are computationally intense, and the

development of numerical methods that allow parameterization of landscape permeability at high spatial resolution is a work in progress [21]. The outputs of the GLM were used to parameterize a circuit model of the landscape using the ResistorArray package v. 1.0-26 for R [22], in which each landscape type has a resistance inversely proportional to the probability of pollination across it. The landscape was first rasterized to produce grid cells of equal size. The maximum spatial resolution of the circuit network possible under the computer systems available was 250 m, giving 2530 cells in total. All 443 trees fell within 45 cells. Each cell was modeled as a resistor with resistance inversely proportional to the probability of pollination across the appropriate land-use type. Each cell was connected to its four cardinal neighbors (except for cells on the boundary). A null model was also created with resistance equal for each land use. The circuit models were solved to give expected resistance between all pairs of cells containing trees, and these expectations were compared with actual pollinations using GLM. The null model gave a significantly better fit to the data than the parameterized model (likelihood ratio test, G = 182.4, df = 3, p < 0.0001).

Discussion

Landscape ecology is often framed in terms of island biogeography-based ideas that (1) habitat and nonhabitat are clearly distinguishable and (2) nonhabitat is wholly hostile for organism travel [4, 23–25]. Consequently, interest in the effects of human modification of landscapes on genetic processes has focused on the impacts of spatial isolation due to habitat fragmentation [26]. This research is frequently framed in terms of how probable it is that an organism will pass through a certain area when moving between habitat patches, also called landscape connectivity and permeability. Although the permeability concept recognizes the potential for variation in

Table 1. General Linear Model of Pollination Probability

Predictor	From Equation 1	VIF	Coefficient	Standard Error	p Value
Intercept	–	–	−3.73	0.15	<0.0001
Proportion of total distance, agriculture	R_A	1.28	0.89	0.85	0.29
Proportion of total distance, plantation	R_P	1.10	1.21	0.14	<0.0001
Proportion of total distance, clearfell	R_C	1.48	−2.08	0.60	<0.0001
log(total distance between the parental trees)	D_{tot}	1.84	−0.46	0.027	<0.0001
Total number of patches crossed	C_{tot}	1.71	−0.063	0.014	<0.0001
Mother tree diameter at 1.3 m height	S_M	1.05	0.025	0.002	<0.0001
Father tree diameter at 1.3 m height	S_F	1.03	0.011	0.002	<0.0001

See Equation 1. The effect of the eight variables on pollination probability for pairs of *Gomortega keule* trees in Maule, Chile, was tested in a general linear model using empirical pollen movement data from paternity analysis of seeds. The coefficients show the strength of the effect of the variable on the logit probability of pollination in comparison to the condition where 100% of the path between a pair of trees is native forest. Over all distances, the correlation between observed and expected probabilities was 0.88. Variance inflation factors (VIF) were small, indicating absence of multicollinearity in predictors.

nonhabitat resistance to pollinator movement, both the connectivity and permeability concepts are strictly based on a binary landscape model wherein the focus remains on organisms' presence in distinct habitat patches and organisms' ability to pass between habitat patches over other land uses with varying degrees of success.

Although there is a recognized need for ecologically explicit models that investigate functional connectivity from the perspective of study organisms [4, 27], and indeed the potential habitat-like contributions of apparently nonhabitat areas, existing models have not incorporated detailed empirical ecological or spatial information about nonhabitat ecosystems or attempted to specifically quantify land-use permeability [28, 29]. Indeed, of reviewed landscape genetics papers, Storfer [30] found that only 0.6% used plants as study organisms and investigated a specific hypothesis of how the landscape between individuals would affect genetic processes. Moreover, models aimed at predicting processes at the ecosystem level have rarely been based on field data [3, 31–33]. The few models that have incorporated variation in land-use permeability have used resistance value optimization with initial land-use permeability values based on expert opinion rather than empirical data [27]. In addition, in these models, genetic distance is frequently used as a surrogate for direct measures of dispersal ([27], but see [21]). Spear et al. [27] note that "the biggest challenge for modeling resistance surfaces is the assignment of resistance values to landscape features, as the actual effects of different cover types on movement, survival, abundance, and reproduction are generally unknown."

The assumptions of pollinator behavior between the two approaches (GLM versus circuit model) are fundamentally different (linear movement versus random walk), and as such, the GLM values cannot be expected to predict movement

under different pollinator movement assumptions. The GLM showed that pollination probability varies significantly over different land-use types, and that landscape arrangement may have major affects on pollination probability in fragmented landscapes when linear pollinator movement between trees is assumed. The GLM results did not provide a better fit to the pollination data than the null model when used to parameterize the circuit model. Parameterization of resistances using circuit models will require the development of efficient optimization algorithms able to test large numbers of parameter values on landscapes rasterized at high spatial resolutions.

Interestingly, our GLM showed not only that land uses differed in their effect on pollination probability but that pollination was most probable when pollinators traveled over areas of pine plantation, even though *G. keule* is mainly found in areas of native forest and is only present as small stands or single trees in plantation and agricultural areas [15] (Figure 1). Low-intensity agriculture showed moderate pollination probability similar to that of native forest, and clearfells were the land use most negatively correlated with pollination probability. Although these results may appear counterintuitive at first, several landscape genetic studies have revealed that features previously assumed to be barriers to gene flow, such as rivers
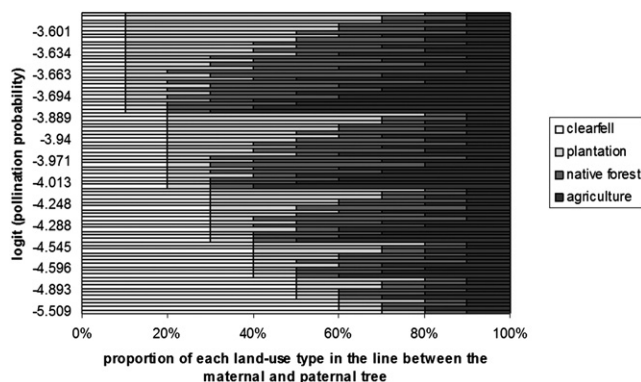
Figure 2. Pollination Probabilities for Landscape Scenarios with Different Proportions of Four Land-Use Types

Probabilities are shown as logits (see Equation 1). The log odds ratio of two scenarios is the difference between the logits of the two scenarios (see Equation 2); e.g., the odds of pollination across one kilometer containing 70% agriculture and 10% each of native forest, plantation, and clearfell (top of graph) are 7.156 times the odds of pollination across one kilometer containing 10% each of agriculture, native forest, and plantation and 70% clearfell (bottom of graph).

Table 2. Pairwise Comparison of Pollination Probability over One Kilometer of Each of the Four Land-Use Types

A (down)	B (across) Clearfell	Native Forest	Agriculture	Plantation
Clearfell	–	8.0	19.5	26.8
Native Forest	–	–	2.4	3.3
Agriculture	–	–	–	1.4
Plantation	–	–	–	–

The values shown are the odds ratios of the probability of pollinator travel and are calculated based on the logit values in Table 1 as shown in Equation 2. In all pairwise comparisons, the probability of travel over land use B (across) is greater than the probability of travel over land use A (down).
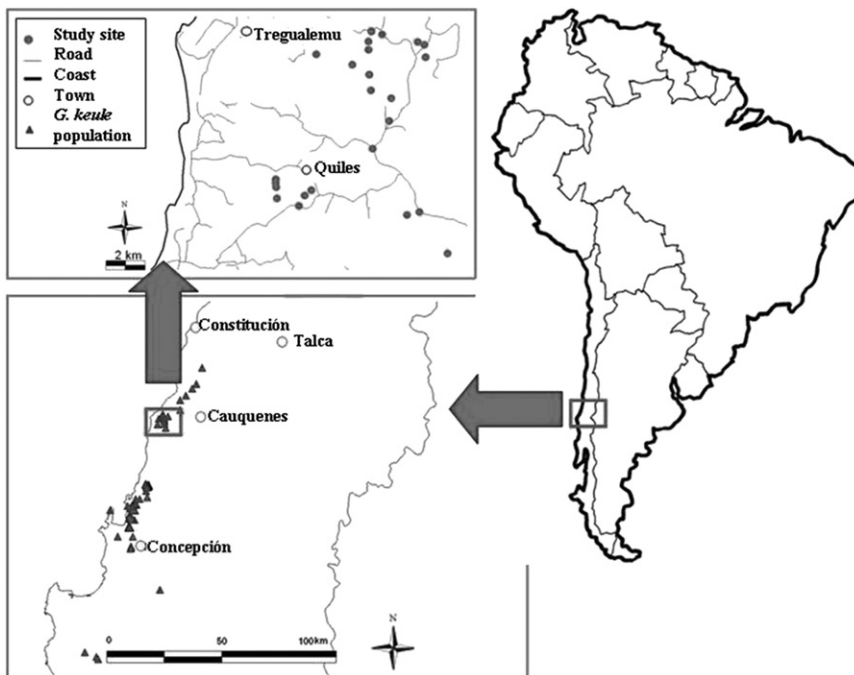
Figure 3. Map of the Study Area
The rectangle on the map of South America (right) shows the global distribution of *G. keule*, which lies within the Maule and Bío-Bío Regions of Chile. The triangles on the map of central Chile (bottom left) represent the known populations of *G. keule* [41]; the rectangle indicates the study area. The study area map (top left) shows the center points of the 26 study sites and local roads.

The low-intensity subsistence agriculture in the study area provides continuous vegetation cover and a variety of flowering plants that are likely to provide pollen and nectar resources for much of the year. The pollinators appear to move out of native forest areas into these agricultural areas [15] but move through the agricultural areas into native forest areas with a lower probability than they move through plantation into native forest. If the pollinators find suitable resources in the agricultural areas, it is reasonable that they remain inside the agricultural areas and do not forage further than necessary, i.e., in agreement with optimal foraging theory [36], which may be applied to most pollinator types. Pine plantations also provide a continuous cover of pollen-producing vegetation, although because the plantations contain a single tree species and little ground cover, the seasonal duration and diversity of resources are more limited than in the agricultural areas. Pollinators may therefore be less likely to find valuable resources in plantation areas than in agricultural areas and thus forage more widely, resulting in a greater probability that they cross the plantation area and reenter native forest. The low probability of travel across clearfell areas may be explained by the lack of vegetation cover, because it has been suggested that breaks in vegetation ground cover present a barrier to syrphid flies [35]. Such complete barriers to organism movement fall outside of the dynamics described by the Circe principle. It must be noted that although pine plantations showed the highest probability of pollination and clearfells the lowest, there is an intrinsic link between plantations and clearfells in most industrial forest plantation management systems. Thus, although the impacts of clearfells and plantations can be modeled separately, in practice their conservation and landscape connectivity impacts are related.

Our results allow specific identification of actions that can improve landscape functionality with respect to this endangered tree species and other species pollinated by generalist insects. Support for subsistence farms and modification of management practices to reduce the size of individual clearfells are likely to have significant positive impacts on the viability of pollinator populations and the probability of pollinators moving across the landscape between fragments of native forest. The results also support the need for a broader vision of biological corridors that embraces a range of land-use possibilities, rather than just continuous corridors of intact habitat. Our results more broadly suggest that the landscape should be viewed as a mosaic of habitats of varying quality and that the probability of pollinator movement must be analyzed on this more complex basis. New models need to

and postfire habitat, may actually facilitate gene flow, depending on the ecology of the study organisms [30].

Based on the general hoverfly (Syrphidae) adult ecology described below, we propose an explanation of our results and present the novel "Circe principle" that arises from these results. Syrphid flies are a globally common pollinator type [34], appear to be the main pollinators of *G. keule*, and were found to carry the pollen of various plant species in the study area [15]. Information on the autoecology of the specific Syrphidae collected on *G. keule* is not available. However, in general, syrphid adults feed on nectar and pollen, with different species utilizing various nectar-bearing and anemophilous trees, shrubs, and herbs. Because the adults feed on both pollen and nectar, are highly vagile, have excellent vision, and appear able to opportunistically use ephemeral resources, they are expected to be able to benefit from various plant resources in complex landscapes [35]. It has been suggested, however, that syrphid flies are less likely to cross areas with breaks in vegetation ground cover, such as clearfells, than areas with continuous vegetation [35].

The Circe Principle

In Homer's *Odyssey*, Circe enchanted Odysseus' crew at a feast at her home on the island of Aeaea. Odysseus bargained with Circe to lift the enchantment, and he and his men remained feasting on the island for a year before recommencing their journey home to Ithaca. Many existing models for organism movement in fragmented landscapes assume that generalist pollinators will travel with higher probability through amenable (permeable) land uses, especially those most similar to native habitat. The Circe principle postulates the reverse: pollinators presented with a wealth of resources, whether inside or outside traditionally defined habitat, are, like Odysseus' crew, likely to move through it slowly or not leave it at all. In contrast, pollinators presented with hostile or resource-poor land uses might not enter, but if they do, they are likely to move through it as quickly as possible.

explicitly recognize the varied nature and the possible positive ecological contributions of the nonhabitat matrix, of spatially isolated individuals and small remnant habitat patches, and to investigate how best to manage these partial habitats. The previous lack of differentiation between nonhabitat land-use types has contributed to the polarization of the conservation debate and left decision makers with the unenviable task of choosing between economic activity or the setting aside of land for conservation. As landscapes around the globe are increasingly fragmented by humans, understanding the effects of land-use type on functional connectivity among populations will become essential for conservation and management [30]. The information presented here could be used to design landscape-level management plans in human-modified landscapes to increase landscape-scale genetic connectivity and support the maintenance of genetic diversity, especially for endangered species such as *G. keule*.

Experimental Procedures

We sampled all 443 adult *Gomortega keule* trees found during an intensive field survey of a 10 × 8 km area on the border between the Maule and Bío-Bío Regions of Chile (Figure 1; Figure 3). We sampled up to 35 seeds from all 144 trees producing seeds in the survey area (1119 seeds) and generated unique genetic fingerprints for each tree and seed using six microsatellite markers [37]. We then identified the specific sire of each seed by paternity analysis (CERVUS [38]; analysis detailed in [14]). We used patterns of paternity among outcrossed seeds of *G. keule* and GIS software (ERDAS Imagine) to construct a matrix that included (1) the distance and direction of pollinator movement responsible for each successful fertilization and (2) the number of patches and proportion of each of the four land-use types over which an insect would have flown in a straight line for every possible combination of pollen tree and seed tree among the sampled trees. The matrix linking 443 trees yielded a total of 195,806 paths (Figure 1). The matrix is asymmetrical (i.e., the path "tree A to tree B" is not equivalent to the path "tree B to tree A") because (1) wind and topography may have different effects depending on the direction of travel, (2) movement from large to small sites is not the same as movement from small to large sites [14], and (3) the empirical data on effective pollination did not produce a symmetrical matrix. Moreover, other authors have found that incorporating the possibility for asymmetrical barriers between sites is important for realistic analyses [39].

Insect pollinators may not travel in a straight line from one tree to the next, and thus travel distances between trees and the distances of each of the land uses used in this study are minimum approximations. According to Spear et al. [27], transect-based methods have the potential to lead to unbiased estimates of landscape connectivity because they correctly use the empirical (i.e., genetic) data as the dependent variable and infer landscape influences on functional connectivity based on these empirical data. This is different from most current landscape genetic studies, which define landscape connectivity a priori, by developing resistance surfaces and then testing whether the empirical data support the assumptions reflected in these surfaces [30]. Because the goal of this research was to measure resistance values, it was inappropriate to assign these values in advance.

G. keule has self-compatible, protogynous flowers [15] that show a generalist pollination syndrome [40]. The species has a long flowering season, from March to June, with individual trees showing a steady-state syndrome of species that produce few flowers but continue to flower for a long period [15]. There may be asynchrony between individual trees' flowering during this long season, and phenological data for all of the trees included in this study are not available. However, because of the steady-state syndrome, the flowering pattern is likely to be similar through the flowering season, and we suggest that phenological asynchrony between individuals is less likely as a source of error in terms of trees included as potential pollen donors than are trees that did not flower at all. Importantly, trees that did not flower will not have donated pollen preferentially to any of the other trees or sites.

Acknowledgments

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