Multiple cryptic species with divergent substrate affinities in the *Serpula himantioides* species complex

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ABSTRACT

Serpula himantioides is a widespread saprotrophic morphospecies mainly colonising coniferous wood in nature, but it appears frequently in buildings as well. From an earlier study, it is known that at least three divergent lineages occur within the *S. himantioides* species complex. In this study, a broader sample of *S. himantioides* isolates has been analysed by multi-locus sequencing, including new isolates from Asia, North and South America. Altogether five phylogenetical species (PS1–5) were detected, all recognised across independent gene phylogenies. A new southern South American phylogenetic species (PS1) was found, representing an early diverging lineage within the *S. himantioides* species complex. The two closely related PS2 and PS3 lineages included isolates from North America only, and PS4 was also dominated by North American isolates. Most of the investigated isolates (76 %) clustered into PS5, a lineage that has been found on most continents, including North America. Overall, little phylogeographical structure was found in PS5, indicating frequent and recent long-distance dispersal events within this widespread lineage. Our analyses indicate that South and North America are the centres of divergence for the *S. himantioides* species complex. Some of the lineages seem adapted to various substrates, but PS5 is able to decay a wide array of angiosperms and gymnosperms, which may have facilitated the spread of this lineage throughout the world.

Introduction

Serpula himantioides (Fr.) P. Karst. is a saprotrophic morphospecies with a wide geographical distribution, observed on all continents except Antarctica. It is mainly found on dead wood of various coniferous tree species, but do also commonly occur in buildings. It produces thin, resupinate and brownish annual basidiocarps and has a heterothallic tetrapolar mating system, based on Northern Hemisphere specimens (Hwang 1955; Harmsen 1960). In a previous study, three genetically well-differentiated lineages were detected within *S. himantioides* across independent gene phylogenies (Kauserud et al. 2006). These three lineages also showed compatible mating within lineages, and incompatible mating between lineages. Thus, as many other basidiomycetes (Nilsson et al. 2003; Geml et al. 2006; Kauserud et al. 2007a), *S. himantioides* seems to represent a species complex including multiple cryptic lineages. Especially when it comes to morphospecies that produces simple, resupinate fruiting structures, such as *S. himantioides*, it might be problematic to detect species boundaries by morphological

means (Taylor *et al.* 2006). Likewise, multiple cryptic species has also been detected in several *Coniophora* species that also produce simple and resupinate fruiting bodies (Ainsworth & Rayner 1990; Kauserud *et al.* 2007a).

Biogeographical studies show that fungi have complex histories of vicariance and dispersal in the same way as plants and animals (Taylor *et al.* 2006; Matheny *et al.* 2009). Although long-distance dispersal events may be rare, it is the best explanation for the present day distribution of many fungal taxa (Hibbett 2001; James *et al.* 2001; Zervakis *et al.* 2004; Hosaka *et al.* 2008; Moncalvo & Buchanan 2008). For some fungi, the natural biogeographical patterns may be blurred by modern spread by man (Brasier & Buck 2001; Coetzee *et al.* 2001; Slippers *et al.* 2001; Kauserud *et al.* 2007b).

In the dry rot fungus *Serpula lacrymans* that is closely related to *S. himantioides*, there seems to have happened a specialization towards growing in buildings (Kauserud *et al.* 2007b). *Serpula himantioides* is also known as a common destroyer of wooden constructions, but whether any adaptations towards this growing habit have happened in any of the *S. himantioides* lineages is not clear.

In this study, a broader sample of S. *himantioides* is included compared to Kauserud *et al.* (2006), including newly obtained isolates from Asia and both of the American continents. The aims of this study were to (1) analyse whether even more phylogenetic species can be found within S. *himantioides*, (2) check whether a biogeographical structure of various S. *himantioides* lineages can be observed, and (3) analyse whether any substrate specialization has happened during the diversification of the S. *himantioides* species complex. To illuminate these topics, the isolates where analysed by multi-locus sequencing of three independent DNA regions.

Material and methods

The material included in this study is listed in Table 1. Compared to Kauserud *et al.* (2006), 40 new isolates of *Serpula himantioides* were included in this study. DNA was extracted from the new cultures following a 2 % CTAB (cetyltrimethylammonium bromide) miniprep method described by Murray & Thompson (1980) with minor modifications: DNA was resuspended in 100 μL distilled sterile H_2O at the final step of extraction. The four DNA markers ITS, LSU, *hsp* and *tub*, were PCR amplified and sequenced as outlined in Kauserud *et al.* (2006). All sequences have been accessioned in GenBank (for accession nos. see Table 1).

Phylogenetic analyses were conducted using TNT (Goloboff *et al.* 2008). Heuristic searches were performed with 1000 random addition sequences and TBR branch swapping. Jack-knife analyses were performed with 10 000 replicates, 36 % removal probability, and absolute frequencies as output. Bayesian analyses were performed in MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003) with models inferred from MrModeltest 2.3 (Posada & Crandall 1998). Two independent runs with five chains (four heated) were run for 10 000 000 generations and summarised after discarding 25 % burn-in. Initially, each DNA region was run separately, but as there was no significant incongruence between datasets, a concatenated dataset were used for all further

analyses. For Bayesian analyses, the different regions were analysed with an independent model for each partition (ITS = GTR + I, LSU = GTR, *tub* = GTR + G, and *hsp* = SYM + G).

Genealogical sorting index (GSI) statistics (Cummings *et al.* 2008) were performed to test for phylogenetic correlation between isolates from different substrates, continents, and habitats. Substrates were categorized as *Pinus*, *Picea*, *Nothofagus*, unknown conifer, and unknown hardwood. Continents were categorised according to geography and habitat categorized as indoor or outdoor.

Results and discussion

In Fig 1, a multi-locus phylogeny of the 67 analysed isolates of *Serpula himantioides* is shown, demonstrating that the isolates group into five different lineages with high support. A high congruence in topology was observed across the four investigated DNA regions when these were analysed separately (Supplementary Information, Fig S1A−C). The five lineages were named PS1−PS5 corresponding to phylogenetic species under the phylogenetic species recognition definition (Taylor *et al.* 2000; Kroken & Taylor 2001, 2009). This, together with earlier mating experiments that has shown that there are compatible matings within the lineages PS3, PS4, and PS5 but incompatible across lineages (Harmsen 1960; Kauserud *et al.* 2006), indicate that PS1−PS5 represent different biological species. As there is only one sample in PS2, and no experimental crosses could be performed, it may be premature to conclude with certainty that this is a distinct species. But as the genetic divergence between PS2 and PS3 is comparable to the divergence to the other phylogenetic species within S. *himantioides*, we will treat it as a separate entity here.

A recent dated molecular phylogeny of the family Serpulaceae has dated the oldest divergence of the cryptic lineages of S. *himantioides* to approx. 12 million years ago (Engh *et al.* in prep). A similar time estimate was made for the split between *Serpula lacrymans* var. *lacrymans* and *Serpula lacrymans* var. *shastensis* that are still able to mate *in vitro* (Harmsen 1960).

Lineage PS1 is sister to the other lineages and includes five South American isolates. PS2, PS3, and PS4 include mainly North American isolates. However, the sample size here is too small to conclude that the lineages are mainly restricted to this continent. PS5 is a widely distributed lineage that has been detected on all continents except for South America and Antarctica. The lack of a distinct phylogeographical structure within PS5 presumably indicates recent long-distance dispersal events. It is well-known that many basidiomycetes have been spread by man on infected timber or plants (Coetzee *et al.* 2001; Gonthier *et al.* 2004; Linzer *et al.* 2008; Pringle *et al.* 2009) and this could also be the case with S. *himantioides*.

Within PS5, a high level of genetic variation is found among the isolates from East Asia and North America. Overall, South and North America seem to have played an important role during the evolution of the S. *himantioides* species complex. The GSI analysis showed that there was a highly significant grouping of the South American samples (GSI 1.00 $p < 0.00001$), but samples from other continents showed no significant grouping. One might speculate that allopatric speciation in South and North America may have happened

Table 1 – Specimens included in this study. Locality information, culture collection, strain number, substrate information, and GenBank numbers are given where they are available.

Code	Locality	Collector	Culture collection[a]	Strain number	Country	Substrate	LSU	ITS	*tub*	*hsp*
SH16	Belgium: Louvain-la-Nueve	G.L. Hennebert	MUCL	30528	BEL	Brick wall	AM076531	AM076498	AJ518086	AM076442
SH17	British Columbia, Aleza Lake	N.a.	MUCL	30795	CAN	*Picea glauca*	AM076527	AM076494	AJ557380	AM076438
SH18	British Columbia, Mt Revelstoke	N.a.	WFPL	49B	CAN	*Callitropsis nootkatensis*	AM076532	AM076499	AJ557377	AM076443
SH19	Bedgebury Pinetum	N.a.	WFPL	49C	GBR	Inner bark, *Pinus* sp.	AM076533	AM076500	AJ518087	AM076444
SH20	British Columbia, Cowichan Lake	N.a.	WFPL	506A	CAN	*Pseudotsuga menziesii*	AM076526	AM076492	AJ557382	AM076436
SH22	UK	N.a.	MUCL	30855	GBR	Log, *Larix* sp.	AM076535	AM076502	AJ518088	AM076446
SH23	Denmark	N.a.	MUCL	30856	DEN	*Pinus* sp. post	AM076536	AM076503	AJ557379	AM076447
SH24	Denmark	N.a.	MUCL	30857	DEN	Pole; decayed	AM076537	AM076504	AJ518089	AM076448
SH25	Antwerpen, Schooten (rue André Ullenslei)	G.L. Hennebert	MUCL	31289	BEL	Bathroom in house	AM076538	AM076505	AJ518090	AM076449
SH26	Manicaland, Chimanimani area, Muguzo Forest Research Station area	Pascal S., Decock C.	MUCL	38575	ZIM	Dead trunk and litter, *Pinus* sp. and *Pinus* litter	AM076539	AM076506	AJ557373	AM076450
SH27	Manicaland, Chimanimani area, Muguzo Forest Research Station area	Pascal S., Decock C.	MUCL	38576	ZIM	Dead trunk and litter, *Pinus* sp. and *Pinus* litter	AM076540	AM076507	AM076430	AM076451
SH28	UK	J. Carrey	MUCL	38935	GBR	Soil	AM076541	AM076508	AM076423	AM076452
SH29	Vosges, Col de la Schlucht, Sentier des roches	Decock C.	MUCL	38979	FRA	Dead standing trunk, coniferous	AM076542	AM076509	AM076427	AM076453
SH30	Bruxelles, St. Josse	Decock C.	MUCL	39729	BEL	Cellar, house	AM076543	AM076510	AM076425	AM076454
SH31	Akershus, Ås, Slørstadskogen	F. Roll-Hansen	NFRI	82-90/7	NOR	*Picea abies*	AM076528	AM076495	N.a.	AM076439
SH96	Maryland, Beltsville	R.W. Davidson	FSC CFS-Atlantic	FSC-31	USA	*Abies* sp.	AM076529	AM076496	AM076825	AM076440
SH99	Bursfelde	H Butin	CBS	383.82	GER	*Picea abies*	AM076547	AM076514	AM076432	AM076458
SH100	Wilsede	O. Schmidt	Schmidt	P218	GER	Spruce stump	AM076548	AM076515	AM076434	AM076459
SH101	Putten, Schovenhorst	J.A. Stalpers	CBS	302.82	NED	Gymnosperm wood	AM076549	AM076516	AM076416	AM076460
SH103	Schleswig-Holstein, Malente	O. Schmidt	Schmidt	P283	GER	Spruce stump	AM076550	AM076517	AM076424	AM076461
SH104	Schleswig-Holstein, Malente	O. Schmidt	Schmidt	P284	GER	Spruce stump	HM135711	HM135661	HM135575	HM135627
SH105	Schleswig-Holstein, Malente	O. Schmidt	Schmidt	P288	GER	Spruce stump	AM076551	AM076518	AM076418	AM076462

SH112	Ceska Trebova	J. Volc	CCBAS	110	CZE	Bric house cellar. Spruce beam	AM076553	AM076520	AM076419	N.a.
SH113	Hedmark: Engerdal: Kvemskjølen SØ.	H. Kauserud	MUCL	46270	NOR	*Pinus sylvestris*	AM076530	AM076497	AM076414	AM076441
SH114	126 Paradise Valley Rd.	Edwards	NZFS	1436	NZL	Ground	AM076554	AM076521	AM076421	AM076465
SH115	Yunnan Province, Chu Xiong, Zi Xi Shan Nature Reserve, 2400 m alt.	Decock C.	MUCL	47005	CHN	Base of a living trunk, *Pinus* sp.	HM135703	HM135653	HM135568	HM135620
SH116	Yunnan Province, Chu Xiong, Zi Xi Shan Nature Reserve, 2400 m alt.	Decock C.	MUCL	47007	CHN	Base of a living trunk, *Pinus* sp.	HM135712	HM135662	HM135576	HM135628
SH117	Limal	Decock C.	MUCL	47155	BEL	Timber, *Pinus* sp.	HM135713	HM135663	HM135577	HM135629
SH120	Brabant Wallon, Ottignies-Louvain-la-Neuve	Hennebert G.	MUCL	47228	BEL	Dead wood in garden, *Chamaecyparis* sp.	HM135714	HM135664	HM135578	HM135630
SH125	Normandie, Le Tilleul Othon	Gesquière P.	MUCL	47679	FRA	House timber, *Pinus* sp.	HM135715	HM135665	HM135579	N.a.
SH127	Yunnan, Chu Xiong, Zi Xi Shan Nature Reserve, 2400 m alt	Decock C.)	MUCL	47928	CHN	Dead stump, *Pinus* sp.	HM135704	HM135654	HM135569	HM135621
SH129	Yunnan, Chu Xiong, Zi Xi Shan Nature Reserve, 2400 m alt	Decock C.	MUCL	47930	CHN	Dead stump, *Pinus* sp.	HM135701	HM135651	HM135566	HM135618
SH130	Yunnan, Chu Xiong, Zi Xi Shan Nature Reserve, 2400 m alt	Decock C.	MUCL	47931	CHN	Dead stump, *Pinus* sp.	HM135702	HM135652	HM135567	HM135619
SH133	British columbia, Snooke		WFPL	506B	CAN	*Pseudotsuga menziesii*	AM076544	AM076511	AM076415	N.a.
SH134	Ontario, Lake Nipigon	J.R. Hansbrough	CFMR	Bud-1908	CAN	*Picea glauca*	HM135716	HM135666	HM135580	N.a.
SH135	Washington; Lewis; Centralia; Weyerhaeuser Timber Co., Forestry Research Centre	K.R. Shea	CFMR	Sh-17	USA	*Picea sitchensis*, 17 y old	HM135717	HM135667	HM135581	HM135631
SH136	Nevada; Nye; G Tunnel, Madison Drift Nuclear test site	R.L. Gilbertson	CFMR	RLG-12941-Sp	USA	*Pseudotsuga menziesii*, white rhizomorph near	HM135718	HM135668	HM135582	HM135632
SH137	Ontario; Ft. William; Lake Nipigon, on Black Sturgion Conc. GLP	G. Englerth	CFMR	Bud-205A	CAN	*Picea glauca*	HM135719	HM135669	HM135583	HM135633
SH139	Munchen, Forstbotanisches Institute	F.F. Lombard	CFMR	R-1	GER	*Picea*, brown and red stain study	HM135720	HM135670	HM135584	HM135634
SH140	Vermont; Warren; Clay Brook area, Green Mt. Nat'l Forest	P.V. Mook	CFMR	PVM-52B-R	USA	*Picea rubens*, 293 y old	HM135721	HM135671	HM135585	N.a.
SH141	Colorado, Bears Ears Ranger District, Routt Nat'l Forest	T.E. Hinds	CFMR	Colo-59-1650	USA	*Picea engelmannii*	HM135705	HM135655	HM135570	HM135622
SH142	Oregon	R. Graham	CFMR	MD-110	USA	*Alnus stake*	HM135722	HM135672	HM135586	N.a.

(continued on next page)

Table 1 – *(continued)*

Code	Locality	Collector	Culture collection[a]	Strain number	Country	Substrate	LSU	ITS	*tub*	*hsp*
SH144	New York; Warren; Warrensburg	J.H. Ginns	CFMR	JHG-459-Sp	USA	*Tsuga canadensis*	HM135723	HM135673	HM135587	HM135635
SH147	Arizona, Portal, Rustler Park, Coronado Nat'l Forest	J.L. Lowe & R.L. Gilbertson	CFMR	L-9729-Sp	USA	*Pinus*	HM135724	HM135674	HM135588	HM135636
SH148	Arizona, Palisades, Santa Catalina Mts, Coronado Nat'l Forest	R.L. Gilbertson	CFMR	RLG-11350-Sp	USA	*Pinus ponderosa*	HM135725	HM135675	HM135589	HM135637
SH150	Georgia, Athens, Oconee National Forest	W.A. Campbell	CFMR	FP-94342-R	USA	*Pinus echinata*	HM135726	HM135676	HM135590	HM135638
SH152	Maryland, Beltsville	R.W. Davidson	CFMR	FP-97366-Sp	USA	*Pinus*	HM135727	HM135677	HM135591	N.a.
SH154	Maryland, Beltsville, Plant industrial station	R.W. Davidson	CFMR	FP-97367-R	USA	*Pinus virginiana*	HM135728	HM135678	HM135592	N.a.
SH155	Maryland, Beltsville, Plant industrial station	R.W. Davidson	CFMR	FP-97439-Sp	USA	*Pinus virginiana*	HM135729	HM135679	HM135593	HM135639
SH156	Maine, Kittern	J.D. Diller	CFMR	FP-97448-Sp	USA	Soil	HM135730	HM135680	HM135594	HM135640
SH157	Maryland, Holiday beech	H.H. McKay	CFMR	FP-104042-T	USA	*Eucalyptus* wood stakes	HM135731	HM135681	HM135595	HM135641
SH158	Maryland, Beltsville	J.D. Diller	CFMR	FP-104137-T	USA	*Pinus* leaves, twigs	HM135732	HM135682	HM135596	HM135642
SH159	Maryland, Beltsville	R.W. Davidson	CFMR	FP-104361-Sp	USA	Hardwood	HM135733	HM135683	HM135597	HM135643
SH160	Maryland, Beltsville	R.W. Davidson	CFMR	FP-104397-Sp	USA	Hardwood	HM135734	HM135684	HM135598	N.a.
SH161	Maryland, Beltsville	R.W. Davidson	CFMR	FP-104405-Sp	USA	Hardwood	HM135735	HM135685	HM135599	N.a.
SH162	Maryland, Beltsville	R.W. Davidson	CFMR	FP-104572-Sp	USA	*Pinus*	HM135736	HM135686	HM135600	HM135644
SH163	Oregon, Hungry Horse, Coram Expt Forest	M.J. Larsen	CFMR	FP-134010-Sp	USA	Conifer	HM135737	HM135687	HM135601	HM135645
SH164	Alaska, North side of Kenai Lake, Kenai Peninsula	N.a.	CFMR	HHB-17587-Sp	USA	*Picea glauca*	AF518648	AM076493	AM076412	AM076437
SH167	Yunnan, Chu Xiong, Zi Xi Shan Nature Reserve	Decock C.	MUCL	46914	CHN	Dead wood, *Pinus* sp.	HM135738	HM135688	HM135602	HM135646
SH168	Concepción	Goetz Palfner	CONC-F	323-2	CHI	From house	HM135699	HM135649	HM135564	HM135616
SH169	Concepción	Goetz Palfner	CONC-F	324-1	CHI	From house	HM135700	HM135650	HM135565	HM135617
SH170	Concepción	Goetz Palfner	CONC-F	324-2	CHI	From house	HM135739	HM135689	HM135603	N.a.
SH171	Tierra del Fuego, Depto. Ushaia, El Valdez	A. Greslebin	CIEFAP	388	ARG	Fallen trunk of *Nothofagus pumilio*	HM135740	HM135690	HM135604	N.a.
SH172	Tierra del Fuego, Depto. Ushaia, Estancia Moat	A. Greslebin	CIEFAP	1517	ARG	Fallen trunk of *Nothofagus betuloides* 'guindo'	HM135741	HM135691	HM135605	N.a.

Isolate	Collector	Locality	Country	Institution	Number	Substrate				
SH175	C. Decock and R. Valenzuela	Durango	MEX	MUCL	52396	Soil and buried wood	AM076555	AM076522	AM076428	AM076466
SH176	C. Decock and R. Valenzuela	Durango	MEX	MUCL	52397	Soil and buried wood	HM159424	HM146135	HM159426	HM159422
SH181	Hallenberg	S. Jutland. Frøslev Plantage	DEN	Hallenberg	2024PS	Picea stump	HM159425	HM146136	HM159427	HM159423

a CBS = Centraalbureau voor Schimmelcultures, Utrecht, Netherlands; CCBAS = Culture Collection of Basidiomycetes, Pragua, Czech republic; CFMR = Centre For Forest Mycology Research, Forest Products Laboratory, USA; CIEFAP = Centro de Investigación y Extensión Forestal Andino Patagónico, Argentinia; CONC-F = From G. Palfner, Concepción, Chile; FSC = Fredericton Stock Culture Collection (Now Atlantic Forestry Centre, Fredericton Canada); Hallenberg = From N. Hallenberg, Gothenburg, Sweden; MUCL = Mycothèque de l'Université catholique de Louvain, Belgium; NZFS = New Zealand Forest Research Institute; NFRI = Norwegian Forest and Landscape Institute, Norway; Schmidt = From O. Schmidt, Hamburg Germany; WFPL = Western Forest Products Laboratory (Now Forintec).
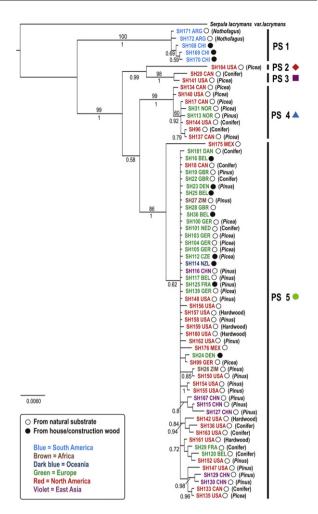

Fig 1 − Phylogenetic tree from a Bayesian analysis of a combined dataset of ITS, LSU, *tef*, and *hsp* sequences. Numbers below branches indicate posterior probability values. Numbers above branches indicate parsimony jack-knife support values (only values above 50 % is shown). The corresponding parsimony trees were of length 350 with CI = 0.763 and RC = 0.674.

in the ancestral lineage splitting into PS1 and the ancestral lineage to PS2−PS5. Our analyses indicate furthermore that PS2, PS3, and PS4 have a primary affinity to North America, but with some northern European representatives. The almost cosmopolitan PS5 may have spread out from North America to Eastern Asia and more recently obtained a world-wide distribution with the help of man. In Fig 2, the geographical distribution of the North American and European isolates is shown. Although speculative, it may be that PS5 has a more temperate distribution on the North American continent while PS4 has a more boreal distribution. In the European samples PS4 was only found in Norway while the other European samples were all in PS5.

There is no evidence for a specialization towards growing on wooden constructions, as has apparently happened in S. *lacrymans* var. *lacrymans* (Bagchee 1954; Kauserud *et al.* 2007b; White *et al.* 2001). In the phylogenetic tree (Fig 1), isolates derived from nature and buildings appear both in PS1
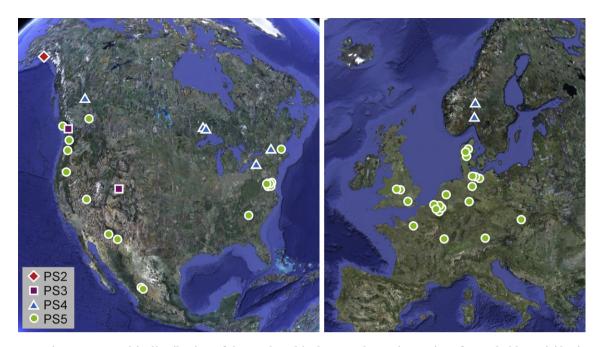
Fig 2 − Approximate geographic distribution of the analysed isolates and cryptic species of *Serpula himantioides* in North America and Europe. Google Maps™ mapping service.

and PS5 without any apparent structuring, indicating that a constant influx of spores happens from nature to buildings and possibly *vice versa*. This is supported by GSI analysis that showed that there was no grouping of outdoor (GSI 0.048 $p = 0.41$) or indoor (GSI 0.051 $p = 0.13$) isolates.

There was however a slightly significant signal in the isolates from *Pinus* substrates (GSI 0.0836 $p = 0.047$). Isolates from *Pinus* substrates were only found in the S4 (one isolate) and S5 lineages. The two PS1 isolates that were found outdoors were obtained from *Nothofagus*, (GSI = 0.239 $p = 0.011$). The substrate from the three indoor isolates in the same clade is unknown, but it is not unlikely that these are also *Nothofagus*, as this is a common source of building material in the region (Martínez Pastur *et al.* 2000). In isolates from PS2, PS3, and PS4, most isolates were from *Picea*, and none of these were from buildings. In the PS5 lineage a lot of different substrates were found, from *Eucalyptus* and *Alnus* to *Abies* and *Pinus*. This indicates that the putative allopatric speciation event leading to the split between PS1 and the PS2−5 lineages was accompanied with a host preference partition as well as a geographic split. In addition, there seems to have been a switch from a predominantly *Abies* host preference seen in the PS2 and PS4 lineages, to a higher degree of non-specific host preference in the PS5 lineage. Although PS5 may initially also have been a host specialist, PS5 has today a wider host range than the other lineages in addition to its much wider geographic distribution. The ability to colonise a wide spectrum of substrates may have facilitated the spread of this lineage throughout the world.

This study underlines the importance of having a broad geographic sample when analysing intraspecies variation and divergence. Undiscovered cryptic species may have a restricted distribution in unsampled areas. We have discovered two new cryptic lineages in this study compared to Kauserud *et al.*

(2006), enabling a better understanding of the biogeography and substrate preferences of the *S. himantioides* species complex.

Supplementary material

Supplementary data related to this article can be found online at doi:10.1016/j.funbio.2010.10.004.

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