Molecular Ecology (2008) **17**, 2865–2879 doi: 10.1111/j.1365-294X.2008.03807.x

Inferring recruitment history from spatial genetic structure within populations of the colonizing tree *Albizia julibrissin* (Fabaceae)

E. A. PARDINI and J. L. HAMRICK
Department of Plant Biology, University of Georgia, Athens, GA 30602-7271, USA

Abstract

Comparative analyses of spatial genetic structure (SGS) among species, populations, or cohorts give insight into the genetic consequences of seed dispersal in plants. We analysed SGS of a weedy tree in populations with known and unknown recruitment histories to first establish patterns in populations with single vs. multiple founders, and then to infer possible recruitment scenarios in populations with unknown histories. We analysed SGS in six populations of the colonizing tree *Albizia julibrissin* Durazz. (Fabaceae) in Athens, Georgia. Study sites included two large populations with multiple, known founders, two small populations with a single, known founder, and two large populations with unknown recruitment histories. Eleven allozyme loci were used to genotype 1385 individuals. Insights about the effects of colonization history from the SGS analyses were obtained from correlograms and *Sp* statistics. Distinct differences in patterns of SGS were identified between populations with multiple founders vs. a single founder. We observed significant, positive SGS, which decayed with increasing distance in the populations with multiple colonists, but little to no SGS in populations founded by one colonist. Because relatedness among individuals is estimated relative to a local reference population, which usually consists of those individuals sampled in the study population, SGS in populations with high background relatedness, such as those with a single founder, may be obscured. We performed additional analyses using a regional reference population and, in populations with a single founder, detected significant, positive SGS at all distances, indicating that these populations consist of highly related descendants and receive little seed immigration. Subsequent analyses of SGS in size cohorts in the four large study populations showed significant SGS in both juveniles and adults, probably because of a relative lack of intraspecific demographic thinning. SGS in populations of this colonizing tree is pronounced and persistent and is determined by the number and relatedness of founding individuals and adjacent seed sources. Patterns of SGS in populations with known histories may be used to indirectly infer possible colonization scenarios for populations where it is unknown.

Keywords: *Albizia julibrissin*, allozymes, colonization, seed dispersal, spatial autocorrelation, spatial genetic structure

Received 8 December 2007; revision received 8 April 2008; accepted 16 April 2008

Introduction

Local spatial genetic structure (SGS), or the nonrandom distribution of genotypes within populations, is determined by a variety of reproductive, ecological, and genetic processes including seed dispersal, spatial distribution of adults, and microhabitat selection. In plants, local distribution of genetic diversity is determined by both pollen and seed dispersal. Because of the sedentary lifestyle of plants, genetic structure may be pronounced within populations. A growing body of literature demonstrates the utility of using patterns of SGS within plant populations to infer breeding behaviour and recruitment history (Premoli &

Correspondence: E. A. Pardini, Biology Department, Washington University in St. Louis, One Brookings Drive, Box 1137, Saint Louis, MO 63130, USA. Fax: 314-935-4432; E-mail: epardini@wustl.edu

Kitzberger 2005; Jones *et al*. 2006; Williams *et al*. 2007). In addition, SGS analyses over time or across size or age cohorts can yield insights into temporal changes in SGS due to recruitment patterns and demographic thinning (Berg & Hamrick 1995; Troupin *et al*. 2006). Comparative analyses across sites or populations (e.g. Parker *et al*. 2001; Miyamoto *et al*. 2002; Jacquemyn *et al*. 2005) provide insights into seed dispersal and colonization history.

In plants, the magnitude of SGS is determined by seed dispersal and the mating system, which together, influence relatedness among individuals. The distance over which structure occurs is influenced primarily by seed dispersal and adult density (Dyer 2007). Localized seed dispersal or animal behaviour such as caching can result in related individuals germinating close to one another and thus higher levels of SGS (e.g. Aldrich & Hamrick 1998; Jones *et al*. 2006). Population density influences seed shadow overlap, and thus the spatial scale at which structure is evident. High density populations with increased overlap of seed shadows exhibit less genetic structure (Hamrick *et al*. 1993; Gapare & Aitken 2005). In addition, the number and relatedness of founding individuals can greatly affect genetic structure in plant populations (McCauley *et al*. 1995; Wade & McCauley 1988; Whitlock & McCauley 1990). Thus, historical events that influence the number, relatedness, and density of seed sources such as colonization (Asuka *et al*. 2004; Litrico *et al*. 2005; Jones *et al*. 2006; Williams *et al*. 2007) and disturbance (Knowles *et al*. 1992; Takahashi *et al*. 2000; Parker *et al*. 2001; Premoli & Kitzberger 2005; Ally & Ritland 2007) can play an important role in structuring local genetic diversity.

SGS analyses estimate average pairwise relatedness among individuals within spatial distance classes relative to individuals drawn randomly from the entire population (Smouse & Peakall 1999; Hardy 2003; Vekemans & Hardy 2004). Results are depicted in a correlogram, in which the *x*-axis represents spatial distance and the *y*-axis represents the average pairwise relatedness of individuals within each distance class. The distance at which relatedness crosses zero can be interpreted as the distance that individuals are on average as genetically related to one another as two randomly sampled individuals. It is highly dependent on the sampling scheme and the arbitrarily set distance classes used in the analysis (Vekemans & Hardy 2004).

The ability to detect SGS is influenced by allele frequencies within the population, sample sizes, and the distance sampled relative to the distance over which structure occurs (Rousset 2002; Vekemans & Hardy 2004; Cavers *et al*. 2005). Absolute values of relatedness can be dependent on the sampling scheme (Dutech *et al*. 2002) and genetic marker system (Ng *et al*. 2004; Cavers *et al*. 2005; Hardy *et al*. 2006; Jump & Penuelas 2007). Note that genetic relatedness is estimated from marker-based similarity between pairs of individuals relative to a reference population, which is often defined as all sampled individuals within the population being analysed (described hereafter as the *local* reference population). By definition, average relatedness over all pairs of individuals within the reference population is zero (Hardy 2003). If the reference population consists of highly related individuals, it may obscure local SGS and lead to incorrect inferences about seed dispersal. For example, a population resulting from a single founder with little immigrant seed recruitment will largely consist of at least half-sibling descendants of the founder. If analysis is performed using a local reference population, it may be difficult to identify significant SGS because, as most individuals are at least half-siblings and background relatedness is high, the average relatedness of pairs of near neighbours may not be (detectably) higher than that of two randomly chosen individuals. A lack of detectable SGS in this case does not indicate panmictic seed dispersal but is a function of the relatedness of individuals in the local population and the estimator. Incorporating regional patterns of allele frequencies can give greater insight into local SGS. Utilizing a *regional* reference population comprised of genotypes from across the landscape, rather than the highly related local reference population, allows detection of subtle, local SGS.

We examined genetic diversity and SGS within populations of the naturalized tree *Albizia julibrissin* (Fabaceae) in Athens, Georgia. *Albizia julibrissin* displays high levels of allozyme polymorphism, and since several populations have been monitored for 10–15 years, observational data about historical recruitment is available. We quantified the existence, strength, and patterns of SGS in sites where *A. julibrissin* has heavily invaded. To fully characterize the effects of recruitment history on structuring of genetic diversity, we examined SGS in two size cohorts (juveniles and adults) within six study populations representing different colonization histories. Study sites included two large populations with multiple, known founders, two small populations with a single, known founder, and two large populations with unknown recruitment histories. We performed further analyses using a regional, rather than local, reference population to elucidate SGS patterns. Here we characterize patterns of SGS between populations with contrasting known colonization histories and then use these patterns to infer likely colonization scenarios in populations with unknown histories.

Individuals within the study populations consist of first-generation founders, second-generation recruits, and immigrant recruits from adjacent reproductive adults. *Albizia julibrissin* is pollinated by generalists including long-distance flyers such as bees and hummingbirds (Godt & Hamrick 1997). Thus, pollen donors to individuals within the study plots could be located within or adjacent to the plot, but also at some distance from the plot. If early recruits are the progeny of a few maternal plants and are sired by a few pollen donors, genetic diversity should be limited in the

larger (adult) cohort. If recruits share seed sources within but not among cohorts, genetic diversity should be structured among cohorts. We hypothesized that SGS in populations with multiple colonists would be present but weak, due to the overlap of many seed shadows. Because our analytical method estimates relatedness relative to the background population sampled, we hypothesized we would visualize a lack of SGS in populations consisting of descendents of isolated founders. We further hypothesized that SGS would be stronger in juveniles and weak or absent in adults due to demographic thinning (e.g. Hamrick *et al*. 1993; Epperson & Alvarez-Buylla 1997).

Materials and methods

Study species

Albizia julibrissin Durazz. (Fabaceae) is native to Asia, from Iran to Japan (Elias 1980). It occurs across the eastern and southern USA, and has become naturalized throughout the southeast where it is listed as invasive in eight southern and mid-Atlantic states (Remaley 2005; USDA 2007). It is a small to medium sized tree with a large, flat crown and numerous flowers grouped in dense inflorescences clustered on indeterminate branches. In Georgia, it flowers from May through August and fruits mature from September to November. Fruits contain 8–12 seeds and are singly sired, so all seeds within the fruit are full-siblings. The light, papery fruits are dispersed by gravity and secondarily by wind at least 90 m (J.L.H., personal observation). A nitrogen-fixing species, *A. julibrissin* tolerates a wide range of soils, grows rapidly, and resprouts from cut shoots. It has exceptionally high seed production and the hard-coated seeds can remain dormant for years (Remaley 2005).

In the southeastern USA, *A. julibrissin* is characterized by frequent colonization and extinction of local populations. Populations experience local extinction because trees are short-lived and susceptible to a soil-borne fungus, *Fusarium oxysporium* var. *perniciosum*, that infects the root system causing vascular wilting and eventual death (DeWolf 1968). This fungus may play a role in demographic thinning over the long-term, but we have observed that *Fusarium* tends to thin the stand at a stage of growth well after the stage we sampled, and only after the canopy closes or the population occurs in a very shady site. New populations are often initiated by isolated colonists resulting from long-distance seed dispersal by wind or humans (E.A.P. and J.L.H., personal observations). The actual patterns of dispersal into an open habitat will be a function of the distance of the site from the nearest seed sources and the number of trees in the source. Based on the size structure of most of the sites in the study region, sites isolated by > 200 m appear to be colonized by one or a few individuals. Once these trees flower, the site 'fills in' with generally even-aged recruits. Sites with many adults nearby generally skip the early colonist phase and just establish dense even-aged stands (E.A.P. and J.L.H., personal observations). Localized dispersal of half- and full-sibling progeny from singly sired fruits could result in strong local structuring of genetic diversity within populations (Pardini & Hamrick 2007). Frequent colonization of open habitats by *A. julibrissin* could leave a distinct imprint on the development and maintenance of genetic structure within its populations.

Study sites

Six study sites were chosen where *A. julibrissin* has heavily recruited in Athens, Georgia, USA (33°57′N, 83°20′W). All sites were primarily characterized by *A. julibrissin*, *Pinus taeda*, *Robinia pseudoacacia*, *Lespedeza cuneata*, *Rubus* sp., and grasses. Study sites included two large populations with multiple, known first-generation founders, two small populations surrounding a single, known founder, and two large populations with patchily distributed individuals but unknown colonization histories and no apparent living founders within the sites. The sites are described as follows:

Sites with multiple, known founders. KNO is a well-established population in a large triangular site in a highway cloverleaf that has been monitored annually for approximately 15 years by J.L.H. The site was initially colonized by five founders and secondarily by about 15 recruits scattered at one end of the site. Initial founders were 41.4–145.0 m (mean = 86.6 ± 38.0 m) from each other and ranged in basal diameter from 31 to 65 cm. Members of the second recruitment phase began producing fruit in 1995 and now range in basal diameter from 10 to 20 cm. Following this phase, seedlings recruited throughout the plot, particularly around the initial founders and along the road edge directly across from (~50 m away) a row of large, reproductive adults (Fig. 1). AWP is a rectangular population on an abandoned hill with a central plateau. There were five founders, identifiable by their large basal diameters and known developmental history in the area. Founders ranged from 1.25 to 53.9 m (mean = 33.83 ± 15.74 m) from each other and ranged in basal diameter from 40 to 65 cm. The closest reproductive adults are approximately 80 m away. The site is somewhat sheltered from wind on two sides by an adjacent building, which may hinder seed movement (Fig. 1).

Sites with a single, known founder. CSL is a small population surrounding a single, known founder located in a cloverleaf adjacent to a highway exit ramp. The founder is surrounded by *A. julibrissin* juveniles that range in basal diameter. There are several other founders at the opposite end of the cloverleaf, separated by approximately 150 m of dense vegetation from the target individual (Fig. 1). JML is a small population surrounding a single founder located on

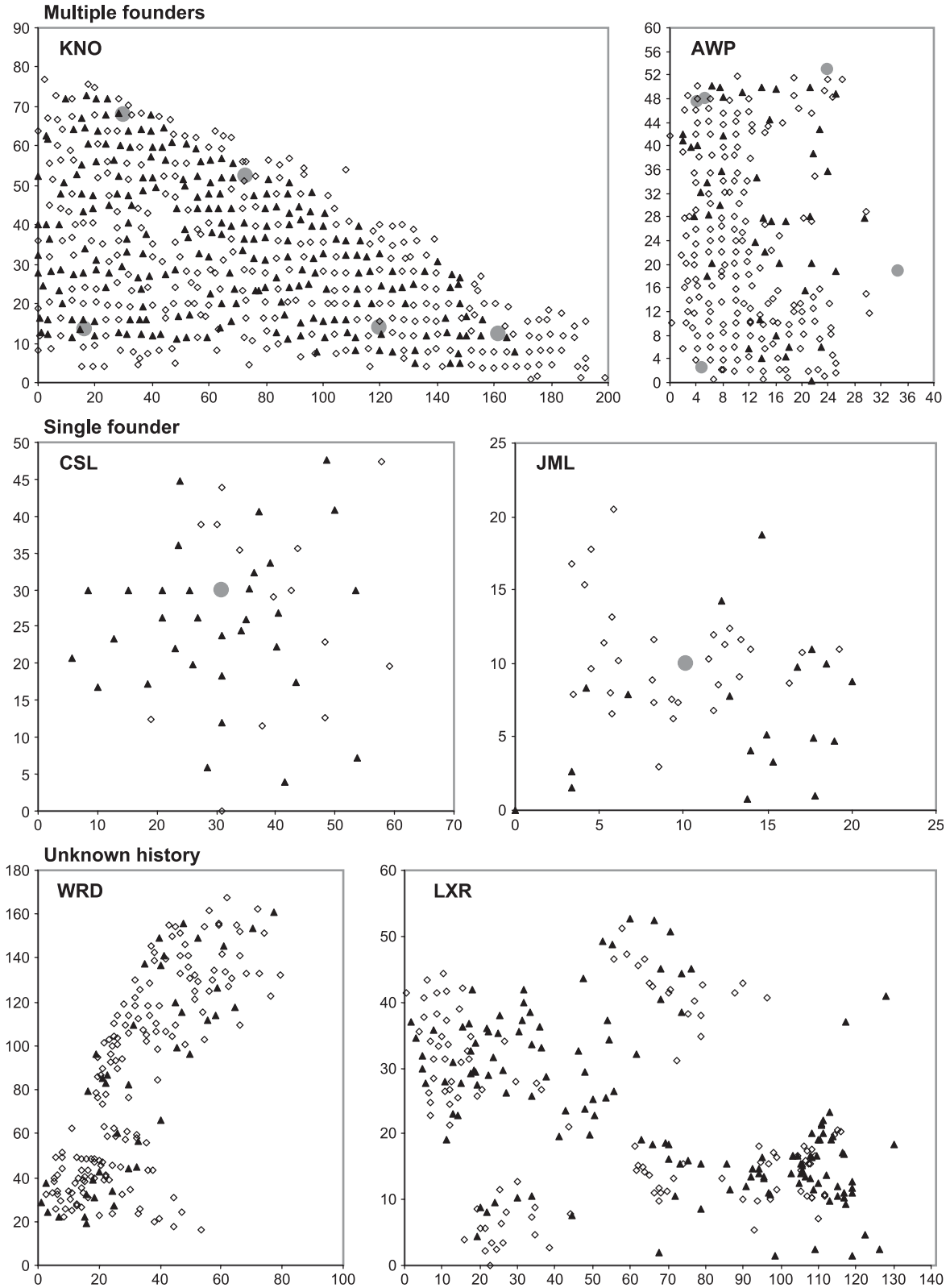

Fig. 1 Maps of the six study populations of *Albizia julibrissin* in Athens, Georgia. Spatial locations of sampled individuals are indicated on the *x*- and *y*-axes in metres. Study sites included two populations in each of three colonization scenarios: (top) multiple, known founders; (middle) single, known founder; (bottom) patchy spatial structure but unknown colonization history. Individuals were classified by basal diameter as juveniles (open diamonds), adults (black triangles), or founders (grey circles).

the side of a highway surrounded by juveniles that range in basal diameter. JML is the most isolated population, approximately 600 m from the nearest reproductive individual (Fig. 1).

Sites with unknown colonization histories. WRD is located in an abandoned lot that is used as a waste site and portions of which are periodically bulldozed. Recruitment within the site has taken place since being initially cleared. *Albizia julibrissin* juveniles are distributed patchily within the site. There are no large founders within the population but there are about 20 large, reproductive adults along roughly one half of the site's perimeter, which likely served as seed sources for recruitment (Fig. 1). LXR is a population located in an abandoned lot. There are no large founders within or adjacent to the plot. Individuals are distributed patchily, and many are aggregated in two main clusters, but its recruitment history is unknown (Fig. 1).

Field methods and size cohorts

We collected samples from 535 mapped individuals at KNO, 232 individuals at AWP, 262 individuals at WRD, 259 individuals at LXR, and 48 individuals surrounding the isolated founders at both CSL and JML. The density of *A. julibrissin* was too high to completely sample the populations, thus individuals were subsampled using a grid or haphazard selection to ensure even coverage of the entire plot. At each site, each sampled individual was mapped on a rectangular coordinate system using metre tapes to record distance from a reference point. Basal diameter of each sampled individual was recorded as a rough proxy for age. One leaf from each individual was collected and stored on ice for transport to the laboratory where enzymes were extracted within 3 h of collection.

In the four large populations (KNO, AWP, WRD, LXR), there were sufficient individuals to divide the populations into juvenile and adults for cohort analyses. Although cohorts are distinguished by size rather than age, field observations suggest that our distinctions are biologically reasonable. Individuals less than 2 cm in basal diameter are typically one to several years old and are not reproductive, while those larger than 2 cm are potentially reproductive (E.A.P., personal observation). For cohort analyses, samples were divided into two size cohorts using basal diameter: juveniles (0.25–2.0 cm) and adults (2.25–31 cm). An additional cohort analysis was performed in KNO where we had adequate samples to group individuals into five size cohorts [0–1.25 cm (n = 151); 1.5–3 cm (n = 149); 3.25–5 cm (n = 72); 5.25–10 cm (n = 52); 10.25–24 cm (n = 26)]. Known and potential founders were not included in cohort analyses because we were interested in genetic diversity among secondary recruits. Individuals from mowed areas at site edges were excluded since their size could not be used as a proxy for age.

Electrophoretic analysis

All individuals were assayed for allozyme polymorphism. Allozymes are highly polymorphic in this species (Godt & Hamrick 1997; Pardini & Hamrick 2007) and have been widely used for studies of SGS (see Vekemans & Hardy 2004). Leaf tissue was crushed with a mortar and pestle and enzymes were extracted using an extraction buffer (Mitton *et al*. 1979) and then absorbed onto 4 × 6 mm filter paper wicks that were stored in 96-well plates at –70 °C. Enzymes were electrophoresed on 11% starch gels using five electrode buffer systems to resolve 11 putatively polymorphic loci [6-phosphogluconate dehydrogenase (6PGDH), isocitrate dehydrogenase (IDH), and phosphoglucoisomerase (PGI) resolved on buffer system 4, alcohol dehydrogenase (ADH) and menadione reductase (MNR) resolved on buffer system 7, aspartate aminotransferase (AAT-1 and AAT-2) and uridine diphosphoglucose pyrophosphorylase (UGPP) resolved on buffer system 10, malate dehydrogenase (MDH) resolved on buffer system 11, and fluorescent esterase (FE) and cathodal peroxidase (CPER) resolved on buffer system 6]. Gel electrode buffers and stain recipes were taken from Soltis *et al*. (1983).The genetic basis of the allozyme banding patterns was inferred from segregation patterns based on subunit structure and alleles were identified based on their migration rate (Wendel & Weeden 1989). All loci were used for analyses of genetic diversity and SGS, except for SGS analyses of KNO and CSL, for which 10 loci were resolved.

Analysis of genetic diversity and inbreeding

Standard genetic diversity and differentiation parameters were calculated for populations and cohorts as described in Hedrick (2005) using a program developed by M. D. Loveless and A. Schnabel. These included the percentage of polymorphic loci (P), mean number of alleles per polymorphic locus (AP), effective number of alleles (A_e), and observed (H_O) and expected (H_E) heterozygosities. Deviations from Hardy–Weinberg expectations were examined for each polymorphic locus in each population using Wright's fixation index (F_{IS}) (Wright 1922). Overall deviations from Hardy–Weinberg were evaluated by averaging F_{IS} over all populations for each polymorphic locus and then averaging over all loci. Significance levels for fixation indices for each locus and population were assessed with chi-squared tests (Li & Horovitz 1953). Population differentiation was estimated using G_{ST} (Nei 1973, 1977), estimated for each polymorphic locus and then averaged over loci to estimate average population divergence. We tested for significant allele frequency heterogeneity among populations at each locus using a chi-squared test (Workman & Niswander 1970).

SGS analysis with a local reference population

We performed standard analyses of SGS of populations, cohorts, and two subpopulations within population LXR. For these analyses, we used the local reference population, which consists of all sampled individuals within the population being analysed. LXR was partitioned into two subpopulations (N and S) comprising the two main clusters based on their spatial locations, as illustrated in the top panel of Fig. 3. We hypothesized these individuals were locally dispersed, related descendants of deceased colonists, and therefore expected patterns of SGS to be similar to those in populations surrounding known isolated founders.

We used the multivariate, multilocus method for spatial autocorrelation of genotypes developed by Smouse & Peakall (1999). This technique determines if genotypes of near neighbours are more genetically similar than those located more distantly. The autocorrelation coefficient (r_{ij}) is similar to Moran's I bounded by (–1, +1) (Peakall *et al*. 2003) and represents average genetic relatedness among pairs of individuals within defined distance classes relative to pairs randomly drawn from the reference population. It produces results similar in value and interpretation to other spatial autocorrelation methods, but is a multivariate approach less sensitive to allelic and locus-to-locus stochasticity (Smouse & Peakall 1999). Expected relatedness among full-siblings is 0.5 and among half-siblings is 0.25, when pairs are compared to a completely panmictic reference population. Because absolute values of relatedness using spatial genetic autocorrelation techniques are sensitive to the sampling scheme, marker system, and relatedness of the reference population, absolute values should be interpreted cautiously.

To quantify SGS, average relatedness among pairs of individuals (r_{ij}) within distance classes was regressed against distance and depicted in correlograms for each population and size cohort. We performed all analyses using the same distance interval (4 m) to allow comparisons among populations, cohorts, or analysis type (see below). Tests of statistical significance were accomplished by permutation and bootstrap estimates of r. For permutation testing, individuals are randomized over all possible spatial positions under the hypothesis of no SGS and r is recalculated 999 times. Ranked values are taken as the 95% confidence intervals (dashed lines in correlograms) and significant genetic structure is inferred where the observed r_{ij} value falls outside this envelope. Upper and lower 95% confidence intervals are constructed around the r_{ij} estimate by 999 bootstrap resamplings of r and ranked values define the 95% confidence interval (error bars in correlograms); significant genetic structure is inferred where the bootstrap confidence interval does not cross $r = 0$. We also report the P value for a one-tailed test for positive autocorrelation; if the probability is less than 0.05, positive spatial genetic structure is accepted (Smouse & Peakall 1999; Peakall *et al*. 2003; Peakall & Smouse 2006). All SGS analyses were carried out using GENALEX 6.1 (Peakall & Smouse 2006).

SGS analysis with a regional reference population

For the estimator we used, relatedness among pairs of individuals is calculated relative to pairs of individuals randomly drawn from the reference population, typically comprised of all sampled individuals. As a result, high levels of relatedness within the population (e.g. half-sibling families) may obscure the relationship between relatedness and distance. For example, if all individuals in a population are highly related, two proximal individuals may not be detectably more related to one another than two randomly drawn individuals; relatedness-based estimators of this type will not detect significant SGS. Because we analysed SGS in recently colonized populations where individuals may be highly related due to a limited number of maternal individuals, we performed subsequent SGS analyses using regional reference populations to increase our ability to detect local SGS in the focal populations. In these analyses, relatedness among pairs of individuals was calculated relative to individuals drawn randomly from a pool of individuals characterized by regional allele frequencies. To create the regional reference population for each of our six focal populations, we randomly sampled 48 genotypes from the five nonfocal populations. Those 240 individuals were assigned mock spatial coordinates such that the shortest distance between any two nonfocal individuals was greater than the greatest distance between pairs of individuals within the focal population. Therefore, relatedness was calculated relative to individuals from a regional sample, rather than just to individuals within the population, allowing SGS to be analysed at smaller spatial scales. Visualization of patterns of SGS at short distances (i.e. mapped) represents average relatedness among pairs of individuals within the focal population relative to the regional reference population and is depicted at a shorter (i.e. mapped) spatial scale in the correlograms. These analyses were performed with GENALEX (Peakall & Smouse 2006).

Analysis of SGS intensity with Sp

To determine the intensity of SGS we estimated the statistic *Sp*, which synthesizes average pairwise relatedness and its relationship with distance. This statistic, which is decoupled from absolute values of relatedness, is useful for comparing the intensity of SGS even if conditions for drift-dispersal–mutation equilibrium are not met and is not sensitive to the sampling scheme (Vekemans & Hardy 2004; Hardy *et al*. 2006). *Sp* is calculated as $-b/(1 - F_1)$, where F_1 is the average kinship (Loiselle *et al*. 1995) among pairs of individuals in the smallest distance interval and b is the slope of the

Table 1 Genetic diversity within six study populations of *Albizia julibrissin* in Athens, Georgia, grouped according to colonization history. Means are averaged across populations; pooled values represent species level variation within the region sampled

Population	*N*	Loci	*P*	*AP*	A_e	H_O (SE)	H_E (SE)	F_{IS} (SE)
Multiple founders								
KNO	535	10	100	2.70	1.44	0.227 (0.016)	0.223 (0.073)	–0.022 (0.017)
AWP	232	11	100	2.82	1.68	0.346 (0.027)	0.309 (0.076)	–0.049 (0.053)
Single founder								
JML	48	11	90.9	2.40	1.66	0.384 (0.061)	0.332 (0.067)	–0.099 (0.083)
CSL	48	10	70.0	2.57	1.76	0.367 (0.049)	0.304 (0.091)	–0.158 (0.073)*
Unknown history								
WRD	263	11	90.9	2.70	1.49	0.226 (0.022)	0.231 (0.070)	0.093 (0.072)
LXR	259	11	100	2.55	1.53	0.289 (0.024)	0.259 (0.071)	–0.062 (0.046)
Mean (SE)			92.0 (3.2)	2.62 (0.15)	1.59 (0.13)	0.306 (0.015)	0.276 (0.031)	
Pooled			100	3.18	1.63		0.282	

Parameters: *N*, number of individuals sampled; *P*, percentage polymorphic loci; *AP*, alleles per polymorphic locus; A_e, effective number of alleles per locus; H_O, observed heterozygosity and its standard error (SE); H_E, expected heterozygosity under Hardy–Weinberg equilibrium and its standard error (SE); F_{IS}, mean fixation index, averaged over loci for each population, and its standard error (SE); *indicates significant differences of F_{IS} from 0 evaluated at $\alpha = 0.05$.

regression of kinship against the natural log of distance (Vekemans & Hardy 2004). To compare *Sp* among populations, regressions of kinship on the natural log of distance should be performed over the same distance range, which is limited by the maximum distance in the smallest population (O. Hardy, personal communication). Thus we performed regressions over the following distance ranges: 0–25 m for all standard and regional analyses of populations and subpopulations; 0–50 m for two-cohort analyses within the four large populations; 0–150 m for the five-cohort analysis within KNO. All analyses for calculation of *Sp* were performed in SPAGEDi (Hardy & Vekemans 2002).

Results

Analysis of genetic diversity and inbreeding

For regional analyses of genetic diversity, 8 of the 11 loci were polymorphic in all of the scored populations. Populations around isolated colonists had slightly lower *P* values but not *AP* or A_e (Table 1). Populations AWP, JML, and CSL had slightly higher H_O and H_E than KNO, WRD, and LXR, but these differences did not correspond to colonization history (Table 1). Observed genotype frequencies were consistent with Hardy–Weinberg expectations for 58.3% of the loci in all populations. Mean F_{IS} across loci was significantly negative in CSL (Table 1), but this was driven by only one locus. Overall, there were no consistent deficiencies or excesses of heterozygotes across loci in any population. Mean F_{IS} across all polymorphic loci and populations was –0.041 and did not differ significantly from zero. Overall genetic differentiation among the six populations was low ($G_{ST} = 0.062$) and chi-squared analyses revealed significant allele frequency heterogeneity at all loci ($P < 0.05$). Such heterogeneity is consistent with low G_{ST} values given the large sample sizes.

Within size cohorts in the four large populations, values of *P* and A_e were similar among juveniles and adults (Table 2). *AP* was higher in juveniles than adults in KNO, AWP, and LXR and lower in juveniles in WRD. H_O was higher in adults than juveniles in KNO, AWP, and WRD and lower in adults in LXR. Among the five size cohorts analysed in KNO, H_O generally increased from the smallest to the largest size cohort (Table 2). Within size cohorts, observed genotype frequencies were consistent with Hardy–Weinberg expectations; there were no consistent negative or positive fixation indices across loci in any size cohort. Differentiation among size cohorts within populations was very low (G_{ST} ranged from 0.002 to 0.006). Hierarchical analysis revealed 5.2% of genetic diversity was distributed among populations, 0.2% among size cohorts within populations, and 94.6% within size cohorts within populations. There was no significant allele frequency heterogeneity between size cohorts within populations. Note that the hierarchical analysis was only conducted in the four large populations that had sufficient individuals to pool into size cohorts and thus the G_{ST} given here differs slightly from that given above in the analysis of all six populations.

SGS analysis with a local reference population

There was pronounced, significant SGS in the four large populations with known (KNO and AWP) and unknown (WRD and LXR) colonization histories (Table 3; Fig. 2, black lines). Average pairwise relatedness in the shortest distance class ($r_{ij}1$) for these populations ranged from 0.066

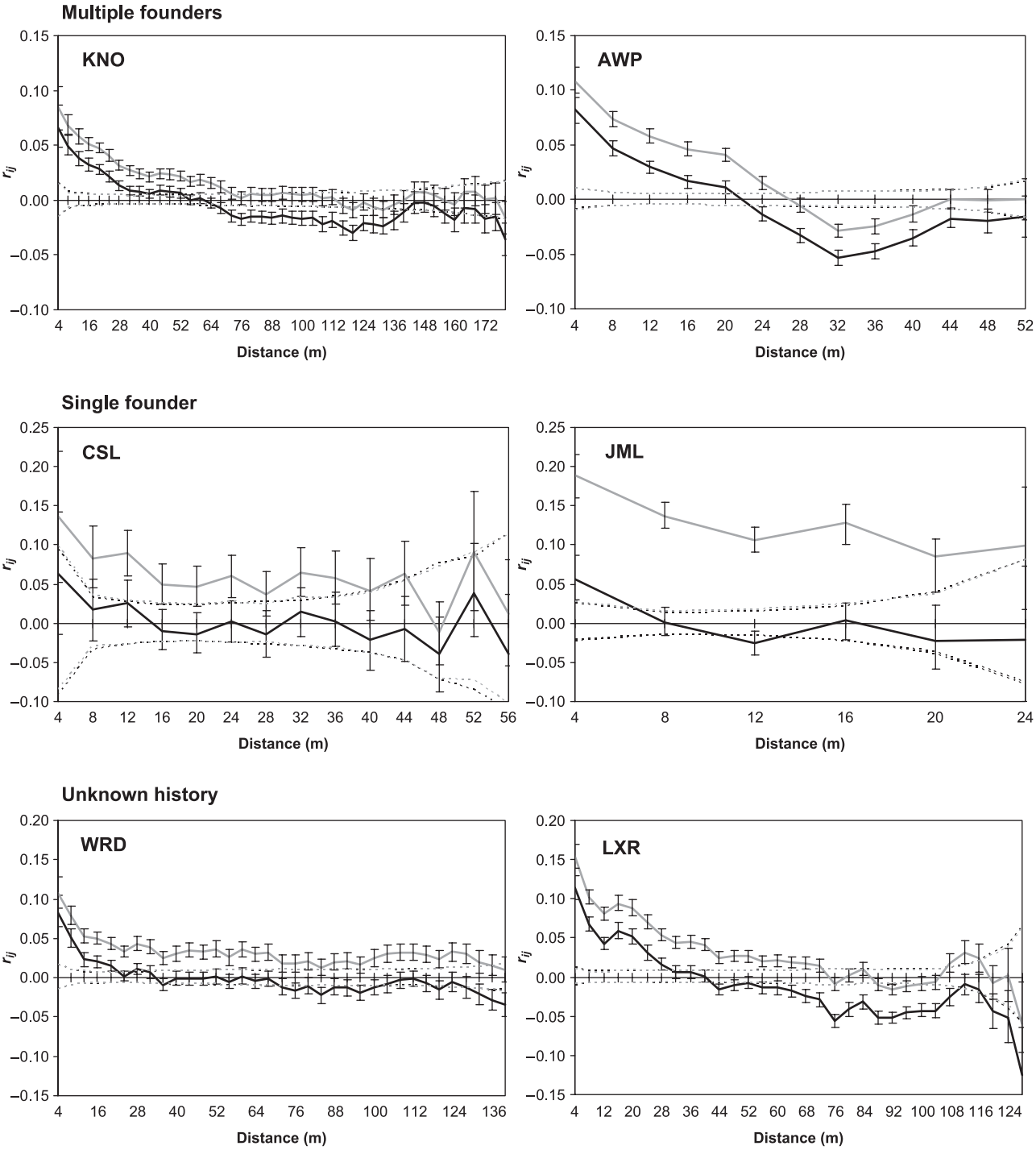

Fig. 2 Correlograms depicting SGS within the six study populations of *Albizia julibrissin* in Athens, Georgia. The solid black and grey lines represent the r_{ij} estimates for analyses conducted with a standard, local reference population and a regional reference population, respectively. The dashed black and grey lines represent upper and lower 95% confidence intervals constructed around the null hypothesis of no SGS estimated by permutation for the local and regional analyses, respectively. Error bars represent upper and lower 95% confidence intervals around r_{ij} estimated by bootstrap resampling.

Table 2 Genetic diversity within size cohorts in four large study populations of *Albizia julibrissin* in Athens, Georgia. For analyses with two size cohorts, juveniles included individuals 0.25–2 cm in basal diameter and adults included individuals greater than 2 cm in basal diameter

Population	Size cohort	*N*	Loci	*P*	*AP*	A_e	H_O (SE)	H_E (SE)	F_{IS} (SE)
Two size cohorts:									
KNO	Juvenile	230	10	100.0	2.70	1.43	0.218 (0.024)	0.221 (0.074)	–0.005 (0.017)
KNO	Adult	220	10	100.0	2.50	1.44	0.242 (0.024)	0.224 (0.073)	–0.051 (0.023)*
AWP	Juvenile	156	11	100.0	2.75	1.65	0.341 (0.033)	0.310 (0.068)	–0.028 (0.065)
AWP	Adult	71	11	91.7	2.45	1.68	0.357 (0.049)	0.315 (0.071)	–0.109 (0.053)*
WRD	Juvenile	161	11	91.7	2.73	1.53	0.252 (0.029)	0.250 (0.067)	0.134 (0.092)
WRD	Adult	102	11	91.7	2.82	1.54	0.283 (0.037)	0.261 (0.068)	0.019 (0.047)
LXR	Juvenile	118	11	91.7	2.73	1.69	0.315 (0.037)	0.299 (0.075)	–0.072 (0.056)
LXR	Adult	141	11	100.0	2.50	1.66	0.295 (0.034)	0.290 (0.074)	–0.058 (0.042)
Five size cohorts:									
KNO	0–1.25 cm	151	10	100.0	2.70	1.44	0.213 (0.029)	0.223 (0.075)	0.011 (0.023)
KNO	1.5–3 cm	149	10	100.0	2.60	1.42	0.233 (0.029)	0.219 (0.073)	–0.041 (0.025)
KNO	3.25–5 cm	72	10	90.0	2.56	1.41	0.231 (0.041)	0.209 (0.072)	–0.061 (0.030)*
KNO	5.25–10 cm	52	10	80.0	2.63	1.48	0.256 (0.051)	0.238 (0.074)	–0.054 (0.046)
KNO	10.25–24 cm	26	10	90.0	2.33	1.45	0.253 (0.073)	0.234 (0.073)	–0.048 (0.024)*

Parameters: *N*, number of individuals sampled; *P*, percentage polymorphic loci; *AP*, alleles per polymorphic locus; A_e, effective number of alleles per locus; H_O, observed heterozygosity and its standard error (SE); H_E, expected heterozygosity under Hardy–Weinberg equilibrium and its standard error (SE); F_{IS}, mean fixation index, averaged over loci for each population, and its standard error (SE); *indicates significant differences of F_{IS} from 0 evaluated at $\alpha = 0.05$.

Table 3 Summary of SGS and *Sp* results for six *Albizia julibrissin* study populations in Athens, Georgia, and for subpopulations within LXR

		Local reference population					Regional reference population				
Population	*N*	r_{ij1}	Dist	F_1	*b* (SE)	*Sp*	r_{ij1}	Dist	F_1	*b* (SE)	*Sp*
Multiple founders											
KNO	535	0.066†	62	0.048	–0.015 (0.008)***	0.016	0.084†	113	0.059	–0.014 (0.007)***	0.015
AWP	232	0.082†	22	0.030	–0.009 (0.003)***	0.009	0.108†	27	0.061	–0.010 (0.012)***	0.010
Single founder											
CSL	48	0.064^{NS}	—	0.043	–0.005 (0.010)^{NS}	0.005	0.137†	47	0.087	–0.005 (0.012)^{NS}	0.006
JML	48	0.056†	8	0.026	–0.011 (0.006)§	0.011	0.189†	—	0.207	–0.025 (0.018)**	0.032
Unknown history											
WRD	263	0.083†	34	0.055	–0.018 (0.008)***	0.019	0.108†	—	0.066	–0.016 (0.007)***	0.018
LXR	259	0.114†	40	0.019	–0.010 (0.004)***	0.010	0.154†	75	0.039	–0.008 (0.004)**	0.009
Subpopulations											
LXR-N	88	0.085†	14	0.039	–0.027 (0.015)***	0.028	—	—	—	—	—
LXR-S	88	0.050†	10	0.007	–0.005 (0.003)§	0.005	—	—	—	—	—

Parameters: r_{ij1}, average pairwise relatedness among individuals in the shortest distance class; Dist, intercept of r_{ij} with 0; F_1, average pairwise kinship among individuals in the shortest distance class; *b*, slope of regression of pairwise kinship F_{ij} on $\ln(d_{ij})$, its standard error (SE); *Sp*, SGS intensity, following Vekemans & Hardy (2004). See text for a discussion of the two analyses. *P* values for r_{ij}: † for $P \leq 0.005$ for one-tailed test that observed $r >$ permuted r; *P* values for *b*: ^{NS} for $P > 0.1$; § for $0.05 < P \leq 0.1$; * for $0.01 < P \leq 0.05$; ** for $0.001 < P \leq 0.01$; *** for $P \leq 0.001$.

to 0.114. The distance at which relatedness among pairs of individuals was no greater than two randomly drawn individuals for these large populations ranged from 22 to 62 m (Fig. 2; Table 3). For populations with a single, isolated founder, CSL exhibited no evidence of SGS, while JML exhibited slight but significant SGS only in the shortest distance class (Table 3; Fig. 2).

Patterns in subpopulations LXR-N and LXR-S behaved qualitatively and quantitatively similarly to those in the populations around known, isolated founders, especially JML (Table 3; Fig. 3). SGS was significant to 8 m in LXR-N and to 4 m in LXR-S.

Estimates of *Sp* for the six study populations ranged from 0.005 to 0.019 (Table 3). The intensity of structure was

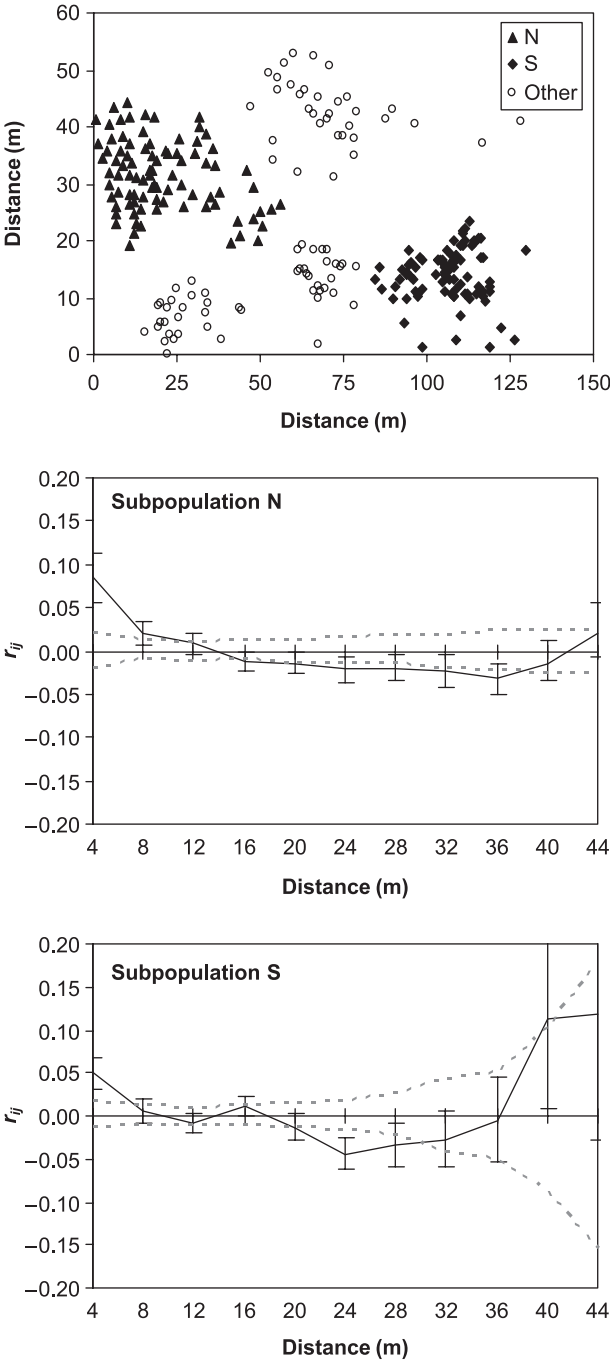

Fig. 3 SGS within subpopulations in study population LXR. The spatial locations of individuals included in subpopulations denoted N and S are indicated in the map (top) on the *x*- and *y*-axes in metres; correlograms (middle and bottom) depict results of SGS analyses.

highest in KNO and WRD, intermediate in AWP, JML, and LXR, and lowest in CSL. The estimate for subpopulation LXR-N was high (*Sp* = 0.028) and low for LXR-S (*Sp* = 0.005) (Table 3).

SGS analysis with a regional reference population

When we analysed SGS relative to a regional reference population, the overall shapes of the relationship between pairwise relatedness and distance did not change. However, r_{ij1} and the values at which pairwise relatedness levelled out were greater in these analyses than in the original analyses (Fig. 2, grey lines). In these analyses, SGS in populations with multiple founders (KNO and AWP) was evident: SGS occurred in KNO up to 113 m and in AWP up to 27 m; relatedness did not become negative in KNO but did in AWP (Table 3, Fig. 2). In populations with a single founder (CSL and JML), SGS occurred over all mapped distances. In sites with unknown colonization histories (WRD and LXR), values of r_{ij} decreased over shorter mapped distances. They differed in the relatedness–distance function at larger distances: SGS remained positive over all mapped distances in WRD while in LXR it was positive to ~76 m and negative from ~76–104 m (Fig. 2). The values of *Sp* for each study population were almost the same for local and regional reference analyses (Table 3).

SGS analyses of size cohorts

Spatial genetic structure was evident in both juvenile and adult size cohorts in the four large populations. Estimates of r_{ij1} were higher in adults than juveniles in AWP, WRD, and LXR and were slightly higher in juveniles in KNO (Table 4; Fig. S1). Within population KNO, SGS was significant in the three smaller size cohorts and not significant in two larger size cohorts (Table 4; Fig. S2). The latter result should be interpreted cautiously, however, because sample sizes in the two largest size cohorts were too small for robust estimates of r_{ij} and confidence envelopes (Queller & Goodnight 1989). Estimates of *Sp* were similar for juveniles and adults in KNO and WRD; *Sp* was higher in juveniles in AWP and higher for adults in LXR (Table 4).

Discussion

Albizia julibrissin frequently initiates populations from one or a few founding individuals, can reproduce in just a few years), and often senesces within 10–20 years (E.A.P. and J.L.H., personal observation). It is clear that colonization patterns of this naturalized tree species play an important role in structuring genetic diversity within its populations. In the four large study populations (KNO, AWP, WRD, LXR), SGS was significant and pronounced. Average pairwise relatedness decreased with increasing distance among pairs of individuals, indicating leptokurtic seed dispersal around maternal individuals and partially overlapping seed shadows. We found contrasting patterns of SGS in populations with multiple vs. single known founders, which are discussed in more detail below.

Table 4 Summary of SGS and *Sp* results for size cohorts within four large study populations of *Albizia julibrissin* in Athens, Georgia

Population		*N*	r_{ij1}	Dist	F_1	*b* (SE)	*Sp*
Two size cohorts (4-m intervals)							
KNO	Juvenile	230	0.077†	32	0.067	–0.018 (0.005)***	0.020
KNO	Adult	220	0.064†	60	0.056	–0.018 (0.010)***	0.020
AWP	Juvenile	156	0.078†	21	0.031	–0.017 (0.008)***	0.017
AWP	Adult	71	0.128†	21	0.039	–0.010 (0.009)§	0.010
WRD	Juvenile	161	0.065†	33	0.036	–0.021 (0.010)***	0.021
WRD	Adult	102	0.082†	32	0.075	–0.018 (0.007)***	0.020
LXR	Juvenile	118	0.105†	30	0.014	–0.006 (0.002)*	0.006
LXR	Adult	141	0.116†	39	0.034	–0.012 (0.004)***	0.013
Five size cohorts (15-m intervals)							
KNO	0–1.25 cm	151	0.031†	60	0.034	–0.023 (0.011)***	0.024
KNO	1.5–3 cm	149	0.044†	67	0.044	–0.031 (0.013)***	0.032
KNO	3.25–5 cm	72	0.063†	65	0.057	–0.050 (0.036)***	0.053
KNO	5.25–10 cm	52	0.014^{NS}	—	0.015	–0.022 (0.024)**	0.022
KNO	10.25–24 cm	26	–0.040^{NS}	—	–0.042	–0.017 (0.009)^{NS}	–0.016

Parameters: r_{ij1}, average pairwise relatedness among individuals in the shortest distance class; Dist, intercept of r_{ij} with 0; F_1, average pairwise kinship among individuals in the shortest distance class; *b*, slope of regression of pairwise kinship F_{ij} on $\ln(d_{ij})$, its standard error (SE); *Sp*, SGS intensity, following Vekemans & Hardy (2004). *P* values for r_{ij}: † for $P \leq 0.005$ for one-tailed test that observed $r >$ permuted *r*; *P* values for *b*: ^{NS} for $P > 0.1$; § for $0.05 < P \leq 0.1$; * for $0.01 < P \leq 0.05$; ** for $0.001 < P \leq 0.01$; *** for $P \leq 0.001$.

The high sample sizes, replication of study sites, and multiple colonization histories in our study allow us to draw inferences about seed dispersal by comparing relative values of relatedness and the behaviour of the relatedness–distance functions. In the two populations with known founders (KNO and AWP), the distance over which SGS occurred was proportional to the distance between founding individuals. Other studies have found a relationship between plant density and local genetic structure (Hamrick *et al*. 1993; Gapare & Aitken 2005). In these two sites, relatedness at short distances was lower in KNO than in AWP. This difference might be due to the presence of many reproductive adults within and adjacent to KNO that could serve as seed sources for recruitment, thus diluting relatedness. In contrast, AWP has fewer reproductive individuals and is unlikely to receive much immigrant seed since it is sheltered on two sides by an adjacent building. This suggests that seed immigration after initial colonization can have a large impact on local genetic structuring in actively colonizing mimosa populations.

In our local reference population analyses, populations surrounding single, known founders displayed little (JML) or no (CSL) SGS. The ability to detect SGS can depend on the allele frequencies in the sampled population and sample sizes (Rousset 2002; Cavers *et al*. 2005; Jump & Penuelas 2007). Given the unavoidably small sample sizes for these two populations, it is difficult to determine if little SGS exists or if it is simply not detectable. Analyses using a regional reference population suggest the latter may be the case, as they revealed significant positive SGS over most of the sampled area in both sites surrounding isolated founders. Elevated relatedness, combined with the lack of a declining relatedness–distance function in the regional analyses suggests that our inability to detect structure in the local analyses was a function of the inherently high background relatedness among individuals in these sites. Together, these results suggest that most individuals within these populations are at least half-siblings, and that there is very little seed immigration from nearby sources. JML displayed significant SGS in the shortest distance class in the local analysis. In another study, estimates of the effective number of pollen donors to crowns of *A. julibrissin* were lower than the actual number of pollen donors, suggesting that progeny consist mostly of half-siblings with some full-siblings resulting from correlated paternity within tree crowns and fruits (Pardini & Hamrick 2007). The very local SGS in this site may indicate that some near neighbours are full-siblings, as might be expected if they come from the same singly sired fruits. *Sp* was intermediate in JML (0.011) and low in CSL (0.005) which might be due to relative amounts of seed immigration. JML is the most isolated site and probably receives very little seed immigration, whereas CSL has more potential seed sources nearby.

Analyses of SGS using a regional reference population also allowed us to use patterns seen in populations with known histories to infer possible colonization scenarios for WRD and LXR. In populations with single founders, regional analyses revealed significant SGS at almost all sampled distances; in populations with multiple founders, SGS was positive at shorter distances and either negative or not

significant at longer distances. Interestingly, the relatedness–distance function was different in the regional analyses of KNO and AWP: AWP displayed significant negative SGS at larger distances while KNO did not. The different responses might be attributed to the amount of immigrant recruitment in the sites. KNO is a well-established population with many adjacent reproductive adults. It may have received more pollen and seed flow over a longer period of time such that distant individuals are on average as related to one another as randomly drawn individuals from the region. Another possibility is that the original founders were somewhat related to each other in KNO but unrelated in AWP.

Populations with unknown colonization histories (WRD and LXR) displayed a combination of patterns seen in populations with multiple vs. single founders. At short distances, SGS was positive and declined with increasing distance in both populations. At greater distances, relatedness values levelled off but remained positive at all distances in WRD while it became nonsignificant or slightly negative at some distances in LXR. The significant but declining SGS at short distances in both populations is consistent with high relatedness among proximal individuals and some degree of seed shadow overlap. In WRD, the flat relatedness–distance function and positive SGS at all greater distances suggest it may have been initiated by recruitment from related individuals. In LXR, the negative SGS in the tail of the relatedness–distance function suggests that it may have been founded by a limited number of individuals that were not necessarily related. The relative amounts of seed immigration in the two populations could also contribute to the difference: WRD is surrounded on two sides by a row of large, even-aged reproductive adults that may be related to one another and probably all contributed to recruitment. The expectation for such a scenario would be a pattern of positive SGS at long distances if distant individuals are on average more related to one another than randomly drawn individuals from the region. In contrast, LXR has no evident remnant or adjacent reproductive individuals.

We suspected the patchy spatial distribution of individuals in LXR was due to limited seed dispersal around deceased founding individuals. With such a colonization history, we would expect to find significant SGS at the entire population level due to the overlapping of seed shadows of different colonists, but little or no SGS within subpopulations (two clusters of aggregated individuals suspected to be seed shadows of deceased founders). Our results were consistent with this hypothesis. Using standard, local analyses, we found significant SGS within the entire study population ($r_{ij1} = 0.114$), indicating proximal individuals (within patches) are much more related to one another, and distant individuals (among patches) are much less related to one another, on average, than randomly drawn individuals. In the two subpopulations, SGS was significant only in the shortest distance classes and relatedness values were lower than for the entire site (N, $r_{ij1} = 0.085$; S, $r_{ij1} = 0.05$). The very local SGS may again be due to clustering of full-sibling individuals dispersed from singly sired fruits. Results for the subpopulations were quantitatively and qualitatively similar to the patterns seen in populations surrounding isolated founders, suggesting the subpopulations represent patches of genetically related individuals. This suggests that LXR may have been initiated by a few colonists and subsequent recruitment around now deceased founders.

Our study populations showed evidence of significant SGS in both juveniles and adults. Several studies of life stages in tree species, with both wind and animal seed dispersal, have found less SGS in adults due to demographic thinning (Hamrick *et al*. 1993; Berg & Hamrick 1995; Epperson & Alvarez-Buylla 1997). A priori, we expected demographic thinning to result in weaker genetic structure in larger size cohorts. Interestingly, we found stronger SGS in adults than juveniles in most populations. The only study population in which SGS was weaker in adults was KNO, but it should be noted that the difference in relatedness between cohorts in this population was not great and the distance over which SGS was significant was much greater in the adults. Furthermore, the five-cohort analysis with larger distance classes revealed generally increasing SGS in the cohorts. The distance over which SGS was significant in the adult cohorts corresponds to the distance between known or putative seed sources in each population. Greater SGS in adults than juveniles has been documented in several tree species and attributed to a combination of generation overlap and selection (Latouche-Halle *et al*. 2003) or population processes such as recruitment pulses and declines (Jones & Hubbell 2006). In our species, the weaker SGS generally found in juveniles is probably due to generation overlap (see below), addition of new alleles by pollen flow, extensive overlap of seed shadows, and seed immigration in the juvenile cohort as the population is filled in. Such persistent SGS in the adults could be due to the general lack of thinning seen in the small and intermediate size cohorts in this invasive species (E.A.P. and J.L.H., personal observations). A similar pattern of significant SGS in adults of the tree *Swartzia simplex* was attributed to a lack of thinning (Hamrick *et al*. 1993). A plausible explanation for the general pattern observed in actively colonizing populations of *A. julibrissin* is that weaker SGS in the younger cohort is due to pollen flow and seed shadow overlap, while persistent SGS in the older cohort is a residual pattern left by the initial genetic footprint of colonization.

We found similar levels of genetic diversity within and little genetic differentiation among size cohorts in the four large study populations. Lack of genetic differentiation among cohorts could result from cohorts sharing similar seed sources across time or overlapping of reproductive

events among generations. Such a mechanism has been proposed to explain similar results in age classes of *Neolitsea sericea* (Chung *et al*. 2000) and in actively expanding populations of the shrub *Myrica cerifera* (Erickson *et al*. 2004). We found no consistent heterozygote excess or deficiency across loci for any population, which is expected given this species is 100% outcrossing (Godt & Hamrick 1997). The mean number of alleles per polymorphic locus (*AP*) was higher in juveniles than adults in three of the four large study populations, which suggests high levels of pollen flow. Observed heterozygosity (H_O) was higher in adults in three of the four populations, which may indicate some selection against more homozygous individuals. A temporal shift towards increasing heterozygosity in older individuals due to selection is a well-documented pattern in forest trees (Bush & Smouse 1992).

Other studies have demonstrated that SGS in tree species is strongly influenced by founding individuals and colonization biology (Premoli & Kitzberger 2005; Jones *et al*. 2006; Troupin *et al*. 2006). *Albizia julibrissin* is a weedy tree for which colonization and extinction are frequent population processes. As a direct result, colonization plays a major role in promoting genetic structure within and among its populations. SGS in colonizing populations is initiated by limited seed dispersal around immigrant seed sources. Extensive pollen flow in this self-incompatible species (Godt & Hamrick 1997; Pardini & Hamrick 2007) appears to rapidly introduce high levels of genetic variation into populations upon colonization. Colonization leaves a genetic footprint in populations of *A. julibrissin* that persists in older trees despite overlapping of many reproductive events. Mating system and pollen flow influence the level of relatedness, but the distance over which SGS occurs is affected primarily by seed dispersal and density of reproductive individuals (see Dyer 2007), thus colonization patterns may have a lasting effect on structuring genetic diversity within populations.

Establishment of *A. julibrissin* populations by a single, isolated founder results in localized dispersal of half- and full-siblings with little off-site recruitment. Initiation of populations by several related founders results in genetic structuring at short distances due to leptokurtic seed dispersal and overlapping seed shadows. Variable colonization histories will result in different visualizations of SGS with standard analyses. As seen here, unless regional analyses are conducted, populations founded by a single individual should display little or no SGS, whereas, populations founded by a few (e.g. two to five) unrelated individuals should display strong SGS with relatively high relatedness values. Finally, populations founded from many individuals should display less SGS. There is no way to formally test from the current data whether these unknown populations actually had the colonization histories ascribed to them. What we can say is that the patterns we observed are consistent with a certain explanation and inconsistent with some other situation. Population genetic assignment methods have been used to reveal founding history in some plants (e.g. Yang *et al*. 2008). Direct measurement of seed dispersal can be difficult in weedy species in which assignment of seed to maternal parents or parent pairs is limited by molecular marker diversity and the abundance of possible seed sources. We have shown that comparative analyses of SGS among populations may have additional utility as a tool for exploring possible colonization history, especially where direct measurement of seed dispersal is difficult. This is an interesting application that deserves further consideration through modelling.

Acknowledgements

We thank Eric Pardini for assistance with field work and Cecile Deen and hourly workers in the Hamrick laboratory for assistance with allozyme analysis. Nick Griffin, Michele Johnson, Russell Blaine and three anonymous reviewers provided comments that greatly improved this manuscript. Funding was provided by USDA NRICGP-2000–00882 to J.L.H. and M.J.W. Godt and by a grant from the Georgia Native Plant Society to E.A.P.

References

Aldrich PR, Hamrick JL (1998) Reproductive dominance of pasture trees in a fragmented tropical forest mosaic. *Science*, **281**, 103–105.

Ally D, Ritland K (2007) A case study: looking at the effects of fragmentation on genetic structure in different life history stages of old-growth mountain hemlock (*Tsuga mertensiana*). *Journal of Heredity*, **98**, 73–78.

Asuka Y, Tomaru N, Nisimura N, Tsumura Y, Yamamoto S (2004) Heterogeneous genetic structure in a *Fagus crenata* population in an old-growth beech forest revealed by microsatellite markers. *Molecular Ecology*, **13**, 1241–1250.

Berg EE, Hamrick JL (1995) Fine-scale genetic structure of a turkey oak forest. *Evolution*, **49**, 110–120.

Bush RM, Smouse PE (1992) Evidence for the adaptive significance of allozymes in forest trees. *New Forests*, **6**, 179–196.

Cavers S, Degen B, Caron H *et al*. (2005) Optimal sampling strategy for estimation of spatial genetic structure in tree populations. *Heredity*, **95**, 281–289.

Chung MG, Chung MY, Oh GS, Epperson BK (2000) Spatial genetic structure in a *Neolitsea sericea* population (Lauraceae). *Heredity*, **85**, 490–497.

DeWolf GP (1968) *Albizia julibrissin* and its cultivar 'Ernest Wilson'. *Arnoldia*, **28**, 29–24.

Dutech C, Seiter J, Petronelli P, Joly HI, Jarne P (2002) Evidence of low gene flow in a Neotropical clustered tree species in two rainforest stands of French Guiana. *Molecular Ecology*, **11**, 725–738.

Dyer RJ (2007) Powers of discerning: challenges to understanding dispersal processes in natural populations. *Molecular Ecology*, **16**, 4881–4882.

Elias TS (1980) *The Complete Trees of North America*. Gramercy Publishing Co, New York.

Epperson BK, Alvarez-Buylla ER (1997) Limited seed dispersal and genetic structure in life stages of *Cecropia obtusifolia*. *Evolution*, **51**, 275–282.

Erickson DL, Hamrick JL, Kochert GD (2004) Ecological determinants of genetic diversity in an expanding population of the shrub *Myrica cerifera*. *Molecular Ecology*, **13**, 1655–1664.

Gapare WJ, Aitken SN (2005) Strong spatial genetic structure in peripheral but not core populations of Sitka spruce [*Picea sitchensis* (Bong.) Carr.]. *Molecular Ecology*, **14**, 2659–2667.

Godt MJW, Hamrick JL (1997) Estimation of mating system parameters of *Albizia julibrissin* (Fabaceae). *Forest Genetics*, **4**, 217–221.

Hamrick JL, Murawski DA, Nason JD (1993) The influence of seed dispersal mechanisms on the genetic structure of tropical tree populations. *Vegetatio*, **107/108**, 281–297.

Hardy OJ (2003) Estimation of pairwise relatedness between individuals and characterization of isolation-by-distance processes using dominant genetic markers. *Molecular Ecology*, **12**, 1577–1588.

Hardy OJ, Vekemans X (2002) SPAGEDI: a versatile computer program to analyse spatial genetic structure at the individual or population levels. *Molecular Ecology Notes*, **2**, 618–620.

Hardy OJ, Maggia L, Bandou E *et al*. (2006) Fine-scale genetic structure and gene dispersal inferences in 10 Neotropical tree species. *Molecular Ecology*, **15**, 559–571.

Hedrick PW (2005) *Genetics of Populations*, 3rd edn. Jones and Bartlett Publishers, Boston, Massachusetts.

Jacquemyn H, Brys R, Honnay O, Hermy M, Roldan-Ruiz I (2005) Local forest environment largely affects below-ground growth, clonal diversity and fine-scale spatial genetic structure in the temperate deciduous forest herb *Paris quadrifolia*. *Molecular Ecology*, **14**, 4479–4488.

Jones FA, Hubbell SP (2006) Demographic spatial genetic structure of the Neotropical tree, *Jacaranda copaia*. *Molecular Ecology*, **15**, 3205–3217.

Jones FA, Hamrick JL, Peterson CJ, Squiers ER (2006) Inferring colonization history from analyses of spatial genetic structure within populations of *Pinus strobus* and *Quercus rubra*. *Molecular Ecology*, **15**, 851–861.

Jump AS, Penuelas J (2007) Extensive spatial genetic structure revealed by AFLP but not SSR molecular markers in the wind-pollinated tree, *Fagus sylvatica*. *Molecular Ecology*, **16**, 925–936.

Knowles P, Perry DJ, Foster HA (1992) Spatial genetic structure in two tamarack [*Larix laricina* (Du Roi) K Koch.] populations with differing establishment histories. *Evolution*, **46**, 572–576.

Latouche-Halle C, Ramboer A, Bandou E, Caron H, Kremer A (2003) Nuclear and chloroplast genetic structure indicate fine-scale spatial dynamics in a neotropical tree population. *Heredity*, **91**, 181–190.

Li CC, Horovitz DG (1953) Some methods of estimating the inbreeding coefficient. *American Journal of Human Genetics*, **5**, 107–117.

Litrico I, Ronfort J, Verlaque R, Thompson JD (2005) Spatial structure of genetic variation and primary succession in the pioneer tree species *Antirhea borbonica* on La Reunion. *Molecular Ecology*, **14**, 1575–1584.

Loiselle BA, Sork VL, Nason JD, Graham C (1995) Spatial genetic structure of a tropical understory shrub, *Psychotria officinalis* (Rubiaceae). *American Journal of Botany*, **82**, 1420–1425.

McCauley DE, Raveill J, Antonovics J (1995) Local founding events as determinants of genetic structure in a plant metapopulation. *Heredity*, **75**, 630–636.

Mitton JB, Linhart YB, Sturgeon KB, Hamrick JL (1979) Allozyme polymorphisms detected in mature needle tissue of ponderosa pine. *Journal of Heredity*, **70**, 86–89.

Miyamoto N, Kuramoto N, Yamada H (2002) Differences in spatial autocorrelation between four sub-populations of *Alnus trabeculosa* Hand. Mazz. (Betulaceae). *Heredity*, **89**, 273–279.

Nei M (1973) Analysis of gene diversity in subdivided populations. *Proceedings of the National Academy of Sciences, USA*, **70**, 3321–3323.

Nei M (1977) *F*-statistics and analysis of gene diversity in subdivided populations. *Annals of Human Genetics*, **41**, 225–233.

Ng KKS, Lee SL, Koh CL (2004) Spatial structure and genetic diversity of two tropical tree species with contrasting breeding systems and different ploidy levels. *Molecular Ecology*, **13**, 657–669.

Pardini EA, Hamrick JL (2007) Hierarchical patterns of paternity within crowns of *Albizia julibrissin* (Fabaceae). *American Journal of Botany*, **94**, 111–118.

Parker KC, Hamrick JL, Parker AJ, Nason JD (2001) Fine-scale genetic structure in *Pinus clausa* (Pinaceae) populations: effects of disturbance history. *Heredity*, **87**, 99–113.

Peakall R, Smouse PE (2006) GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes*, **6**, 288–295.

Peakall R, Ruibal M, Lindenmayer DB (2003) Spatial autocorrelation analysis offers new insights into gene flow in the Australian bush rat, *Rattus fuscipes*. *Evolution*, **57**, 1182–1195.

Premoli AC, Kitzberger T (2005) Regeneration mode affects spatial genetic structure of *Nothofagus dombeyi* forests. *Molecular Ecology*, **14**, 2319–2329.

Queller DC, Goodnight KF (1989) Estimating relatedness using genetic markers. *Evolution*, **43**, 258–275.

Remaley T (2005) *Silk Tree*. Plant Conservation Alliance, Alien Plant Working Group, Washington DC. Retrieved from http://www.nps.gov/plants/alien/fact/alju1.htm on October 1, 2007.

Rousset F (2002) Inbreeding and relatedness coefficients: what do they measure? *Heredity*, **88**, 371–380.

Smouse PE, Peakall R (1999) Spatial autocorrelation analysis of individual multiallele and multilocus genetic structure. *Heredity*, **82**, 561–573.

Soltis DE, Haufler CH, Darrow DC, Gastony GJ (1983) Starch gel electrophoresis: a compilation of grinding buffers, gel and electrode buffers, and staining schedules. *American Fern Journal*, **73**, 9–27.

Takahashi M, Mukouda M, Koono K (2000) Differences in genetic structure between two Japanese beech (*Fagus crenata* Blume) stands. *Heredity*, **84**, 103–115.

Troupin D, Nathan R, Vendramin GG (2006) Analysis of spatial genetic structure in an expanding *Pinus halepensis* population reveals development of fine-scale genetic clustering over time. *Molecular Ecology*, **15**, 3617–3630.

USDA (2007) *Alliaria petiolata* (Bieb.) Cavara & Grande. *USDA Plants Database*. Retrieved from http://plants.usda.gov/java/profile?symbol=ALPE4 on April 27, 2007.

Vekemans X, Hardy OJ (2004) New insights from fine-scale spatial genetic structure analyses in plant populations. *Molecular Ecology*, **13**, 921–935.

Wade MJ, McCauley DE (1988) Extinction and recolonization – their effects on the genetic differentiation of local populations. *Evolution*, **42**, 995–1005.

Wendel JF, Weeden NF (1989) Visualization and interpretation of plant isozymes. In: *Isozymes in Plant Biology* (eds Soltis DE, Soltis PS), pp. 5–45. Dioscorides Press, Portland, Oregon.

Whitlock MC, McCauley DE (1990) Some population genetic consequences of colony formation and extinction – genetic correlations within founding groups. *Evolution*, **44**, 1717–1724.

Williams DA, Muchugu E, Overholt WA, Cuda JP (2007) Colonization patterns of the invasive Brazilian peppertree, *Schinus terebinthifolius*, in Florida. *Heredity*, **98**, 284–293.

Workman PL, Niswander JD (1970) Population studies on southwestern Indian tribes. II. Local genetic differentiation in Papago. *American Journal of Human Genetics*, **22**, 24–49.

Wright S (1922) Coefficients of inbreeding and relationship. *American Naturalist*, **56**, 330–338.

Yang S, Bishop JG, Webster MS (2008) Colonization genetics of an animal-dispersed plant (*Vaccinium membranaceum*) at Mount St Helens, Washington. *Molecular Ecology*, **17**, 731–740.

Eleanor Pardini is a Postdoctoral Research Associate at Washington University in St. Louis. She is interested in understanding the evolutionary and ecological consequences of seed dispersal. Her current research uses demographic modelling and genetic tools to understand plant population biology and inform management of invasive and rare plants. Jim Hamrick is a Regents Professor in the Department of Plant Biology at the University of Georgia. He is a plant evolutionary biologist interested in gene movement and its impacts on the structuring and maintenance of plant population genetic diversity.

Supplementary material

The following supplementary material is available for this article:

Fig. S1 Spatial genetic structure in juvenile and adult size cohorts within four large populations of *Albizia julibrissin* in Athens, Georgia. The solid lines represent the r_{ij} estimates; the dashed lines represent upper and lower 95% confidence intervals constructed around the null hypothesis of no SGS estimated by permutation; error bars represent upper and lower 95% confidence intervals around r_{ij} estimated by bootstrap resampling.

Fig. S2 Spatial genetic structure in five size cohorts within the large KNO population of *Albizia julibrissin* in Athens, Georgia. The solid lines represent the r_{ij} estimates; the dashed lines represent upper and lower 95% confidence intervals constructed around the null hypothesis of no SGS estimated by permutation; error bars represent upper and lower 95% confidence intervals around r_{ij} estimated by bootstrap resampling.

This material is available as part of the online article from:
http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-294X.2008.03807.x
(This link will take you to the article abstract).

Please note: Blackwell Publishing are not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.