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Table 1 FDR significant* results from weighted GWAS

SNP	Location (Chr: BP in hg18)	A1	OR	Original p value†	Original rank	Weighted p value‡	Gene (distance from gene)	Norway p value§	NETT–NAS p value	Eclipse p value	Costa Rica RCHH		
											Cases (%)	Controls (%)	RCHH p value
rs1903003	4:90105320	C	0.75	7.18E–8	1	6.87E–8	FAM13A(0)	4.3E–4	1.4E–3	9.1E–3	1 (2%)	0 (0%)	0.2126
rs7671167	4:90103002	C	0.76	8.59E–8	2	8.22E–8	FAM13A(0)	7.9E–4	2.7E–4	7.8E–3	1 (2%)	0 (0%)	0.2126
rs1062980	15:76579582	C	0.76	4.81E–7	3	9.53E–8	IREB2(0)	9.9E–3	1.0E–2	3.6E–2	5 (9%)	0 (0%)	0.0164
rs13180	15:76576543	C	0.76	5.01E–7	4	9.93E–8	IREB2(0)	7.9E–3	1.6E–2	4.3E–2	5 (9%)	0 (0%)	0.0164
rs8034191	15:76593078	C	1.32	5.37E–7	5	1.06E–7	IREB2 (+12.22 kb)	1.5E–4	8.7E–3	8.2E–1	5 (9%)	0 (0%)	0.0164
rs12914385	15:76685778	T	1.29	1.42E–6	9	2.81E–7	CHRNA3(0)	1.4E–3	9.8E–3	9.5E–1	5 (9%)	0 (0%)	0.0164
rs1051730	15:76681394	A	1.29	2.80E–6	14	5.54E–7	CHRNA3(0)	4.3E–4	2.1E–2	8.4E–1	5 (9%)	0 (0%)	0.0164
rs17404727	15:47791375	C	1.28	4.71E–6	15	7.17E–7		1.9E–2	2.2E–2	3.4E–2	7 (12%)	0 (0%)	0.0049
rs996414	9:26570067	G	0.76	1.80E–6	11	8.76E–7		6.2E–4	8.8E–1	2.6E–1	2 (3%)	0 (0%)	0.1063
rs4480740	15:47543134	A	1.27	6.75E–6	17	1.03E–6	FGF7(0)	4.0E–2	2.5E–2	2.1E–2	7 (12%)	0 (0%)	0.0049
rs12591300	15:47492033	A	1.27	8.78E–6	21	1.34E–6	FGF7 (–10.72 kb)	3.9E–2	8.3E–2	2.5E–2	7 (12%)	0 (0%)	0.0049
rs2656069	15:76532762	C	0.75	6.82E–6	18	1.35E–6	IREB2(0)	1.6E–1	2.6E–3	1.0E–2	5 (9%)	0 (0%)	0.0164
rs2036534	15:76614003	C	0.75	6.98E–6	19	1.38E–6	PSMA4 (–5.798 kb)	5.8E–2	7.4E–3	9.4E–2	5 (9%)	0 (0%)	0.0164
rs2869967	4:90088355	C	1.29	1.48E–6	10	1.41E–6	FAM13A1 (0)	4.7E–4	7.6E–3	4.4E–3	1 (2%)	0 (0%)	0.2126

*An FDR-corrected p value of 1.43E–6 was used as the cut-off for genome-wide significance.
†Results previously published by Cho *et al*.[1]
‡The weighted p value is the original p value divided by the weight constructed from the RCHH (not shown).
§p Values for individual cohorts are the original, unweighted p values.
COPD, chronic obstructive pulmonary disease; ECLIPSE, Evaluation of COPD Longitudinally to Identify Predictive Surrogate Endpoints; FDR, false-discovery rate; FGF7, fibroblast growth factor-7; GWAS, genome-wide association study; NAS, Normative Aging Study; NETT, National Emphysema Treatment Trial; PSMA4, proteasome subunit, α-type, 4; RCHH, region of conserved homozygosity haplotype; SNP, single nucleotide polymorphism.

There are several plausible methods for weighting chromosomal regions in GWAS, including upweighting previously identified candidate genes, coding variants, exons and promoter regions. However, these weighting strategies work counter to one of the strengths of a GWAS: its hypothesis-free nature. Using HHs as a weighting method avoids the pitfall of these

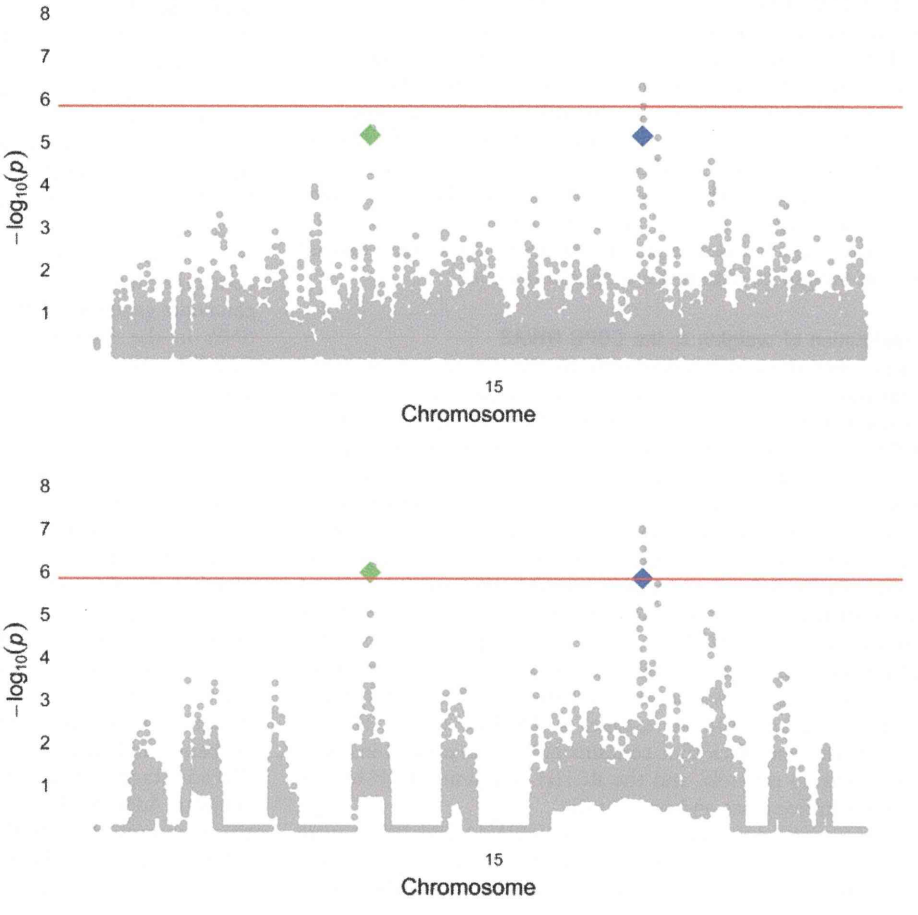

Figure 1 Manhattan plot of chromosome 15, before (top) and after weighting. rs4480740 (Green) is in the gene FGF7 and rs2036534 (blue) is in the promoter of PSMA4. The red line indicates the FDR corrected α level for genome-wide significance. FDR, false-discovery rate; FGF7, fibroblast growth factor-7; PSMA4, proteasome subunit, α-type, 4.

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Table 2 Combined p values for replication of FGF7 SNPs

SNP	COPD consortium OR (two-sided p value)	Lovelace (all subjects) OR (one-sided p value)	Lovelace (Hispanics) OR (one-sided p value)	Combined one-sided p value (all subjects)	Combined one-sided p value (Hispanics only)*
rs12591300	1.27 (8.78E−6)	1.21 (0.01)	1.5 (0.06)	7.9E−7	3.9E−6
rs4480740	1.27 (6.75E−6)	1.15 (0.05)	1.64 (0.025)	2.8E−6	1.5E−6

*Fisher's combined p value using original two-sided p values.
COPD, chronic obstructive pulmonary disease; FGF7, fibroblast growth factor-7; SNP, single nucleotide polymorphism.

other weighting strategies because they are constructed using a hypothesis-free method, so the weights are unbiased with respect to prior knowledge.

One of the main strengths of our study is that it shows the power of using HH analysis in an isolated population to investigate common diseases. While our sample size was small, Miyazawa *et al*[9] have previously shown in simulated data that HH analysis has the ability to identify the region containing an SNP inherited identity-by-descent from a distant common ancestor using only 45 cases and 45 controls. In our own data, we were able to show that the previously identified candidate genes *IREB2* and *CHRNA3* fall within an RCHH that is significantly over-represented in subjects with COPD. When combined with results from a weighted GWAS in an independent cohort with adequate sample size, we were able to show that variants in these genes are significant after correction for multiple testing.

Two novel genes are contained within significant regions of conserved homozygosity, and after weighting they are significant by FDR correction. The first, *FGF7*, was identified in cultured human embryonic lung fibroblasts,[22] and plays a role in promoting wound healing[23] and protecting airway epithelium from oxidant injury in mice.[24] One of the SNPs identified in this study (rs4480740) is in an intron of *FGF7*, and the other (rs12591300) lies immediately upstream of *FGF7* in an intron of hypothetical protein LOC196951. In a GWAS of FEV_1 in the British 1958 Birth Cohort, five out of the nine SNPs genotyped in FGF7 were significantly ($p<0.05$) associated with differences in lung function, although not the two SNPs identified in this study.[25] FGF7 has been shown to protect against oxidative stress response specifically in the lung epithelium,[24] so increases in expression associated with disease progression may indicate a greater burden of injury. A limitation of our study is the lack of experimental evidence for an effect(s) of the SNPs identified in *FGF7* on gene expression. We hypothesise that these SNPs cause decreased expression of *FGF7*, which could affect antioxidant mechanisms protecting against detrimental effects of cigarette smoking on the lung. Alternatively, *FGF7* may play a role in disease susceptibility through its role in epithelial development during embryogenesis by influencing epithelial responses to cigarette smoke. Since it is unclear whether increased *FGF7* expression is a marker of exposure to oxidant injury or a cause of epithelial damage, further work must be done to characterise the role of these SNPs on *FGF7* expression.

The HHAnalysis algorithm works best under certain assumptions, namely that (1) the risk alleles were introduced into the population from a population of common ancestors within the last several hundred years, (2) the target population is genetically isolated, (3) the number of common ancestors introducing the risk allele is small and that (4) the risk of the disease allele is moderate to high. Violations of these assumptions reduce the theoretical expected size of the RCHH and/or the association of the RCHH with disease, which reduces the power of the algorithm to detect them. Genetic and historical data for the population of the Central Valley of Costa Rica suggest that the first three assumptions are met. As in most association studies of complex disease, the effect size of a risk allele is likely small to moderate at most, and we expect that this has somewhat reduced our power.

Whereas other homozygosity mapping methods are primarily designed to detect recessive alleles, the HHAnalysis method instead uses homozygosity to identify ancestral regions inherited from a common ancestor. These regions from a common ancestor can harbour risk alleles that operate under recessive, dominant or additive models. However, the HHAnalysis algorithm would also detect copy number variation that results in the deletion of a single allele. While this may explain a fraction of the regions identified, the top novel SNPs identified in *FGF7* do not fall within known regions of copy number variation according to the Database of Genomic Variants.[26]

In summary, we have shown that weights obtained from HH analysis in an isolated population can improve the power to detect novel variants in GWAS in non-isolates. In addition to confirming results for previously identified variants in *IREB2* and *CHRNA3*, we have identified variants in a novel candidate gene (*FGF7*) for COPD. The validity of this gene is supported by replication in an independent cohort of smoking adults, and expression data showing consistent and significant patterns associated with COPD intermediate lung function phenotypes. Further analysis of these genes in the Costa Rican cohort and functional studies should yield insights into the causative SNPs or haplotypes that underlie the associations identified in this study.

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Competing interests None.

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Contributors Manuscript preparation: JMB, JCC; data analysis and study design: JMB, YT, SB, TJM, SB, NB, JPZ, MES-O, LA, MHC, BH, AAL, FJ, EF, SD, EKS, JCC; data collection: YT, TJM, MES, LA, AAL, PB, AG, WHA, DAL, EKS, JCC; statistical analysis: JMB, KH, MHC.

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Journal club

The increasing importance of innate antimicrobials

The protein short palate, lung and nasal epithelium clone 1 (SPLUNC1) is found in airway epithelium. It is known to have reduced expression in chronic airways diseases and in smokers. This study aimed to demonstrate its antimicrobial properties against *Mycoplasma pneumoniae* infection. The investigators compared the inflammatory and antibacterial responses to *M pneumoniae* infection in transgenic mice deficient in expressing this protein with the responses in mice overexpressing the protein.

The overall results showed SPLUNC1 has antibacterial effects by inhibiting bacterial adherence proteins, thereby inhibiting *M pneumoniae* growth. Following *M pneumoniae* infection, a reduction in tissue inflammation and increase in neutrophil elastase production was seen in those mice with expression of SPLUNC1. Neutrophil elastase is important in relation to infection and was shown to reduce *M pneumoniae* growth when incubated with human sputum neutrophil elastase.

This study shows the potential antibacterial and immunomodulatory functions of SPLUNC1, which may help in the development of novel treatments for chronic airway diseases. In an ever-increasing climate of drug resistance, it emphasises the importance of focusing on host endogenous antimicrobial responses.

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研究成果の刊行に関する一覧表

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