MOLECULAR ECOLOGY

Molecular Ecology (2012) doi: 10.1111/mec.12055

Long-distance dispersal and genetic structure of natural populations: an assessment of the inverse isolation hypothesis in peat mosses

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Abstract

It is well accepted that the shape of the dispersal kernel, especially its tail, has a substantial effect on the genetic structure of species. Theory predicts that dispersal by fat-tailed kernels reshuffles genetic material, and thus, preserves genetic diversity during colonization. Moreover, if efficient long-distance dispersal is coupled with random colonization, an inverse isolation effect is predicted to develop in which increasing genetic diversity per colonizer is expected with increasing distance from a genetically variable source. By contrast, increasing isolation leads to decreasing genetic diversity when dispersal is via thin-tailed kernels. Here, we use a well-established model group for dispersal biology (peat mosses: genus *Sphagnum*) with a fat-tailed dispersal kernel, and the natural laboratory of the Stockholm archipelago to study the validity of the inverse isolation hypothesis in spore-dispersed plants in island colonization. Population genetic structure of three species (*Sphagnum fallax*, *Sphagnum fimbriatum* and *Sphagnum palustre*) with contrasting life histories and ploidy levels were investigated on a set of islands using microsatellites. Our data show (ϕ'_{st}, AMOVA, IBD) that dispersal of the two most abundant species can be well approximated by a random colonization model. We find that genetic diversity per colonizer on islands increases with distance from the mainland for *S. fallax* and *S. fimbriatum*. By contrast, *S. palustre* deviates from this pattern, owing to its restricted distribution in the region, affecting its source pool strength. Therefore, the inverse isolation effect appears to hold in natural populations of peat mosses and, likely, in other organisms with small diaspores.

Keywords: genetic structure, inverse isolation hypothesis, island colonization, long-distance dispersal, *Sphagnum*

Received 6 December 2011; revision received 27 August 2012; accepted 29 August 2012

Introduction

Dispersal is one of the most critical phases of an organism's life history because of its effects on distribution and evolution (Ronce 2007; Travis *et al.* 2010). Short-distance dispersal (SDD) is relatively easy to detect because of its frequent occurrence, and is thought to impact within-population variation patterns (Vekemans & Hardy 2004; Broquet & Petit 2009; Chybicky & Burczyk 2010). Nevertheless, it is agreed that long-distance dispersal (LDD) and not SDD is the major determinant governing

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the dynamics of colonization and large-scale genetic structure of species (Nichols & Hewitt 1994; Ibrahim *et al.* 1996; Nathan 2005; Nathan *et al.* 2005; Bialozyt *et al.* 2006; Klein *et al.* 2006; Fayard *et al.* 2009).

Long-distance dispersal may be rare, and thus, difficult to measure, even using genetic markers, but its effect on the spatial distribution of genetic diversity is well characterized by theoretical models. Experimental evidence suggests that the highly stochastic process of dispersal can be reasonably well approximated by a small number of mathematical functions that mainly differ in the frequency with which LDD occurs (Bullock & Clarke 2000; Austerlitz *et al.* 2004; Devaux *et al.* 2005; Klein *et al.* 2006). When LDD is present, the dispersal process can be approximated by either a thin-tailed kernel where LDD events are rare or alternatively by a fat-tailed distribution where LDD events are more frequent. It is now accepted that the shape of the dispersal kernel, in particular its tail, is a primary determinant of expansion dynamics and the spatial genetic structure of colonizing populations (Bialozyt *et al.* 2006; Klein *et al.* 2006; Wingen *et al.* 2007; Fayard *et al.* 2009).

In thin-tailed kernels, rare establishment by a few founders ahead of the expanding front dominates the dispersal process and is expected to lead to a dramatic reduction of genetic diversity and to a coarse-grained patchy distribution of genotypes (the embolism effect, Bialozyt *et al.* 2006; Fayard *et al.* 2009; Ray & Excoffier 2010). Furthermore, when LDD events are rare, most colonizing propagules at a given location are expected to originate from the closest source, resulting in a propagule pool with low diversity (Klein *et al.* 2006). By contrast, when LDD events are more frequent, establishment of individuals ahead of the colonization front, and from a wider array of sources is expected. Frequent LDD events can preserve genetic diversity at the regional scale because of the mixing of genetically diverse propagules (reshuffling effect, Nichols & Hewitt 1994; Ibrahim *et al.* 1996; Bialozyt *et al.* 2006; Fayard *et al.* 2009).

Predictions of dispersal models can be validated only in organism groups, where details of the dispersal process and the shape of the dispersal kernel are known in natural populations. Organisms with considerable dispersal power, in particular spore-dispersed plants, provide a tractable model system where genetic consequences of LDD can be investigated. Peat mosses (members of the genus *Sphagnum*) represent an appropriate model system to study the genetic consequences of LDD with a fat-tailed kernel because dispersal curves and their effects on the spatial structuring of genetic diversity have been investigated experimentally (Sundberg 2005, 2010). Experimental evidence shows that deposition of peat moss spores in natural populations follows a fat-tailed inverse power law curve of the form $D = a \times r^b$ (where D is the number of spores deposited per unit area (m^{-2}) at radius r (m) from the centre of a colony, a is the spore density at 1 m from the centre and b is the rate of decline with distance from the source; Sundberg 2005). Both dispersal from individual patch sources (rates of decline $b \approx -1.8$ to -2.3) and from larger sources at regional scales (including background deposition; $b \approx -0.28$ to -0.57) indicate frequent LDD events, which is supported by high recorded spore deposition densities at isolated sites (Sundberg 2005, 2012). Furthermore, available ecological and genetic data also support frequent LDD in *Sphagnum* (Stenøien & Såstad 1999; Hanssen *et al.* 2000; Thingsgaard 2001; Sundberg *et al.* 2006; Szövényi *et al.* 2008; Stenøien *et al.* 2011).

Recently emerged networks of islands represent an appropriate system to study the effect of LDD on the genetic structure of populations. In general, island populations are expected to be genetically less diverse than their mainland counterparts, and genetic diversity should decrease with an increasing distance from the mainland if dispersal is restricted (Barrett 1996; Franks 2010). However, in spore-producing plants with a fat-tailed dispersal curve, theory suggests an inverse isolation effect in which higher genetic diversity per colonizer is expected on islands with increasing distance from the mainland (Sundberg 2005; Klein *et al.* 2006; Wingen *et al.* 2007).

Simple mathematical models predict that an inverse isolation effect is expected to develop in a mainland–island system if (i) dispersal is mainly from the mainland to the islands; (ii) contribution of islands to the propagule pool is negligible; (iii) dispersal follows a fat-tailed kernel; and (iv) colonization of the islands can be approximated by a random process. Given these assumptions, island colonization is predicted to take place from a continuously diluting propagule cloud penetrating the archipelago in which a higher proportion of propagules is expected to originate from more distant and spatially more diverse sources with increasing distance from the mainland source (Sundberg 2005; Klein *et al.* 2006). This is in sharp contrast to traditional models of island colonization involving thin-tailed dispersal kernels where diversity of colonizing propagules, is expected to decrease with distance from the mainland (Barrett 1996; Franks 2010).

Contrasting diversity of the colonizing propagule pool under classical 'isolation by distance' (IBD), and the inverse isolation hypothesis has significant implications for the genetic diversity of island populations. In particular, no relationship between geographic and genetic distances (IBD) and only weak among island

genetic differentiation is expected as a result of the inverse isolation effect. Furthermore, allelic richness per unit island area is either expected to increase or remain more or less constant with increasing distance from the source because dilution of the spore cloud is predicted to be balanced by the rate at which genetic diversity of propagules per unit island area increase (Sundberg 2012). This is expected to lead to higher genetic variability (in terms of allelic richness) per colonizer on more distant islands, a central prediction of the inverse isolation hypothesis (Sundberg 2005).

It has been shown that island colonization in the Stockholm archipelago by peat mosses is predicted to lead to an inverse isolation effect (Sundberg *et al.* 2006), so here, we compare expected and observed patterns of genetic structure of peat moss populations on islands of the Stockholm archipelago to test that prediction. Our study involves three peat moss species (*Sphagnum fallax* (Klinggr.) Klinggr., *Sphagnum fimbriatum* Wils. and *Sphagnum palustre* L) with contrasting mating systems and ploidal levels, in order to distinguish species-specific and species-independent processes.

Materials and methods

Study area

The study included ten sites along a mainland–island gradient in the boreo-nemoral vegetation zone in the province of Uppland, East-central Sweden (Fig. 1, Table 1). Six sites were small islands in the Stockholm archipelago located two to 39 km from the mainland, of varying size (7–55 ha) and age (3100–4100 years; Table 1). In the area, continuous land uplift proceeds at 4–5 mm/year since the last glaciation that terminated ca 10 000 years ago (Mörner 1991). Thus, age can be predicted from island height (Sundberg *et al.* 2006). On the islands, *Sphagnum* occurs in periodically wet depressions among exposed granite or gneiss bedrock (Sundberg *et al.* 2006). Another site (no. 7) was part of coastal areas of the large island Väddö (38-km long, highest point at 50 m asl), close to the mainland, where *Sphagnum* occupies rock pools. On the mainland, three peatlands were sampled in which *Sphagnum* species occurred as relatively well-defined patches: a swamp forest surrounding open peatlands (no. 8; Table 1); a former peatland drained for forestry 55 years ago (no. 9); and peat pits in a former bog, where peat extraction ceased 60 years ago (no. 10).

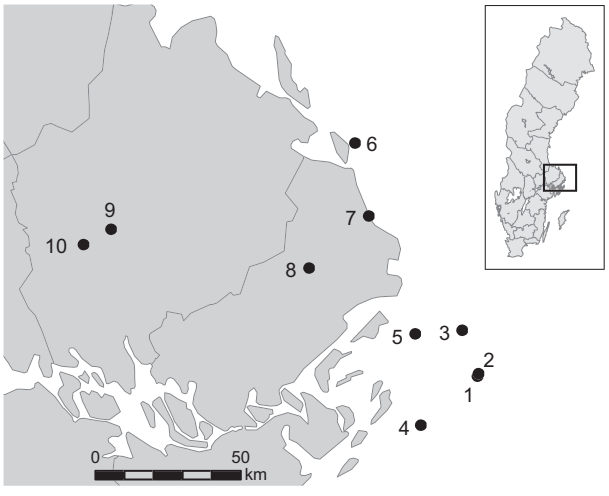

Fig. 1 The geographical setting of the ten sites sampled in the province of Uppland, East-central Sweden. Site numbers refer to Table 1.

Sampling

The three most common *Sphagnum* species in the archipelago were chosen as study subjects: *Sphagnum fallax* (Klinggr.) Klinggr., *Sphagnum fimbriatum* Wils. and *Sphagnum palustre* L. All species are also common on the mainland. The species have contrasting life histories, reflecting their mating systems and frequency of spore capsule production. *Sphagnum fallax* is dioecious and rarely (not seen by us) produces capsules in the archipelago, *S. fimbriatum* is monoecious and produces capsules frequently (46% of the sampled patches bore capsules at a generally high density), while *S. palustre* is dioecious and produces capsules occasionally (11% at a lower density). The first two species are haploid ($n = 19$), while *S. palustre* is supposedly an allodiploid ($n = 38$; Karlin *et al.* 2010). The three species have overlapping habitats in the archipelago and frequently grow together (Sundberg *et al.* 2006).

At each site, between 30 and 43 patches were sampled for each species. Table 1 reports the number of individuals for which complete genotypic information could be obtained. Individuals with missing data were excluded from further analyses. These patches represented a majority of the extant patches found at the sites. Samples of 5–10 shoots, 5–10-cm long, were generally taken from the centre of each patch and stored in paper bags until further analysis. A patch was distinguished as separate if it was isolated by at least 5 cm. The position of each patch was recorded with a GPS (Garmin GPSmap 60CSx) providing an estimated horizontal error of 2–3 m. Distances smaller than 2–3 m were ascertained using a measuring tape. Elevation was based on a combination of calibrated barometric pressure in the GPS, position in relation to 5 m contour lines in maps and comparison with the height of a person standing at the shoreline. Samples were put in labelled paper bags and air-dried before extraction and genetic analysis.

Table 1 Description of the sampling sites in the province of Uppland, East-central Sweden (cf. Fig. 1), and the number of samples collected of three *Sphagnum* species. Site numbers refer to Fig. 1

Site no.	Name	Type of site*	Area† (ha)	Height† above sea level (m)	Age (years)	Dist. from the (mainland‡ (km)	Site midpoint (WGS84)	No. of samples analysed		
								Sphagnum fallax	*Sphagnum fimbriatum*	*Sphagnum palustre*
1	Storön	I	55	17.5	4100	39.3	59°26′34.8″N; 19°30′10.6″E	24	34	29
2	Manskär	I	7	17.5	4100	38.8	59°27′02.5″N; 19°30′43.6″E	13	39	3
3	Röder (storskär)	I	21	15	3500	24.6	59°35′17.2″N; 19°25′48.7″E	26	40	33
4	Horssten	I	31	12.5	3100	24	59°18′10.7″N; 19°08′35.6″E	29	34	32
5	Enskär	I	25	16	3600	14.3	59°35′11.9″N; 19°08′28.7″E	33	37	31
6	Måssten	I	23	17.5	3300	9.1	60°11′15.6″N; 18°50′38.1″E	32	37	30
7	Väddö	M	12 790 (150)	50 (12)	>10000 (c 1600)	0	59°57′33.6″N; 18°54′05.9″E	37	33	23
8	Lohärad (Mårdsjön/ (Kärrmossen)	M	(10)	(25)	>4400	−20	59°48′32.2″N; 18°30′59.6″E			41
9	Långmossen	M	(9)	(52)	55§	−70	59°57′18.2″N; 17°18′36.4″E		40	
10	Stormossen	M	(20)	(68)	60¶	−80	59°54′39.6″N; 17°08′13.9″E	40		

*I, island; M, mainland.
†Areas and heights in parentheses include the extensions of sampled areas of mainland or large island sites, whereas those for smaller islands include the whole islands.
‡Linear distance from the coast; negative distances refer to inland sites.
§A former peatland that was drained 55 years ago – most *Sphagnum* colonization probably happened after that.
¶A former peat harvested peatland – much of the *Sphagnum* colonization should have occurred after its abandonment 50–60 years ago.

Genetic analysis

From each bag (corresponding to a single patch), we randomly selected one shoot, and the uppermost 3–5 mm of the capitulum was used for DNA extraction. The rest was preserved, as a voucher in the Duke University Herbarium (DUKE). DNA extraction followed the methods described in Shaw *et al.* (2008). Initially, a sample of eight individuals per species (two each of the four distant islands) and a set of 30 microsatellite markers were used for screening marker variability. Microsatellite loci with an unambiguous banding pattern and with the highest variability were kept. Microsatellite markers were amplified in a multiplex PCR by combining 3–4 primers, and labelled with FAM, HEX and NED fluorofores. The final set of microsatellite loci included the following (numbers refer to Shaw *et al.* 2008 and to Stenøien *et al.* 2011; with multiplex mixes in brackets): 1. *Sphagnum fimbriatum*—15 loci: (9, 20, 22, 85); (28, 60, 68); (7, 10, 30, 87); (14, 17, 19, 49). 2. *Sphagnum fallax*—16 loci: (1, 7, 22, 30); (4, 15, 19, 68); (6, 10, 28, 49); (14, 20, 29, 94). 3. *Sphagnum palustre*—13 loci: (18, 20, 54, 84) (30, 65, 87) (5, 19, 94) (1, 22, 85). Details of PCR conditions, multiplexing and fragment size scoring followed Shaw *et al.* (2008). The numbers of samples analysed are given in Table 1.

Genetic diversity, AMOVA and IBD pattern

Genetic variability was described by estimating the following statistics for each species (population and species-wide): allelic diversity calculated as the effective number of alleles (A_e) and allelic richness expressed as the average number of alleles per locus (A) (Peakall & Smouse 2006). For each species and for each site, extent of clonality was estimated as the proportion of distinguishable genotypes (number of different multilocus genotypes/number of individuals analysed, Ellstrand & Roose 1987). Allelic richness (A) was rarified to correct

for uneven sampling intensities across sites using the software HP-Rare (Kalinowski 2005). Genetic diversity indices were compared among the three species using a Kruskal–Wallis test (Sokal & Rohlf 1995).

Genetic structure of populations was investigated using a nested AMOVA model (Excoffier *et al.* 1992), with populations nested within regions (island populations: sites 1,2,3,4,5,6 vs. mainland populations: sites 7,8,9,10; site numbers refer to Fig. 1 and Table 1). In order to account for species-wide and within-population genetic diversity differences, the AMOVA was conducted by calculating the standardized metric of genetic differentiation (ϕ'_{st}) developed by Meiermans (2006). For all AMOVA calculations, clonal replicates within each population were removed to correct for the difference in the extent of clonality among species. Pairwise population differentiation was estimated as ϕ'_{st} and its significance tested by randomly permuting individuals among sites 10 000 times. *P*-values were adjusted using the standard Bonferroni correction (Sokal & Rohlf 1995). Estimates for genetic diversity statistics were obtained, and AMOVA analyses were conducted using GenoDive (Meirmans & Van Tienderen 2004) and GenAlex 6.4 (Peakall & Smouse 2006). Site #2 for *S. palustre* (with three individuals sampled) was only used when calculating descriptive statistics, but was excluded from the AMOVA and correlation analyses.

If migration among populations is limited, IBD may develop (Hutchison & Templeton 1999). By contrast, in organisms with a fat-tailed dispersal kernel, no IBD is expected, owing to the well-mixed and diverse propagule pool (Sundberg 2005; Klein *et al.* 2006). In order to test this, correlations between geographic (linear distance among populations) and standardized genetic distances ($Y'_{st} = \phi'_{st}/(1 - \phi'_{st})$) were tested using the whole data set (both island and mainland populations) and significance was assessed by randomly permuting geographic coordinates among spatial locations 10 000 times. IBD was calculated on the total data set, but clonal replicates within each population were removed (only one individual per genetic clone per population was kept) to correct for the difference in the extent of clonality among species. Calculations were conducted in SPAGEDI-1.3.c (Hardy & Vekemans 2002).

Correlation among genetic diversity statistics and island parameters

Predictions of the inverse isolation hypothesis on the genetic diversity of island populations were investigated by calculating nonparametric partial correlation coefficients and testing their significance (Sokal & Rohlf 1995). In order to describe the genetic diversity of island populations, three statistics were used that are predicted to show contrasting patterns under the inverse isolation and the classical island colonization scenarios. The average number of alleles per locus was calculated as an estimate of the allelic richness of island populations. A composite measure was also obtained by dividing allelic richness by the number of unique multilocus genotypes to measure the genetic variability per colonizer per island. This measure was used to compensate for fewer colonizers (dilution effect) on more isolated sites. Both measures were rarified using the software HP-Rare (Kalinowski 2005), in order to correct for uneven sampling intensities across sites. Finally, we also calculated Nei's unbiased estimate of heterozygosity (gene diversity, Nei 1975). Island age, island area and minimum distance of the island from the mainland were used as predictors, whereas the average number of alleles per locus, per genetic clone and expected heterozygosity were tested as response variables. Nonparametric partial correlation between each predictor and response variable was calculated using Spearman's rho statistic, while controlling for the rest of the predictors (Sokal & Rohlf 1995). To correct for multiple testing, *P*-values were adjusted using the Holm-Bonferroni method (Sokal & Rohlf 1995). Correlation analysis and statistical testing were conducted in the R statistical package (R Development Core Team 2011).

Results

Genetic diversity

Within-population (islands = populations) allelic diversity (A_e) was highest in the unisexual haploid *Sphagnum fallax*, lowest in the bisexual haploid *Sphagnum fimbriatum* and intermediate in the unisexual diploid *Sphagnum palustre* (Table 2). Nevertheless, within-population allelic richness estimates (A) were not significantly different between *S. palustre* and *S. fallax* but both species' allelic diversity was significantly higher than that of *S. fimbriatum*.

The three species also showed differences in their average clonal richness (PD, Table 2). The proportion of distinguishable genotypes (number of clones divided by the number of sampled individuals) was greatest in *S. fallax* (PD = 0.851), intermediate in *S. fimbriatum* (PD = 0.638) and lowest in *S. palustre* (PD = 0.581). Clonal richness values of *S. fallax* and *S. palustre* were significantly different, whereas *S. fimbriatum* did not differ significantly from either of those two species.

AMOVA and genetic differentiation among populations

In all the three species, most of the genetic variance occurred within populations (Table 3). The proportion of

Table 2 Average genetic diversity of populations for the three species investigated. Significantly different values among species ($P \leq 0.05$, Kruskal–Wallis test) are marked with different capital letters (A, B)

		N	*A*	Ae	PD
Sphagnum fallax	Mean	29.266	4.219^{A}	2.589^{A}	0.851^{A}
	SE	0.720	0.053	0.186	0.050
Sphagnum fimbriatum	Mean	36.750	3.017^{B}	1.932^{B}	0.638^{AB}
	SE	0.241	0.270	0.170	0.062
Sphagnum palustre	Mean	27.712	3.250^{C}	2.331^{AB}	0.581^{B}
	SE	1.028	0.149	0.090	0.047

N, average number of individuals per population analysed, A, average number of alleles per locus averaged over all populations, Ae, the effective number of alleles averaged over all populations, PD, proportion of distinguishable genotypes (number of multilocus genotypes/number of individuals analysed) averaged over all populations, SE, standard error of the mean.

among-population genetic variance was highest in *S. fimbriatum* (6%, $P = 0.001$), intermediate in *S. palustre* (2%, $P = 0.001$) and smallest in *S. fallax* (1%, $P = 0.005$). According to the nested AMOVA, populations of all three species were significantly albeit weakly differentiated (Table 3). The among-population ϕ'_{sc} value was greatest in *S. fimbriatum* ($\phi'_{sc} = 0.088$, $P = 0.001$), intermediate in *S. palustre* ($\phi'_{sc} = 0.046$, $P = 0.001$) and smallest in *S. fallax* ($\phi'_{sc} = 0.027$, $P = 0.005$). Island and mainland populations showed significant but weak differentiation in *S. fimbriatum* and *S. palustre* but not in *S. fallax*, where differentiation was essentially zero and nonsignificant (Table 3).

Average pairwise population ϕ'_{st} values among-islands (AI) and among-island vs. mainland populations (IM) were very similar but the former tended to be slightly greater in all three species studied with a marked difference in *S. fallax* (*S. fallax* ϕ'_{st} AI:0.039, IM:0.023; *S. fimbriatum* ϕ'_{st} AI:0.12, IM:0.11; *S. palustre* ϕ'_{st} AI:0.051, IM:0.050; Table 4). Nevertheless, this difference was not statistically significant according to a Mantel test ($R_{S.\ fimbriatum} = 0.16$, $P = 0.16$; $R_{S.\ fallax} = -0.202$, $P = 0.70$; $R_{S.\ palustre} = 0.07$, $P = 0.26$; Mantel 1967). The proportion of significantly differentiated population pairs was greatest in *S. palustre*, intermediate in *S. fimbriatum*, and negligible in *S. fallax* (Table 4). Mainland populations tended to harbour slightly higher allelic richness in *S. fimbriatum* and *S. fallax* but not in *S. palustre*. By contrast, the effective number of alleles did not show a consistent difference among island and mainland populations in any of the three species investigated (Table 4).

Isolation by distance and correlation between genetic variability and island parameters

No IBD was detected in *S. fimbriatum* ($\beta = -0.01$, $P = 0.76$) and *S. fallax* ($\beta = 0.00$, $P = 0.70$), but *S. palustre* ($\beta = 0.01$, $P = 0.01$) showed a weak but significant IBD across the mainland–island system investigated (Table 5 and Fig. 2). The average number of alleles per genet was significantly positively correlated with the distance from the mainland in *S. fimbriatum* and *S. fallax*, whereas this relationship was nonsignificant in *S. palustre*. By contrast, neither island age nor area had a significant effect on the average number of alleles per genet in any of the species investigated (Table 6). Furthermore, partial correlations among island variables and other statistics describing genetic diversity of populations (average number of alleles per locus, expected heterozygosity) were nonsignificant (Table 6).

Discussion

Weak genetic differentiation and lack of IBD across the archipelago

Multiple studies have shown that organisms producing large numbers of small airborne, wind-dispersed

Table 3 Results of the nested AMOVA for the three species investigated

Species	Source	d.f.	%var	ϕ_xx	ϕ-value	*P*-value	ϕ′-value
Sphagnum fallax	Among Island–Mainland sites	1	0	ϕ_ct	0.000	0.133	−0.013
	Among Populations	6	1	ϕ_sc	0.013	0.005	0.027
	Within Populations	227	99	ϕ_is	0.995	0.001	—
Sphagnum fimbriatum	Among Island–Mainland sites	1	3%	ϕ_ct	0.030	0.026	0.045
	Among Populations	6	6	ϕ_sc	0.060	0.001	0.088
	Within Populations	286	88	ϕ_is	0.968	0.001	—
Sphagnum palustre	Among Island–Mainland sites	1	1	ϕ_ct	0.006	0.029	0.013
	Among Populations	6	2	ϕ_sc	0.023	0.001	0.046
	Within Populations	428	97	ϕ_is	0.971	0.001	—

d.f., degrees of freedom; %var: percentage of molecular variance explained; ϕ′-value, ϕ-value divided by its maximum possible value given within-population allele frequencies.

Table 4 Allelic diversity and pairwise genetic differentiation of populations for the three species studied. ϕ'_{st} values are shown in the lower triangular, Y'st values in the upper triangular and allelic richness values in the diagonal (Ae: effective number of alleles/ A: average number of alleles per locus) of the matrix. Gray shading indicate mainland–island comparisons and numbers in brackets refer to Table 1. Statistically significant ($P \leq 0.05$) among-population ϕ'_{st} values after Bonferroni correction are shown in bold

Sphagnum fimbriatum								
	(1) Storön	(4) Horssten	(3) Röder	(6) Måssten	(5) Enskär	(2) Manskär	(9) Långmossen	(7) Väddö
(1) Storön	1.27/2.40	0.135	0.095	−0.021	0.070	0.261	0.240	0.295
(4) Horssten	0.119	2.24/3.40	0.110	0.231	0.017	0.127	0.089	0.212
(3) Röder	0.086	**0.099**	1.95/3.15	0.138	0.020	0.156	0.116	0.136
(6) Måssten	−0.021	**0.187**	0.121	1.59/2.40	0.105	0.278	0.260	0.284
(5) Enskär	0.066	0.016	0.020	0.095	2.31/3.12	0.065	0.042	0.099
(2) Manskär	**0.207**	**0.112**	**0.135**	**0.217**	0.061	1.43/2.52	−0.014	0.005
(9) Långmossen	0.193	**0.081**	**0.104**	**0.206**	0.041	−0.014	2.70/3.84	0.018
(7) Väddö	0.228	0.175	**0.119**	**0.221**	0.090	0.005	0.018	1.97/3.20
Sphagnum fallax								
	(1) Storön	(4) Horssten	(3) Röder	(6) Måssten	(5) Enskär	(2) Manskär	(10) Stormossen	(7) Väddö
(1) Storön	2.45/3.84	0.041	−0.010	−0.004	0.023	0.013	−0.011	0.006
(4) Horssten	0.042	2.29/3.35	0.109	0.087	0.111	0.138	0.064	0.072
(3) Röder	−0.010	0.099	2.73/4.14	−0.016	0.037	−0.025	−0.002	0.029
(6) Måssten	−0.004	0.080	−0.016	2.94/3.90	0.036	0.017	−0.014	0.032
(5) Enskär	0.024	0.125	0.038	0.037	2.53/3.54	0.058	0.021	−0.001
(2) Manskär	0.013	0.122	−0.024	0.017	0.055	2.5/3.44	0.051	0.035
(10) Stormossen	−0.011	**0.060**	−0.002	−0.014	0.021	0.049	2.74/3.97	0.026
(7) Väddö	0.006	0.067	0.028	0.031	−0.001	0.034	0.027	2.54/3.79
Sphagnum palustre								
	(1) Storön	(4) Horssten	(3) Röder	(6) Måssten	(5) Enskär	(2) Manskär	(8) Lohärad	(7) Väddö
(1) Storön	2.46/2.68	0.050	0.040	0.087	0.037	−0.010	0.045	0.068
(4) Horssten	**0.048**	2.40/2.23	0.053	0.032	0.040	0.073	0.061	0.052
(3) Röder	**0.039**	**0.050**	2.44/2.57	0.095	0.034	0.033	0.058	0.046
(6) Måssten	**0.080**	**0.031**	**0.086**	2.28/2.26	0.077	0.112	0.090	0.095
(5) Enskär	**0.036**	**0.039**	**0.033**	**0.072**	2.40/2.59	0.048	0.050	0.049
(2) Manskär	−0.010	0.079	0.034	0.101	0.050	1.97/2.10	0.001	0.058
(8) Lohärad	**0.043**	**0.057**	**0.055**	**0.083**	**0.048**	0.001	2.41/2.59	0.030
(7) Väddö	**0.064**	**0.050**	**0.044**	**0.087**	**0.046**	0.055	0.031	2.29/2.29

Table 5 Regression of pairwise genetic distances ($\phi'_{st}/(1-\phi'_{st})$) on geographic distances [ln(distance)]

Species	Number of permutations	*a*	R^2	β	*P*
Sphagnum fallax	10 000	0.06	0.03	0.00	0.70
Sphagnum fimbriatum	10 000	0.19	0.02	−0.01	0.76
Sphagnum palustre	10 000	−0.07	0.26	0.01	0.01

a, intercept; R^2, coefficient of determination; β, slope; *P*, significance of a one-sided test, H1: obs > exp.

particles, such as spores, are capable of frequent LDD (Brown & Hovmøller 2002; Sundberg 2005, 2012, Sundberg *et al.* 2006; Hutsemékers *et al.* 2008; Vanderpoorten *et al.* 2008; Geml *et al.* 2010). This is especially true for the organisms studied here (peat mosses), producing huge numbers of small spores and having a specialized spore discharge mechanism (Sundberg 2002, 2005; Whitaker & Edwards 2010). Island colonization of peat mosses in the Stockholm archipelago involving frequent LDD events is expected to result in an inverse isolation effect. That is, colonization is assumed to take place from a continuously diluting spore cloud penetrating the archipelago in which a higher proportion of propagules is expected to originate from more distant and spatially more diverse sources with increasing distance from the mainland source (Sundberg 2005; Klein *et al.* 2006; Sundberg *et al.* 2006). This will lead to the lack of IBD and to weak genetic differentiation among islands that is in sharp contrast to classical models of island colonization, where IBD and strong among-population genetic differentiation is predicted to develop.

Our genetic data are in line with predictions of the inverse isolation hypothesis by providing evidence for essentially random dispersal of peat moss spores across the island–mainland system in two of the three species investigated. In *Sphagnum fimbriatum* and *Sphagnum fallax*, effective dispersal is indicated by the lack of a

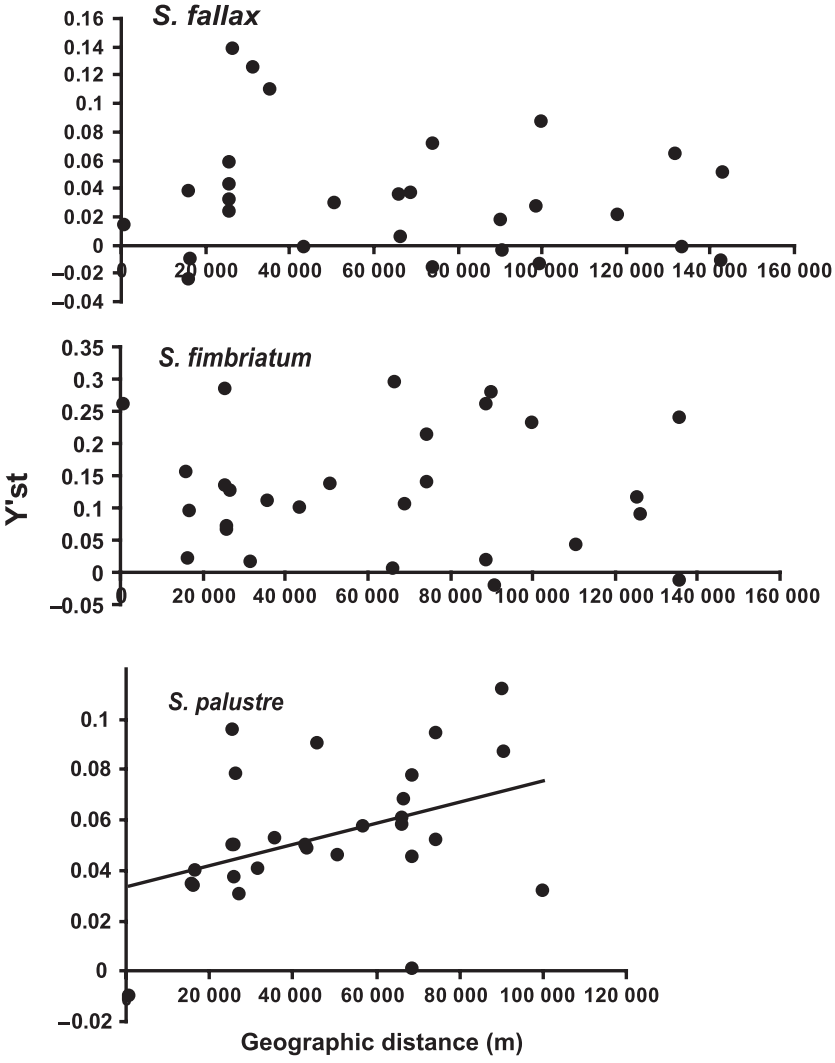

Fig. 2 Regression of pairwise genetic distances $\left(Y'_{st} = \phi'_{st}/(1 - \phi'_{st})\right)$ on geographic distances (m). Significant isolation by distance detected in *Sphagnum palustre* is indicated by the fitted regression line.

relationship between genetic and geographic distances and by the weak genetic differentiation of populations (AMOVA). Only one of the three species, *S. palustre* showed a significant, albeit weak, IBD indicating somewhat restricted dispersal across the archipelago. Nevertheless, genetic differentiation among populations was significantly greater than what would be expected by chance alone in all the three species (AMOVA). Therefore, weak population structure in the two species lacking IBD is likely maintained by forces other than distance *per se* (Table 3). Altogether, these observations imply that dispersal of peat mosses (at least in *S. fimbriatum* and *S. fallax*) is highly efficient, for over some 100 km in the island–mainland system studied. Therefore, the dispersal process of most peat mosses at regional scales can be well approximated by a simple model in which spores are sampled randomly from the pool of available particles (Sundberg *et al.* 2006). These findings are in line with assumptions of the random colonization hypothesis, fit previous ecological observations (Sundberg *et al.* 2006), and add to the continuously accumulating ecological, genetic and phylogenetic evidence suggesting efficient LDD in this group (Stenøien & Såstad 1999; Thingsgaard 2001; Sundberg 2005, 2010, 2012; Sundberg *et al.* 2006; Szövényi *et al.* 2008; Stenøien *et al.* 2011). However, dispersal limitation might develop at larger (intercontinental) spatial scales, and thus, the random approximation may not be applicable (see Szövényi *et al.* 2008; Stenøien *et al.* 2011).

Dispersal kernel and genetic structure

It has been shown that the dispersal kernels of peat moss spores tend to better fit a power law (fat-tailed) than an exponential function (Sundberg 2005). Dispersal of such propagules results in a continuously diluting spore cloud in which the number of propagules per unit island area is expected to decrease, whereas their

Table 6 Nonparametric partial correlation analysis between genetic diversity statistics and island parameters

Species	Response variable tested	Predictor variable	Spearman's Rho	Significance
Sphagnum fallax	AR	Island area	−0.170	0.807
		Island age	0.080	0.909
		Distance from the mainland	−0.106	0.880
	NAPG	Island area	−0.766	0.092
		Island age	−0.777	0.081
		Distance from the mainland	0.870	**0.013**
	uHe	Island area	−0.655	0.220
		Island age	−0.039	0.955
		Distance from the mainland	0.107	0.879
Sphagnum fimbriatum	AR	Island area	−0.153	0.827
		Island age	−0.605	0.282
		Distance from the mainland	0.492	0.424
	NAPG	Island area	0.086	0.919
		Island age	0.696	0.125
		Distance from the mainland	0.999	**0.003**
	uHe	Island area	−0.188	0.787
		Island age	−0.339	0.610
		Distance from the mainland	0.348	0.600
Sphagnum palustre	AR	Island area	0.494	0.570
		Island age	0.906	0.032
		Distance from the mainland	0.623	0.425
	NAPG	Island area	0.593	0.462
		Island age	−0.018	0.986
		Distance from the mainland	−0.503	0.561
	uHe	Island area	−0.072	0.942
		Island age	−0.660	0.380
		Distance from the mainland	0.623	0.425

AR, average number of alleles per locus; NAPG, average number of alleles per locus per genetic clone; uHe, unbiased estimate of expected heterozygosity.
P-values passing an experiment-wise error rate of 0.05 after Holms-Bonferroni correction are shown in bold.

diversity of origin increases with increasing distance from the source (Sundberg 2005; Klein *et al.* 2006). In such a system, an inverse isolation effect is expected to develop in which higher genetic diversity per colonizer is expected with increasing distance from sources (Sundberg 2005).

Here, we report for the first time that the inverse isolation effect on within-population diversity (expressed as the magnitude of the average number of alleles per genet) is a real and detectable effect of fat-tailed dispersal kernels in peat mosses. Distance from the mainland and the genetic diversity per colonizer were positively correlated in *S. fimbriatum* and *S. fallax*, suggesting that the inverse isolation effect may apply for other species with frequent dispersal across the archipelago. This relationship appears to hold for species with contrasting life history characteristics (bisexual *S. fimbriatum* and unisexual *S. fallax*), and thus, seems to be species independent. Our findings suggest that the inverse isolation effect might well be valid for other organisms producing large numbers of propagules that are dispersed according to a fat-tailed dispersal kernel.

In contrast to *S. fimbriatum* and *S. fallax*, *S. palustre* did not follow the expectations of the inverse isolation hypothesis. We detected no significant correlation in *S. palustre* between genetic diversity per colonizer and distance from the mainland. Furthermore, *S. palustre* was the only species with a weak but significant IBD, implying restricted dispersal even at the spatial scale of the archipelago. Therefore, colonization of *S. palustre* appears to be restricted. A plausible reason for this is that *S. palustre* is at its northern limit of distribution, whereas *S. fallax* and *S. fimbriatum* extend much further north (Daniels & Eddy 1990). This should limit the number of available sources, their allelic variability and establishment potential (in *S. palustre*), especially on climatically extreme sites such as the islands. These findings are in line with the expectation of theoretical studies predicting that, below certain source strength and (realized) LDD frequency thresholds, the inverse isolation effect diminishes (Sundberg 2005; Klein *et al.* 2006; Wingen *et al.* 2007).

Another important finding of our study is that only allelic richness per colonizer increased significantly with distance from the mainland. By contrast, neither allelic richness *per se* nor expected heterozygosity responded to the isolation effect. This finding is in line with the observation of Sundberg (2012) that the spore cloud dilutes by increasing distance from the source, which may counteract the diversity-increasing effect of geographic mixing. Therefore, a decreasing number of colonizers from more diverse sources are expected per unit island area with increasing distance from the source. Our data provide evidence that dilution of the spore cloud is sufficient to balance the effect of geographic mixing in our study area because statistics

not corrected for the dilution effect (allelic richness *per se* and expected heterozygosity) show no significant isolation effect. Therefore, allelic richness per colonizer, a statistic that compensates for fewer colonizers (dilution effect) on more isolated sites, is the preferable indicator of genetic diversity under the inverse isolation hypothesis.

Very few studies have assessed the validity of the inverse isolation effect in natural populations. The inverse isolation effect may have caused the genetic structure differences in *Pogonatum dentatum* (Hassel *et al.* 2005), where recently colonized sites along newly constructed forest roads harboured on average more genetic diversity than their well-established counterparts in the mountains. Simulations incorporating LDD have also shown that within-population genetic diversity can be well preserved during range expansions owing to the reshuffling effect that is the mechanistic basis for the inverse isolation hypothesis (Bialozyt *et al.* 2006; Klein *et al.* 2006).

Dispersal following a fat-tailed kernel has far reaching consequences for the large- and small-scale population genetic structure of peat mosses in particular, and organisms experiencing similarly fat-tailed dispersal in general. It increases genetic diversity of the dispersing propagule pool, and thus, helps mixing of the genetic material at regional to intercontinental scales. Owing to a well-mixed and diverse propagule pool, no IBD effect is expected to develop in populations of organisms with fat-tailed dispersal kernel. This prediction is supported by multiple studies describing the population genetic structure of bryophytes and fungi (Lekberg *et al.* 2011; Shaw *et al.* 2011; Travadon *et al.* 2011). Dispersal following a fat-tailed kernel also helps explaining a possible cause for the weak relationship between latitude and diversity in spore-dispersed organisms (Hillebrand & Azovsky 2001; Shaw *et al.* 2005; Hedenäs 2007), the lack of distance effects on island species richness (Sundberg *et al.* 2006), and the generally wide distribution of peat moss species. Furthermore, in organisms with fat-tailed dispersal kernels, islands (and similarly isolated habitats) may function as refuges conserving genetic diversity, which may have an important implications in connection with species range contractions and expansions, such as during glaciations (cf. Hutsemékers *et al.* 2011).

In contrast, highly leptokurtic dispersal kernels promote the origin and conservation of local genetic structure, because at local scales (up to approximately 1 km) propagules from the closest source would dominate the propagule pool. Overall, dispersal following fat-tailed kernels has complex effects on the genetic structure of populations, promoting genetic mixing at larger-spatial scales while conserving genetic structure at local scales. Indeed, observations on the genetic structure of peat mosses are in line with these predictions, showing a complex pattern of local genetic structure yet effective large-scale mixing of genetic material (Stenøien & Såstad 1999; Thingsgaard 2001; Szövényi *et al.* 2008; Stenøien *et al.* 2011).

Conclusions

It is well established that the tail of the dispersal kernel affects the genetic structure of populations. Our study provides a quantitative test of the hypothesis that dispersal with a fat-tailed kernel results in higher genetic diversity per colonizer with increasing distance from the source (inverse isolation effect). We found that this prediction holds in natural populations of organisms with a fat-tailed dispersal kernel, regardless of the mating system of the species studied. Existence of the inverse isolation effect in natural populations of peat mosses suggests a major difference between the genetic structuring of colonizing populations in seed and spore-dispersed plants. In seed plants, island colonization is expected to promote genetic diversification, while in spore-dispersed plants, the inverse isolation effect is predicted to lead to genetic homogenization and conservation. Nevertheless, evolutionary consequences of contrasting genetic composition of colonizing populations in seed and spore-dispersed plants remain to be explored more deeply.

Acknowledgements

We thank Jesper Hansson and Baptiste Regnery for help with sample collection, Jenny Ahlén and Amelia Merced Alejandro for sample sorting, Per Stolpe for the map and Megan Ramaiya for help with DNA isolation. The study was financed by grants no. 215 – 2006-1062 and 215 – 2008-587 from the Swedish research council Formas to S. Sundberg; NSF grant no. DEB-0918998 to A.J. and B. Shaw. Financial support from the Duke University IGSP, the DAAD, the Alexander von Humboldt Foundation and the SNSF (Ambizione fellowship) to P. Szövényi is gratefully acknowledged. Detailed comments of an anonymous reviewer are also acknowledged.

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P.S., S.S., and A.J.S. designed the research, P.S. and S.S. performed the research, P.S. generated and analyzed the data, P.S. and S.S. wrote the paper and all authors commented on multiple drafts of the manuscript.

Data accessibility

Microsatellite data are available under the doi:10.5061/dryad.13kr7 DRYAD entry.