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Genetic population structure of the ground beetle, *Pterostichus oblongopunctatus*, inhabiting a fragmented and polluted landscape: Evidence for sex-biased dispersal

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Abstract

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Keywords: gene flow, microsatellite markers, spatial structure
Abbreviations: AMOVA, analysis of molecular variance; ***F***, the probability that two genes share a common ancestor within a population; F_{IS}, inbreeding coefficient of an individual relative to subpopulation; F_{ST}, fixation index (the effect of subpopulations compared to total population); mAI_C, mean of genetic assignment index; vAI_C, variance of genetic assignment index
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Introduction

Anthropogenic disturbance may drive species to extinction or to local adaptation. Extinction probability and micro-evolutionary processes are strongly linked to the organism's mobility, especially in fragmented landscapes (Thomas 2000; Carroll et al. 2007; Garant et al. 2007). Carabid beetles form a major family (Carabidae) of predacious and omnivorous species inhabiting a wide range of terrestrial habitats (Lindroth and Bangsholt 1985). They are widely used in biological surveys, especially to study effects of habitat alteration (Butterfield et al. 1995; Niemelä et al. 2002; Rainio and Niemelä 2003). Numerous studies have investigated the response of carabid species to changing environmental conditions resulting from human impact, such as forest fragmentation or management practices (Rainio and Niemelä 2002; Koivula 2000). Carabids are known to differ significantly in their dispersal abilities; flightless beetles are considered to be able to move a few hundred meters per day by walking, while species with good flight capability can move longer distances and are less dependent on dispersal corridors (Thiele 1977).

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Materials and Methods

Study species

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Sample collection

Site No. | Site description | Site code | N | Zn (N=4) | Patch size
1 | Przeginia-Zederman | PRZ | 15 | 0.28 ± 0.17 | 0.52
2 | Kogutek-Sieniczno | KOG | 15 | 0.33 ± 0.08 | 0.84
3 | Olkusz-stacja benzynowa | OSB | 16 | 0.35 ± 0.10 | 1.05
4 | Olkusz-leśniczówka | OLE | 15 | 0.33 ± 0.09 | 1.08
5 | Osiek | OSI | 15 | 0.67 ± 0.53 | 0.03
6 | Witeradów | WIT | 14 | 0.93 ± 0.54 | 1.96
7 | Srebrna Góra | SRG | 15 | 1.67 ± 0.74 | 0.49
8 | Pustynia Starczynowska | PUS | 13 | 6.85 ± 8.67 | 20.7
9 | Starczynów | STA | 15 | 15.98 ±13.05 | 8.54
10 | Bukowno-śmietnik | BUS | 15 | 11.79 ± 14.64 | 0.12
11 | Stary Olkusz | SOL | 15 | 5.97 ±7.33 | 11.57
12 | naprzeciwko Grodziska | GRO | 15 | 5.47 ± 7.81 | 11.57
13 | Droga na Klucze | DRK | 14 | 0.69 ± 1.00 | 18.61
14 | Laski | LAS | 14 | 7.48 ± 6.26 | 2.6
15 | Bukowno-Krążek | BUK | 15 | 7.75 ± 5.81 | 0.27
16 | Bukowno-Wodąca | BUW | 15 | 4.59 ± 6.62 | 0.29
17 | Sławków 312 | SLA | 15 | 2.25 ± 2.58 | 14.98
18 | Olkusz - huta | OLK | 14 | 2.89 ± 2.18 | 1.19
19 | Bolesław | BOL | 15 | 1.43 ± 1.03 | 0.11
20 | Hutki | HUT | 16 | 0.60 ± 0.42 | 18.61
21 | Klucze | KLU | 13 | 0.37 ± 0.38 | 18.61

Table 1. Characterization of the sampling sites.

N - number of sampled individuals

Zn - pollution level expressed as zinc concentration [g/kg] in soil humus layer (mean ± standard deviation based on four samples from each site)

Patch size - size of a woodland habitat patch around the sampling site [km²] !!

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Microsatellite typing

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Genetic diversity and gene flow between populations

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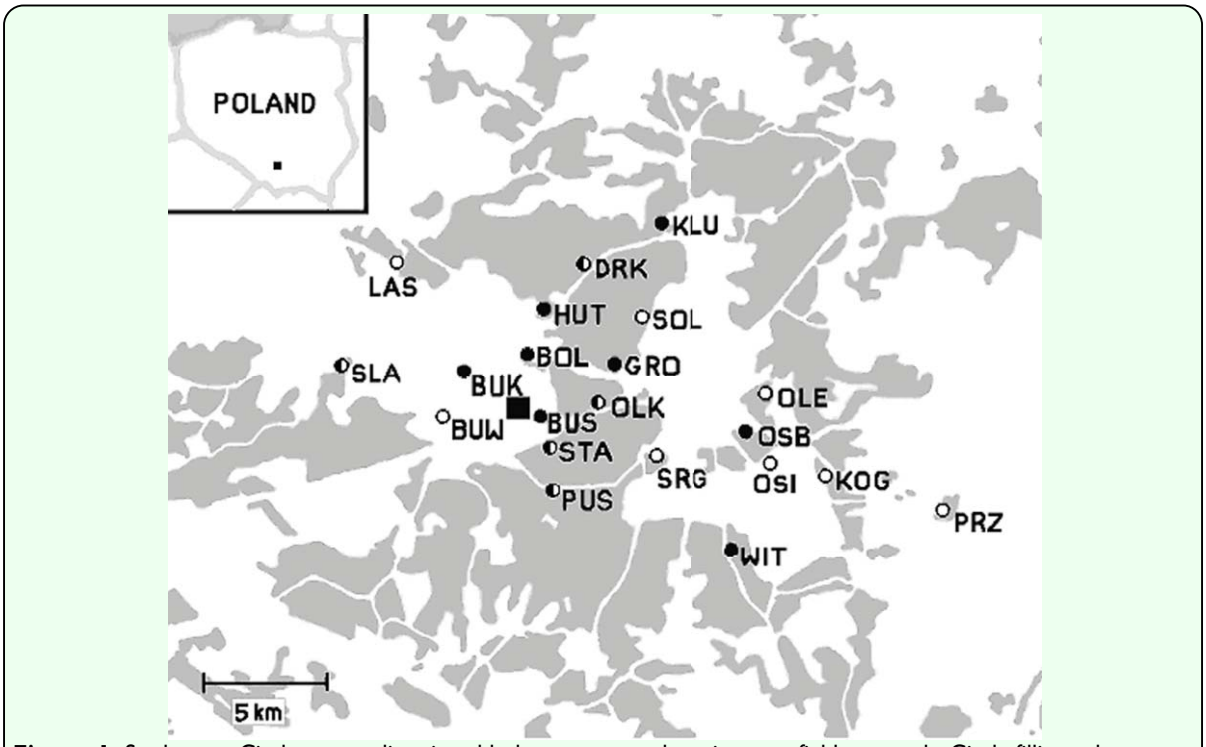


Figure 1. Study area. Circles – sampling sites, black square – smelter site, grey fields – woods. Circle filling colours show membership in genetic clusters according to Bayesian clustering method: Black and white-filled circles represent two main clusters with individuals' membership of at least 60%. Half-filled circles represent "unclustered" sites, comprised of individuals from two clusters in almost equal proportions (40-60% ancestry for each of the two clusters). High quality figures are available online.

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Sex-biased dispersal

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Environmental correlations: geographic distance, pollution, and fragmentation

Population clustering analyses

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Results

Genetic diversity and gene flow between populations

L++!0.:)!3 .1#$,–*)++.*)!+$1.! &:),*./–*)’! =)#)!4$+23 $#47.1!=.*7&!–&’!–3 $&/! 4$4%+–*.$&,!=.*7!*7)!);1)4*.$&!$0!+$1%,! J$(D!&!*7)!4$4%+–*.$&!QUW!–&’!J$(V!&! *7)!4$4%+–*.$&!SO8!?*7)!*7#))<+)**)#!1$’),! #)0)#!*$!,–3 4+&/!,.*),!))>./%#)!H!–&’! R–(+)!HB5IR7)!&%3 ()#!$0!–++)+),9!–:)#–/)’! $:)#!–++!+$1.9#–&/)’!0#$3 !D5E!&!SO8!*$!V5Z! &!,.*),!] 8R96^R!–&’!WK^5U#.:–*)!–++)+),!!

Table 2. Genetic diversity measures of *P. oblongopunctatus* populations at 5 microsatellite loci.

Site	Pob1			Pob3			Pob4			Pob5			Pob14			all (average)		
	A	*He*	*Ho*	*A*	*He*	*Ho*	*A*	*He*	*Ho*	*A*	*He*	*Ho*	*A*	*He*	*Ho*	*A*	*He*	*Ho*
PRZ	4	0.58	0.73	3	0.38	0.47	5	0.76	0.67	3	0.25	0.20	3	0.60	0.80	3.6	0.51	0.57
KOG	4	0.72	0.73	3	0.35	0.13	5	0.78	0.67	3	0.31	0.00	4	0.58	0.80	3.8	0.55	0.47
OSB	4	0.69	0.31	4	0.39	0.25	6	0.80	0.75	7	0.83	0.44	6	0.68	0.69	5.4	0.68	0.49
OLE	4	0.60	0.67	3	0.39	0.47	6	0.83	0.80	2	0.19	0.00	3	0.60	1.00	3.6	0.52	0.59
OSI	3	0.63	0.73	3	0.30	0.33	5	0.77	0.87	1	-	-	3	0.55	0.87	3.0	0.56	0.70
WIT	4	0.70	0.71	6	0.53	0.50	7	0.70	0.62	5	0.76	0.43	6	0.62	0.46	5.6	0.66	0.54
SRG	3	0.70	0.73	4	0.41	0.27	5	0.62	0.47	4	0.36	0.27	3	0.56	0.73	3.8	0.53	0.49
PUS	4	0.74	0.69	3	0.34	0.15	6	0.82	0.54	6	0.77	0.46	4	0.70	0.50	4.6	0.67	0.47
STA	4	0.70	0.73	5	0.59	0.47	6	0.79	0.80	6	0.69	0.40	4	0.61	0.33	5.0	0.68	0.55
BUS	4	0.78	0.47	2	0.19	0.00	7	0.75	0.73	6	0.81	0.20	4	0.68	0.53	4.6	0.64	0.39
SOL	4	0.71	0.73	3	0.30	0.27	6	0.79	0.80	3	0.31	0.13	2	0.55	0.80	3.6	0.53	0.55
GRO	4	0.65	0.73	3	0.25	0.20	4	0.61	0.40	3	0.54	0.40	4	0.57	0.53	3.6	0.51	0.43
DRK	3	0.68	0.71	1	-	-	3	0.57	0.43	4	0.68	0.36	4	0.61	0.57	3.0	0.64	0.52
LAS	3	0.74	0.64	4	0.27	0.14	5	0.71	0.50	3	0.54	0.64	3	0.56	0.50	3.6	0.56	0.48
BUK	4	0.69	0.47	5	0.41	0.40	5	0.77	0.33	7	0.81	0.40	4	0.77	0.77	5.0	0.69	0.47
BUW	5	0.74	0.73	4	0.31	0.27	6	0.84	0.40	3	0.52	0.80	3	0.45	0.33	4.2	0.57	0.51
SLA	4	0.68	0.53	4	0.41	0.40	6	0.65	0.73	5	0.66	0.20	5	0.64	0.67	4.8	0.61	0.51
OLK	3	0.67	0.71	4	0.43	0.36	5	0.72	0.64	6	0.77	0.50	5	0.60	0.64	4.6	0.64	0.57
BOL	3	0.65	0.60	3	0.41	0.27	6	0.71	0.53	8	0.85	0.33	3	0.40	0.40	4.6	0.60	0.43
HUT	3	0.62	0.63	5	0.52	0.50	7	0.67	0.38	7	0.82	0.63	6	0.69	0.75	5.6	0.66	0.58
KLU	4	0.69	0.69	4	0.34	0.38	7	0.81	0.85	7	0.89	0.38	6	0.70	0.77	5.6	0.69	0.61

A - number of alleles
He, Ho - expected and observed heterozygosity.

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=)#) !0$%&' !-*!) -17 !+$1%,9!) ;1) 4*!J$(H!b9! -&' !/)&) #-+2 !$11%##) ' !-*!+$= !0#) C%) &1.) ,5! M%3 ()#,! $0! -+)+) ,! -&' ! $(,)#:) ' ! -&' ! %&(.-,) ' !) ;4) 1*) ' !7) *) #$I2/$,.*2 !:-+%) ,! -#) !/.:) &!,) 4-#-*) +2 !0$#!) -17 !,-3 4+&/! ,.*) !-&' !+$1%,! &!R-(+) !G5!Y) 1-%,) !*7) ! &%3 ()#!$0!+$1.!%,) ' ! &!*7.,!,*%' 2!= -,! ,3 -+9!-&' !,-3 4+) !,.I) !0#$3 !) -17 !+$1-*.$&! = -,!+.3 .*) ' 9!,$3) !1-%*.$&!= -,!&) 1),,-#2! &! *7) ! &*) #4#) *-*.$&! $0! *7) ! #),%+*,5! R7) #) 0$#) 93 %+*.4+) !-44#$-17),!=)#) !%,) ' ! *$!1$&0.#3 !*7) !#$(%,*&),,!$0!*7) !3 -&! 0&' &/,5!

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>$#!*7) !+&N-/) !' .,) C%.+.(#.%3 !*),*9!$&+2 !D! 4-.#,! $0! +$1.!$%*! $0! GHE! 4-.#,! /-:) ! -! ,./&.01-&*!4<:-+%) !-*!*7) !4+o !E5EEEH!+) :) +5! O&/+) <+$1%,! *),*,! 0$#! ') :.-*.$&,! 0#$3 ! 6-#'2<]) &()#/!) C%.+.(#.%3 ! #) :) -+) ' ! ,./&.01-&*!') 4-#*%#) !?-*!4+o !E5EEEVB!.&!c! $%*!$0HEV!-&-+2,),AG!1-,),!0$#!+$1%,U$(b! -&' !Z!0$#!+$1%,!J$(V5!6-#'2<]) &()#/! ') :.-*.$&,! =)#)! &$*! #),*#.1*) ' ! *$! 4-#*.1%+-#!,-3 4+&/!,.*),5!8&!-++!c!1-,),9! *7) !$(,)#:) ' !7) *) #$I2/$,.*2 != -,!+$=)#! *7-&!) ;4) 1*) '9!= 7.17 != -,!4#$(-(+2 !&$*

!1-%,) ' !(2!&%++!-++) +),!()1-%,) !&$!&%++! 7$3 $I2/$*) !/) &$*24),!=)#) !$(,)#:) '5! R7) #) != -,!-! ' .00) #) &1) ! &! /) &$*24) ! ' .,*#.(%*.$&!()*=))&!*7) !,) ;),9!),4) 1.-+2! &!*7) !3 $,*!:-#.-(+) !+$1%,9!J$(V9!= 7) #) ! $(,)#:) ' ! 7) *) #$I2/$,.*2! +) :) +,! =)#) ! /) &) #-+2 !+$=)#!.&!3 -+),!*7-&!.&!0) 3 -+),! ?' -*-!&$*!,7$= &B5Q) :.-*.$&!0#$3 !6-#'2<]) &()#/!) C%.+.(#.%3 ! 3 -2! &' .1-*) ! ,./&.01-&*! .3 3 ./#-*.$&9! ' #.0*9! ,) +) 1*.$&! -&' d$#&$&<#-&' $3 !3 -*&/5!

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R7) ! -&-+2,.,! $0! 3 $+) 1%+-#! :-#.-&1) ! ?LP S\LB!#) :) -+) ' !,*-*.,*.1-+2 !,./&.01-&*! /) &) *.1!,*#%1%#&/!-3 $&/!*7) !,-3 4+&/! ,.*),A!/) &) *.1!:-#.-*.$&!= .*7 &!,-3 4+&/! ,.*),! -3 $%&*) ' ! *$! FD5Dj 9! = 7) #) -,! :-#.-*.$&!-3 $&/!*7) !,-3 4+&/!,.*),!= -,! Z5aj !?\= .*7 &!p!H5bEacH9! ' 0= .*7 &!p!VFa9! \-3 $&/!p!E5HEHH9! ' 0-3 $&/!p!GE9>!p!D5HGa9!4! o!E5EEEHB5K$1%,!(2!+$1%,!LP S\L!,7$=) ' ! *7-*! +$1%,!J$(V! .,! #),4$&,.(+) !0$#! *7) ! +-#/),*!4-#*!$0!*7) !*$*-+!/) &) *.1!:-#.-*.$&! $(,)#:) ' !() *=))&!*7) !,.*),5>$#!*7.,!+$1%,9! *7) !:-#.-*.$&!-3 $&/!*7) !,-3 4+&/!,.*),! -3 $%&*) ' !*$!GHj 5K$1.U$(H9U$(b9-&' !

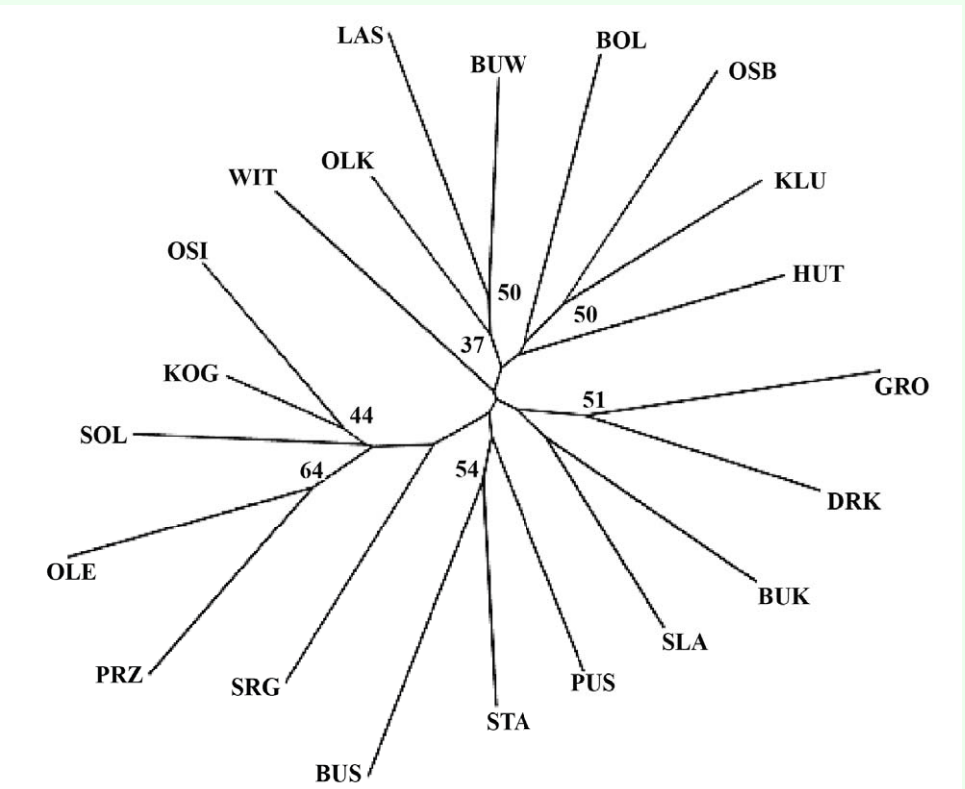


Figure 2. Unrooted neighbour-joining tree of 21 populations based on distances between populations estimated from Cavalli–Sforza and Edwards's chord distances. Phylogenetic trees were bootstrapped over loci (10,000 replicates). Numbers indicate percentage support of each branch in the topology; only the values > 30 are presented. High quality figures are available online.

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UJ$(Hb! –+,$! #)0+)1*)'! ,./&.01–&*!'.00)#)&*.–*.$&9!(%*!*$!–!,3 –++)#!);*)&*!?G9!G5F!–&'!G5bj 9!#),4)1*.:)+2B5!J$4%+–*.$&!4–.#= .,)!),*3 –*),!$0!6<=+=)#)!+),,!*7–&!I)#$!&!HG!1–,),9!= 7.17!=)#)!,)*!*$!E5E5!R7)!3)–&!4–.#= .,)!:–+%),!0$#!–++!,–3 4+&/!,.*),!:–#.)'!()*=))&!E5EG!–&'!E5HE5!

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R$!–,,),,!= 7)*7)#!*7)!–++)+1!'.,*#.(%*.$&,!= .*7&!*7)!,–3 4+&/!,.*),!7–'!())&!,7.0*)'!(2!17–&/),!&!4$4%+–*.$&!,.I),!'%)!*$!*7)!4–,*!4$4%+–*.$&!')1+&)!$#!1$+$&.I–*.$&!):)&*,9!*7)!YSRRKhMh@W!4#$/#–3 != –,!%,)'!?@$#&%)*!–&'!K%.N–#*!HFFZB5!Y–,)'!$&!*7)!*= $<47–,)!3 $')+9!&$!4$4%+–*.$&!);7.(.*)'! ,./&.01–&*! 7)*)#$I2/$,.*2!);1),,!$#!')0.1.)&129!&'.1–*.:)!$0!#)1)&*!($**+)&)1N,!?*= $<*–.+)'!] .+1;$&!*),*!#%&!0$#!)–17!,–3 4+&/!,.*),!)4–#–*)+29!–++!4+q!E5EVB5!

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Table 3. The relative interaction between gene flow and drift in sampled populations of the ground beetle *P. oblongopunctatus*.

Site	*F*	*M*
PRZ	0.024 ± 0.0001	19.726 ± 0.215
KOG	0.164 ± 0.0003	1.525 ± 0.004
OSB	0.218 ± 0.0004	1.099 ± 0.003
OLE	0.021 ± 0.0001	28.369 ± 0.417
OSI	0.146 ± 0.0003	1.806 ± 0.006
WIT	0.071 ± 0.0002	4.240 ± 0.015
SRG	0.039 ± 0.0001	13.352 ± 0.201
PUS	0.165 ± 0.0003	1.482 ± 0.004
STA	0.063 ± 0.0001	4.645 ± 0.012
BUS	0.161 ± 0.0003	1.518 ± 0.004
SOL	0.028 ± 0.0001	302.803 ± 23.88
GRO	0.081 ± 0.0002	3.553 ± 0.012
DRK	0.086 ± 0.0002	3.252 ± 0.009
LAS	0.049 ± 0.0001	6.107 ± 0.021
BUK	0.036 ± 0.0001	11.473 ± 0.076
BUW	0.170 ± 0.0003	1.420 ± 0.003
SLA	0.286 ± 0.0004	0.706 ± 0.002
OLK	0.105 ± 0.0003	2.919 ± 0.011
BOL	0.034 ± 0.0001	17.057 ± 0.254
HUT	0.196 ± 0.0003	1.195 ± 0.003
KLU	0.010 ± 0.0001	214.363 ± 5.647

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F - probability that two genes share a common ancestor within a population
M - immigration rate obtained from F (Ciofi et al. 1999)
Shown: mean ± standard error

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Sex-biased dispersal

Environmental correlations: geographic distance, pollution and fragmentation

Table 4. Partial Mantel r correlations between genetic differentiation (pairwise F_{ST}) and geographic distance, pollution level and patch size, calculated for all samples, and for females and males, separately.

Dependent variable - genetic differentiation of:	Comparison	Partial *r* correlation with genetic differentiation	*P*
Both sexes			
	Geographic distance	0.155	0.010
	Pollution index	-0.072	0.260
	Patch size	-0.153	0.027
Females			
	Geographic distance	0.051	0.204
	Pollution index	-0.064	0.280
	Patch size	-0.227	0.002
Males			
	Geographic distance	0.209	0.002
	Pollution index	-0.074	0.288
	Patch size	-0.015	0.837

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1$##) +-*) ' %, &/ !- !P -&*) +!*) , *!?$ p E5HVV94 + p ! E5EHEB5! R7 ., ! #) , %+*! -+, $! #) 0+) 1*, ! 7 ./7 ! 3 ./#-*.$&! #-*) , ! ( )*=)) &! &) ./7 ($#&/ ! , -3 4+&/ !, .*) , 5! 6 $=) :) #9! = 7) &! ' -*-! 0$#! 0) 3 -+) , ! -&' ! 3 -+) , ! =) #) ! -&-+2 I) ' ! ,) 4 -#-*) +2 != .*7 !- !P -&*) +!*) , *9! 1$##) +-*.$&! ( )*=)) &!/) $/#-47 .1!-&' !/) &) *.1!' ., *-&1) ! = -, !, ./&.0.1-&*!0$#!3 -+) , !?$!p ! E5GEF9 4 + p ! E5EEGB! -&' ! &, ./&.0.1-&*!0$#!0) 3 -+) , !?$+p ! E5EVH9 4 + p ! E5GEbB5!

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J-#*.-+!P -&*) +g !*) , *, !=) #) !%,) ' !*$!*) , *!0$#!) 00) 1*, !$0!7-(.*-*!1$&*-3 &-*.$&!+) :) +, !-&' ! 7-(.*-*! 4-*17 ! , .I) ! $&! ' ., *#.(%*.$&! $0! /) &) *.1! ' .:) #, .*29! = 7 .+) ! 1$&*#$++&/ ! 0$#! 4$*) &*.-+!) 00) 1*, !$0!, 4-*.-+!-%*$1$##) +-*.$&5! M$! , ./&.0.1-&*! -, , $1.-*.$&, !=) #) ! 0$%&' ! ( )*=)) &! /) &) *.1! ' .00) #) &*.-*.$&! -&' ! 4$+%*.$&!$:) #!-+!! &' .:.' %-+, 9! -, !=) +!-, ! 0$#!0) 3 -+) , !-&' !3 -+) , !,) 4-#-*) +2 !?R-(+) ! bB5M) /-*.:) !1$##) +-*.$&!( )*=)) &!+) :) +, !$0! /) &) *.1!' .00) #) &*.-*.$&!-&' !7-(.*-*!4-*17 ! , .I) !?$+p !<E5HVD9 4 + p ! E5EGcB! = -, !$(,) #:) ' ! &!4-#*.-+!P -&*) +!*) , *, !1-+1%+-*) ' !$:) #!-+!! , -3 4+) , 5! 6 $=) :) #9! = 7) &! -&-+2,) , !=) #) ! 4) #0$#3) ' ! 0$#! *= $! ,) ;) , ! ,) 4-#-*) +29! /) &) *.1!' .:) #, .*2 !$0!0) 3 -+) , != -, !#) +-*) ' !*$! 0$#) , *!4-*17 !, .I) !?$+p !<E5GGa9 4 + p ! E5EEGB9!

!= 7) #) -, !0$#!3 -+) , !*7 ., !#) +-*.$&, 7 .4 != -, ! &, ./&.0.1-&*!?$+p !<E5EHV9 4 + p ! E5cDaB!?R-(+) ! bB5!

Population clustering analyses

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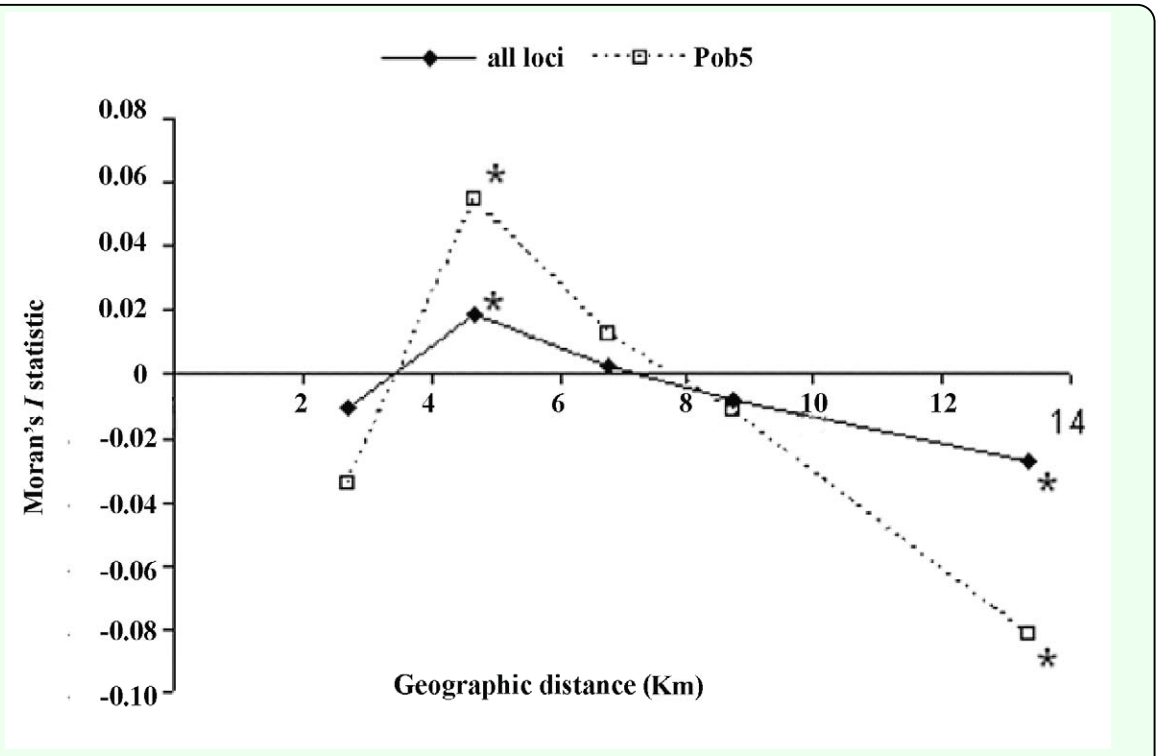


Figure 3. Spatial autocorrelogram estimated from multilocus microsatellite genotypes and for locus Pob5 only. * - Moran's I significant at p 0.05. High quality figures are available online.

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Discussion

Genetic diversity and gene flow among populations

Table 5. Characterization of the genetic population clusters.

Cluster 1 ("eastern")		Cluster 2 ("western")	P[a]
Sampling sites assigned to cluster	PRZ, KOG, OLE, OSI, SRG, SOL, LAS, BUW	OSB, WIT, BUS, GRO, BUK, BOL, HUT, KLU	
Allelic richness, *AR*	3.49	4.79	< 0.001
Observed heterozygosity, *Ho*	0.53	0.49	0.265
Gene diversity, *HS*	0.49	0.62	< 0.001
Inbreeding coefficient, *FIS*	-0.06	0.21	< 0.001
Genetic distance between sites, *FST*	0.07	0.03	0.081
Metal pollution, Zn [g/kg] in soil humus	2.66	3.59	0.624
Habitat patch size, [km²]	2.17	6.53	0.202

[a] P values were calculated using permutation tests in FSTAT for genetic variables, and ANOVA for environmental variables.

Mean values of genetic diversity statistics and environmental parameters computed for sampling sites grouped according to the results of the genetic clustering test.

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Sex-biased dispersal

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Environmental correlations: geographic distance, pollution, and fragmentation

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Population clustering analyses

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Conclusions

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Acknowledgements

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References

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!"#$%&"'()*&#,–%./%0*.("1"*&►5?@$+59!
@–#–(.'–)B!–&'!!)'–%.")*&I#(%$*&+"#–:5!
?@$+5D0*–472+&.'–)B5J#")#$–1.I&#%*$.1–+
%5L%%–%/:!DH?GBAbHc<bVG5!

Y%**)#0.)+' !T9K%00!PK9Y–&),!P 9h2#)!PQ5!
HFFV5@–#–(.'!())*+)!1$3 3 %&.*.),!–,!
&'.1–*$#,!$01$&,)#:–*.$&!4$*)&*.–+!.&!
%4+–&'!0$#),*,56%$#&"+H(%–%/:–L.I+
>1./#7 #."!aF?H<GBAZD<aa5!

@–##$++DJ96)&'#2!LJ9J)I&.1NQM9►$;!
@] 5GEEa5h:$+%*.$&!$&!)1$+$/.1–+!*.3)<
,1–+),56*.("%.1–H(%–%/:GH?DBADca<DFD5!

@–%'.++@@5GEED5P)–,%#&/!'.,4)#,–+!.&!–!
3)*–4$4%+–*.$&!%,&/!,*–(+)!.,$*$4)!
)&#.173)&*A6./7#–*),!$0!,);<(.–,)'!
'.,4)#,–+!()*=))&!4–*17),!.&!–!3 –20+2!
3)*–4$4%+–*.$&5F'G%&!HEH?DBAZGb<ZDE5!

@7–4%.,!PJ9h,*$%4!L5GEEa5!
P.1#$,–*)++.*)!&%++!–+)+),!–&'!),*3 –*.$&!
$0!4$4%+–*.$&!'.00)#)&*.–*.$&5> %–#(*–1$+
M'%–%/:–L.I+H3%–*"%.!Gb?DBAZGH<ZDH5!

@.$0.!@9Y)–%3 $&*!PL9O=&/+–&'!8U9!
Y#%0$#'!P]5HFFF5")&)*.1!'.:)#/)&1)!
–&'!%&.*,!0$#!1$&,)#:–*.$&!.&!*7)!W$3 $'$!
'#–/$&!N1$1.*&+G%7 %I%#.&'&5!$%(##I'./&+
%5+")#+O%:1–+%('#":+%5P%.I%.+<#$'#&+M!
ZZ?HbDVBAGGZF<GGab5!

@$#&%)*!TP 9K%.N–#*!"5HFFZ5Q),1#.4*.$&!
–&'!4$=)#!–&–+2,.,!$0!*=$!*),*,!0$#!
')*)1*&/#)1)&*!4$4%+–*.$&!($**+)&)1N,!
0#$3 !–++)+)!0#)C%)&12!'–*–5Q#."'(&!
Hbb?bBAGEEH<GEHb5!

Q),)&')#!W9O)##–&$!T5HFFF5L!/)&)*.1!
1$3 4–#.,$&!$0!L*+–&*.1!–&'!P)'.*)##–&)–&!
4$4%+–*.$&,!$0!–!,–+*3 –#,7!())*+)5M#–/'1.+
K%*$.1–%5L%%–%/:!HGF?HBAcD<Fb5!

Q),)&')#!W9O3 –++h9"–%(+$3 3)!h9!
\)#'21NU5GEEV5U%#–+<%#(–&!/#–'.)&*,!
–&'!*7)!4$4%+–*.$&!/)&)*.1!,*#%1*%#)!$0!
=$$'+–&'!/#$%&'!())*+),52%.&#$31"%.+
Q#.#"'(&Z?HBAVH<ZG5!

Q),)&')#!W9\)#'21NU5GEEH5")$/#–47.1!
,1–+&/!–&'!/)&)*.1!'.00)#)&*.–*.$&!&!*=$!
7./7+2!3 $(.+)!h%#$4)–&!,–+*3 –#,7!
())*+),5M#–/'1.+K%*$.1–%5L%%–%/:!HDH?HBA!
DH<bG5!

h:–&&$!"9U)/&–%*D9"$%')*T5GEEV5!
Q)*)1*&/!*7)&%3 ()#$01+%,*)#,!$0!
&'.:.'%–+,%,&/!*7)!,$0*=–#)!
ORU^@R^UhAL!,.3 %+–*.$&!,%'25!
>%–#(*–1$+H(%–%/:!Hb?cBAGZHH<GZGE5!

h;1$00.)#K9O3 $%,)Uh9L%–**#$!TP 5HFFG5!
L&–+2,.,!$03 $+)1%+–#!:–#.–&1)!&0)##)'!
0#$3 !3)*#.1!.,*–&1),!–3 $&/QML!
7–4+$*24),!<!–44+.1–*.$&!*$!7%3 –&!
3 .*17&'#.–+QML#),*#.1*.$&!'–*–5!
Q#.#"'(&HDH?GBAbaF<bFH5!

"–&'$&D5HFFF5W.&!1$3 4)*.*.$&9*7)!1$,*!
$0!&(#))'&/!–&'!*7)!):$+%*.$&!$0!
'.,4)#,–+5K%*$.1–%5=)#%$#"'(1–M'%–%/:!
GEE?bBADbV<DZb5!

"–#–&*Q9►$#')Dh96)&'#2!LJ5GEEa5R7)!
3 %+*.0–#.$%,!)00)1*,!$0!'.,4)#,–+!–&'!/)&)!
0+$=!5&!1$&*)3 4$#–#2!–'–4*–*.$&5!
6*.("%.1–H(%–%/:GH?DBAbDb<bbD5!

"$%')*T5HFFV5►ORLR!:)#,.$&!H5GAL!
1$3 4%*)#4#$/#–3 !*$!1–+1%+–*)►><
,*–*.,*.1,5K%*$.1–%5R#$#I'":!cZ?ZBAbcV<
bcZ5!

"$%')*T9U)##&M9] –,)#U5GEEG5R),*,!
0$#!,);<(.–,)'!.,4)#,–+%,&/!(.<
4–#)&*–+2!&7)#.*)'!/)&)*.1!3 –#N)#,5!
>%–#(*–1$+H(%–%/:!HH?ZBAHHED<HHHb5!

"#))&=$$'UT5HFcE5P –*&/!,2,*)3 ,9!
47.+$4–*#2!–&'!'.,4)#,–+!&!(.#',!–&'!
3 –3 3 –+,5?.'7 1–M#)13'%*$Gc?bBAHHbE<
HHZG5!

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6–#'2!ST9\)N)3 –&,!w5GEEG5OJL"hQ.AL!
:)#,–*.+)!1$3 4%*)#!4#$/#–3 !*$!–&–+2,)!
,4–*.–+!/)&)*.1!,*#%1*%#)!–*!*7)!&'.:.'%–+!
$#!4$4%+–*.$&!+):)+,5> %–#(*–1$+H(%–%/:+
J%"#&!G?bBAZHc<ZGE5!

6–#'2!ST9\)N)3 –&,!w5HFFF58,$+–*.$&!(2!
'.,*–&1)!&!–!1$&*&%$%,!4$4%+–*.$&A!
U)1$&1.+.–*.$&!()*=))&!,4–*.–+!
–%*1##)+–*.$&!–&–+2,.,!–&'!4$4%+–*.$&!
/)&)*.1,3 $')+,5R#$#I'":!cD?GBAHbV<HVb5!

6–#*+QK9@+–#N!L"5HFFa5!$'.('0–#&%5+
0%0*–1"%.+/#.#"'(&DD#')'.*.$&5O.&–%)#!
L,,$1.–*),5!

6)()#*!UQM9K%N)#!P P 5HFFZ5!")&)*.1!
)00)1*,!01&*–3 .&–&*!);4$,%#)!<!*$=–#',!
–&!–,,),,3)&*!$0!.3 4–1*,!$&!–&.3 –+!
4$4%+–*.$&,5<('#.(#%5#")#+=%"1–+
H.3'$%.7#."!HFH?HBAGD<Vc5!

6.#$*–!R5GEEb5R7)!):$+%*.$&!$0!,);<
(.–,)'!'.,4)#,–+!(2!4#)<'.,4)#,–+!
1$4%+–*.$&!–&'!0%1*%–*.&/!)&:.#$&3)&*5!
K%*$.1–%5?.'7 1–H(%–%/:!aD?ZBAHHHV<
HHGE5!

T!$44!>9U)%*)#!65GEEV5Q.,4)#,–+!$0!
1–#–(.'!())*+),!x!)3)#/)&1)!$0!
'.,*#.(%*.$&!4–**)#&,5H(%–%/'(1–> %I#—'./!
HcZ?bBADcF<bEV5!

W–=)1N.!RT5GEED5O);<(.–,)'!'.,4)#,–+!
–&'!–'–4*–*.$&!*$!3 –#/&–+!7–(.*–*,5!
?7#$'(1.+U1"*$1–&"!HZG?bBAbHV<bGZ5!

W)+)#!89K–#/.–')#!@U5GEED5U)1)&*!
7–(.*–!0#–/3)&*–*.$&!1–%,)'!(2!3 –X$#!
#$–',!+)–',!*$!#)'%1*.$&!$0!/)&)!0+$=!–&'!
+$,,$0!/)&)*.1!:–#.–(.+*2!&!/#$%&'!
())*+),5!$%(##I'./&%5")#–0%:1–<%('":–%5+
P%.I%.–<#$'#&MGaE?HVHDBAbHa<bGD5!

W$.:%+–!P 5GEEG5L+*)#&–*.:)!7–#:),*&/!
3)*7$',!–&'!($#)–+!1–#–(.'!())*+),!
?@$+)$4*)#–9@–#–(.'–)B56%$#&"!H(%–%/:+
1.I+> 1.1/#7#."!HZa?H<DBAHED<HGH5!

K–/.,I!P 9W#–3 –#IU9K–,N$=,N.U9R$($#!
P 5GEEG5U$4%+–*.$&!4–#–3)*)#,!$0!*7)!
())*+)!!"#$%&"'()*&%,–%./%0*.("1"*&>5!
0#$3 !3)*–+1$&*–3 &–*)'!–&'!#)0)#)&1)!
–#)–,5M*–#"'.%5H.3'$%.7#."1–+
2%."17'.1"%.–1.I+=%8'(%–%/:!ZF?GBAGbD<
GbF5!

K–/.,I!P 9W#–3 –#IU9M.N+.t,N–!P 5GEEV5!
P)*–+N&)*.1,!–&'!#),4.#–*.$&!#–*),!&>H!
/)&)#–*.$&!$01–#–(.'!())*+),!
?!"#$%&"'()*&%,–%./%0*.("1"*&+>5B!
$#./&–*&/!0#$3 !3)*–+<1$&*–3 &–*)'!–&'!
#)0)#)&1)!–#)–,5?$()'3#&%5H.3'$%.7#."1–+
2%."17'.1"%.–1.I+=%8'(%–%/:!bc?bBAbcb<
bcF5!

K–/.,I!P 9K–,N$=,N.U5GEEc5h:.')&1)!0$#!
()*=))&</)&)#–*.$&!)00)1*,!&!1–#–(.',!
);4$,)'!*$!7)–:2!3)*–+,!4$+%*.$&5!
H(%"%8'(%–%/:!Ha?HBAVF<ZZ5!

K–/.,I!P 9] $+00W5GEEb5P .1#$,–*)+.*)!
QML!3 –#N)#,!0$#!*7)!/#$%&'!())*+)+
!"#$%&"'()*&%,–%./%0*.("1"*&>5!
>%–#(*–1$+H(%–%/:+U%"#&!b?HBAHHD<HHV5!

K–&/)++–!S5GEEH5!F!SP?=9FJ<€;T;TEU+
!%0*–1"%.–Q#.#"'(+<"$*("*$#+V9.I'3'I*1–%$+
!%0*–1"%.+4'&"1.(#&D!):–%/#.#"'(+=$##&W;!
L:–.+–(+)!$&+&)A7**4Add===54/)5L&#,<
/.05#d($.&0$d4$4%+–*.$&,d5!

K&'#$*7!@69Y–&/,7$+*>5HFcZ5=)#+
21$1,'I1#+V2%–#%0"#$1W%56#..%&(1.I'1+
1.I+4#.7 1$G;#!1$"+T;D1–&'&–:.–&!
O1.)&1)U#),,5!

K&'#$*7!@69Y–&/,7$+*>5HFcV5=)#+
21$1,'I1#+V2%–#%0"#$1W%56#..%&(1.I'1+
1.I+4#.7 1$G;#!1$"€5O1–&'&–:.–&!
O1.)&1)U#),,5!

P –#N$=!RL9@–,*#)I–&–!O5GEEE5Q.,4)#,–+!
&!1–1*$47.+.14$%&%0)'–15F'G%&bcF?GBA!
Dac<DcZ5!

P –*–+&!L\5GEED5\–#.–*.$&,!&!0+./7*!
–(.+.*2!=.*7!,);!–&'!–/)!&!/#$%&'!())*+),!

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?@$+)$4*)#–9@–#–(.’–)B!$0!,$%*7<=),*)#&!
P $+’$:–5!#I%,’%–%/’1!ba?bBADHH<DHF5!

P ./%+–U9y–,I1I21–U9L%/%,*2&.–N!P 9!
] .+1I)N!"9U$I4z’)N!W9W–0)+L9!] i,I2&!
P 5GEEb5L&*.$;.’–*.:)!’)0)&1)!)&I23),!
&!())*+),!0#$3 !–!3)*–+!4$+%*.$&!/#–’.)&*5!
M’%–%/’1BM$1"’&–131!VF?VBAZbV<ZVb5!

P $,,3 –&!@L9] –,)#UP 5HFFF5")&)*.1!
’)*)1*.$&!$0!,);<(.–,)’!’.,4)#,–+5!
> %–#(*–1$+H(%–%/:!c?ZBAHEZD<HEZa5!

P %++)#!KL69!\–&/#$&,:)+’!U9@$+4–)#*U\5!
GEEa5")&)*.1!,*#%1*%#)!$0!<*’—*&+*"#*&+
4$4%+–*.$&,!&!7)–:23)*–+!4$+%*)’!–&’!
&$&4$+%*)’!7–(.*–*,5> %–#(*–1$+H(%–%/:!
HZ?GGBA!baGc<baDa5!

P e++)#!U9W–,17%(–L5HFcZ5Y.$+$/.1–+!
,./&.0.1–&1)!$0!*7)!,)–,$&–+!’.,*#.(%*.$&!$0!
–1*.:.*2!$0!!"#$%&"’()*&%,–%./%0*.("*&!
?>B5?@$+)$4*)#–9@–#–(.’–)B5&&AY$)#U9!
K%00P K9P $,,–N$=,N.Q9])()#>9)’.*$#,5+
21$1,’I–M##"–#&U=)#’$+?I10"1"%.&–L.I+
4:.17 ’(&;+445HaD<HcH5"%,*–:>.,17)#5!

M).!P 5HFac5h,*3 –*.$&!$0!–:)#–/)!
7)*)#$I2/$,.*2!–&’!/)&)*.1!’.,*–&1)!0#$3 !
–!,3 –++&%3 ()#$0!&’.:.’%–+,5Q#.#"’(&!
cF?DBAVcD<VFE5!

M)./)+U!h5GEEG58,>,*$(,$+)*){!
2%.&#$31"%.–Q#.#"’(&D?GBAHZa<HaD5!

M.)7%),>T96$1N3 –&&U9])()#>5HFFZ5!
")&)*.1,!–&’!’2&–3 .1,!$0!–+21$1,*&+
1*$%.’"#.&!3)*–4$4%+–*.$&!&!*7)!
]),*47–+.–&!$= +–&’,!?@$+)$4*)#–9!
@–#–(.’–)B5?..1–#&+L%%–%/’(’+6#..’(’!
DD?HBAcV<F’Z5!

M.)3)+|U9W$*I)!QT9!\)&&D9U)&):K9!
O*$2–&$:!89O4)&1)U96–#*+)2!Q9!’)S1–!hP 5!
GEEEG5@–#–(.’!())*+)!–,,)3 (+–/),!
?@$+)$4*)#–9@–#–(.’–)B!–1#$,,%#(–&<
#%#–+!/#–’.)&*,A!L&!&*)#&–*.$&–+!
1$3 4–#.,$&5P1.I&(10#+H(%–%/:!Ha?VBA!
Dca<bEH5!

J–/)!UQP 5HFFZ5R#))\.)=A!L&!
–44+.1–*.$&!*$!’.,4+–24!472+$/)&)*.1!*#)),!
$&!4)#,$&–+!1$3 4%*)#,52%7 0*"#$+
?00–’(1"%.&+’.+")#+M’%&(’#.(#&!HG?bBADVa<
DVc5!

J)##.&M9P –I–+$:!\5GEEE5K$1–+!
1$3 4)*.*.$&9!.&(#))’ .&/9!–&’!*7)!
):$+%*.$&!$0!,);<(.–,)’!’.,4)#,–+5!
?7 #$’(1.+J1"*$1–’&"!HVV?HBAHHZ<HGa5!

J#.*17–#’!U!W9O*)47)&,!P 9Q$&&)+2!U5!
GEEE58&0)#)&1)!$0!4$4%+–*.$&!,*#%1*%#)!
%,&/3 %+*.+$1%,!/)&$*24)!’–*–5Q#.#"’(&!
HVVA!FbV<F’VF5!

J#%/&$++)>9’)!P))%,!R5GEEG58&0)##.&/!
,);<(.–,)’!’.,4)#,–+0#$3 !4$4%+–*.$&!
/)&)*.1!*$$+,A!L#):.)=5R#$#I’":!cc?DBA!
HZH<HZV5!

U–&.$!U9M.)3)+|!YL5GEEE583 4–1*,!$0!
);4)#.3)&*–+!7–(.*–*0#–/3)&*–*.$&!$&!
/#$%&’!()))*+),!?@$+)$4*)#–9@–#–(.’–)B!&!
–!($#)–+!,4#%1)0$#),*5?..1–#&+L%%–%/’(’+
6#..’(’!Da?DBAGEH<GHG5!

U–&.$!U9M.)3)+|U5GEED5"#$%&’!()))*+),!
?@$+)$4*)#–A@–#–(.’–)B!–,!(.$.&’.1–*$#,5!
M’%I’3#$&":+1.I+2%.&#$31"%.!HG?DBA!bca<
VEZ5!

U$%,,)*>5HFFa5")&)*.1!’.00)#)&*.–*.$&!
–&’!),*.3 –*.$&!$0!/)&)0+$= 0#$3 >><
,*–*.,*.1,!%&’)#!.,$+–*.$&!(2!’.,*–&1)5!
Q#.#"’(&!HbV?bBAHGHF<HGGc5!

O–++\!L9L!#*7$0)#!] 9K.)%*.)#>9O*–%00)#!@9!
W)#’)+7%)!@5GEEa5U72+$/)$/#–472!$0!–!
7$,*<,4)1.0.1!&,)1*A!")&)*.1!,*#%1*%#)!$0!
90&":0%/$10)*&+&h%#$4)!’$),&$*!#)0+)1*!
4–,*0#–/3)&*–*.$&!$0!.*,!7$,*5M’%–%/’(1–+
K%*$.1–%5+")#+P’..#1.+<%(’#":!FE?GBAGDF<
GbZ5!

O17&).’)#D9W%)00)#!R+P 9U$),,+.Q9!
h;1$00.)#K5HFFa5?$–#X*’.–3#$;€¡CUP?+
&%5"Y 1$#–%$+0%0*–1"%.+/#.#"’(–E1"1+

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1.1–:&'&5")&)*.1,!–&'!Y.$3)*#2!
K–($#–*$#29^&.:)#,.*2!$0!")&):–5!

O3 $%,)UTh9K$&/!I@9O$N–+UU5HFcZ5!
P %+*.4+)#)/#),,.$&!–&'!1$##)+–*.$&!
);*)&,.$&,!$0!*7)!P –&*)+!*),*$03 –*#.;!
1$##),4$&')&1)5K:&"#7 1"'(+L%%–%/:!
DV?bBAZGa<ZDG5!

O*$&)!Q9D)4,$&UT9W#–3 –#IUT9K–,N$= ,N.!
U5GEEH5R.3)!*$!')–*7#),4$&,)!&!
1–#–(.'!())*+),!);4$,)'!*$03 %+*.4+)!
,*#),,$#,!–+$&/!–!/#–'.)&*!$07)–:203)*–+!
4$+#%*.$&5H.3'$%.7 #."1–+!%–*"'%.!HHD?GBA!
GDF<Gbb5!

O*$&)!Q9D)4,$&UT9K–,N$= ,N.U5GEEG5!
R#)&',!&!')*$;.01–*.$&!)&I23),!–&'!
7)–:203)*–+!–11%3 %+–*.$&!&!/#$%&'!
())*+),!?@$+)$4*)#–A@–#–(.'–)B!&7–(.*&/!
–!/#–'.)&*!04+#%*.$&52%7 01$1"'3#+
M'%()#7 '&"$:–Z+!):&'%–%/:;=%8'(%–%/:–1.I+
!)1$7 1(%–%/:–2!HDG?HBAHEV<HHG5!

O%&',*#_3 !K9W)++)#!K9@7–4%.,–*!P 5GEED5!
8&(#))'&/!–&'!,);<(.–,)'!/)&)!0#$= !&!
7)!–&!6%$7 '(1–#8&#("15H3%–*"'%.!Va?aBA!
HVVG<HVZH5!

R7.)+)!6<^5HFaa521$1,'I+M##"–#&+'.+=)#'$+
H.3'$%.7 #."&UP?+<"*I:–%.+R1,'"1"+<#–#("'%.+
,:+?I10"1"'%.&+'.+!):&'%–%/:–1.I+
M#)13'%*$;!D4#&/)#<\)#+–/5!

R7$3 –,!@Q5GEEE5Q.,4)#,–+!–&'!
);*&1*.$&!&!0#–/3)&*)'!+–&',1–4),5!
!$%(##I'./&%5")#–O%:1–+<%('":–%5P%.I%.+
<#$'#&MTGZa?HbDFBAHDF<HbV5!

\–&!Q)#!] %#00L] "98,––N,!TL9h#&,*&/!"9!
\–&!O*#––+)&!MP 5GEED5U$4%+–*.$&!
,%(,*#%1*%#),!&!*7)!,$.+!&:)#*)(#–*)!
F$()#&#–1+('.("19+–,#):)–+)'!(2!
3 .1#$,–*)++.*)!–&'!Rh<L>KJ3 –#N)#,5!
>%–#(*–1$+H(%–%/:!HG?ZBAHDbF<HDVF5!

\–&!6%.I)&!R6J5HFcE5O4)1.),!$0!
@–#–(.'–)!?@$+)$4*)#–B!&!= 7.17!*7)!
$11%##)&1)!$0!'.,4)#,–+!(2!0+./7*$0!
&'.:.'%–+,!7–,!())&!,7$=&5!
H."%7 %–%/'&()#–M#$'()"#.!bE?HHBAHZZ<
HZc5!

\–&!S$,*)#7$%*!@9%6%*17&,$&!] >9] .++,!
QJP 9O7.4+)2UT5GEEb5P 8@US<@6h@WhUA!
O$0*= –#)!0$#!.')&*.02&/!–&'!1$##)1*&/!
/)&$*24&/!)##$#,!&!3 .1#$,–*)++.*)!'–*–5!
>%–#(*–1$+H(%–%/:+U%"#&!b?DBAVDV<VDc5!

:–&!D17–.1N!f.++),)&U"9Y#%&,*&/!LP 65!
HFcb5R7)!&0%)&1)$0!0$'!C%–&*.*2!–&'!
47$*$4)#.$'!'%#&/!*7)!4#)<–'%+*!,*–/),!
$&!0+./7*3 %,1+)!'):)+$43)&*!&!–'%+*!
!)'%.")*&+#(%$*&+?@$+)$4*)#–A!
O*–47.+&.'–)B!–&'!!"#$%&"'()*&+
%,–%./%0*.("1"*&+?@$+)$4*)#–A!
@–#–(.'–)B5H."%7 %–%/'1+Q#.#$1–'&F?DBA!
HbD<Hba5!

])#!YO9@$1N)#7–3 !@@5HFcb5h,*.3 –*&/!
><,*–*.,*.1,!0$#!*7)!–&–+2,.,!$0!4$4%+–*.$&!
,*#%1*%#)5H3%–*"'%.!Dc?ZBAHDVc<HDaE5!

]7.*)7)–'!L9L&')#,$&!DK9W%.:.+–!WP 9!
U$–17!TK9P –2!Y5GEED5")&)*.1!:–#.–*.$&!
–3 $&/!&*)#1$&&)1*)'!4$4%+–*.$&,!$0!
21"%&"%7 *&+%((’I#."1–’&A83 4+.1–*.$&,!0$#!
'.,*&/%.,7&/!.3 4–1*,!01&*–3 &–&*,!
0#$3 !(.$/)$/#–47.1–+!,*#%1*%#.&/5!
>%–#(*–1$+H(%–%/:!HG?HEBAGcHa<GcDD5!

f2/3 %&*UT9P –#2–t,N.!P 9K–,N$= ,N.U5!
GEEZ5Y$'2!3 –,,!–&'!1–+$#.1!:–+%)!$0!*7)!
/#$%&'!())*+)!?!"#$%&"'()*&+
%,–%./%0*.("1"*&B!?@$+)$4*)#–9!
@–#–(.'–)B!–+$&/!–!/#–'.)&*!$07)–:2!
3)*–+!4$+#%*.$&5H.3'$%.7 #."1–+=%8'(%–%/:+
1.I–2)#7 '&"$:GV?HEBAGaEF<GaHb5!

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