

Supplementary Information: Loss of flight promotes beetle diversification

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Supplementary Table S1 | GenBank accession numbers of *COI-II* gene sequences used in this study.

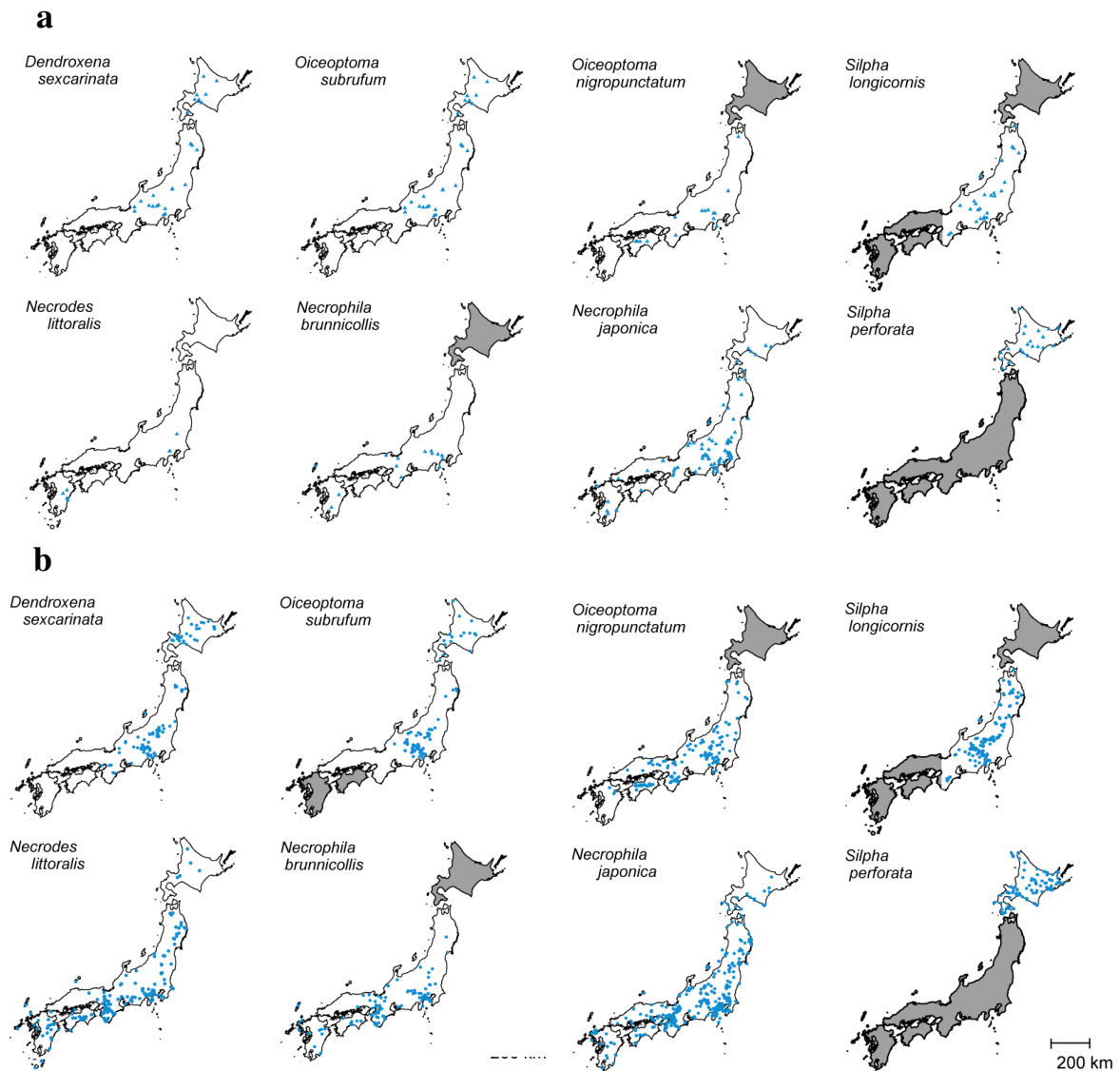
Supplementary Table S2 | GenBank accession numbers of *Pepck* and *Wg* gene sequences used for AMOVA.

Supplementary Table S3 | The contribution of each environmental variable to the estimation of distribution areas.

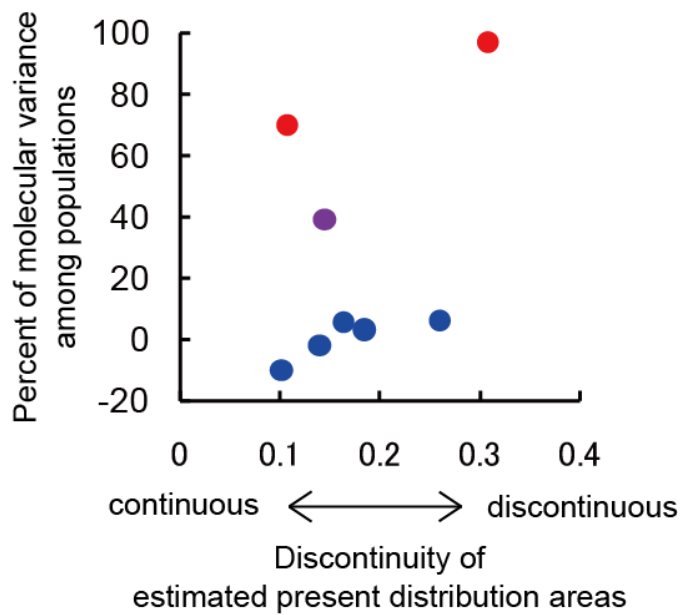
Supplementary Table S4 | The data used in the meta-analysis of the relationship between flight ability and genetic differentiation in beetles.

Supplementary Methods

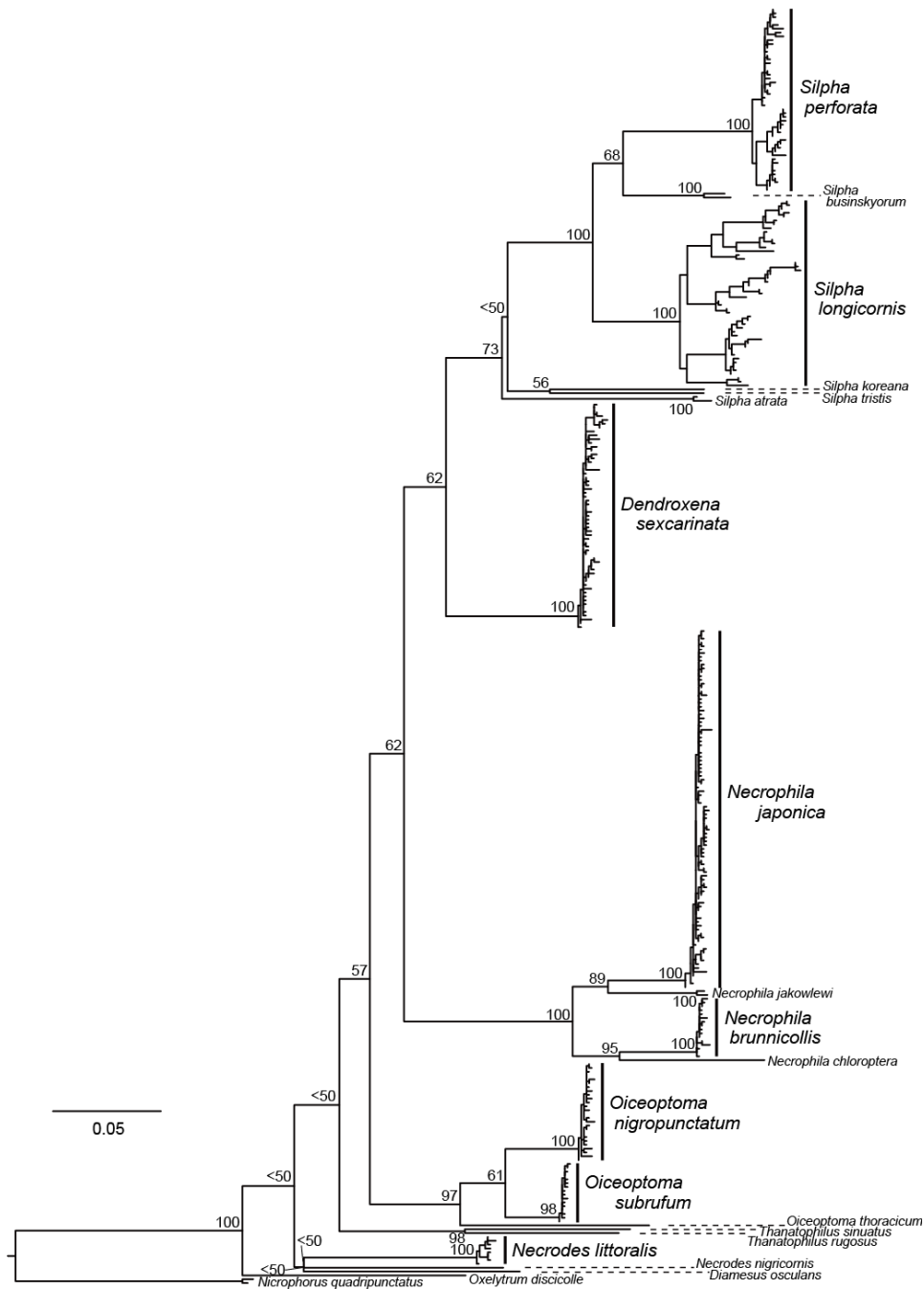
Supplementary References



Supplementary Figure S1 | Sampling localities used for genetic analysis and estimation of distribution areas. (a) Sampling localities used for genetic analysis. Localities are shown in light blue circles. The areas in which the species do not occur are shown in light gray. **(b)** Sampling localities used for estimation of distribution areas. Localities are shown in light blue triangles.

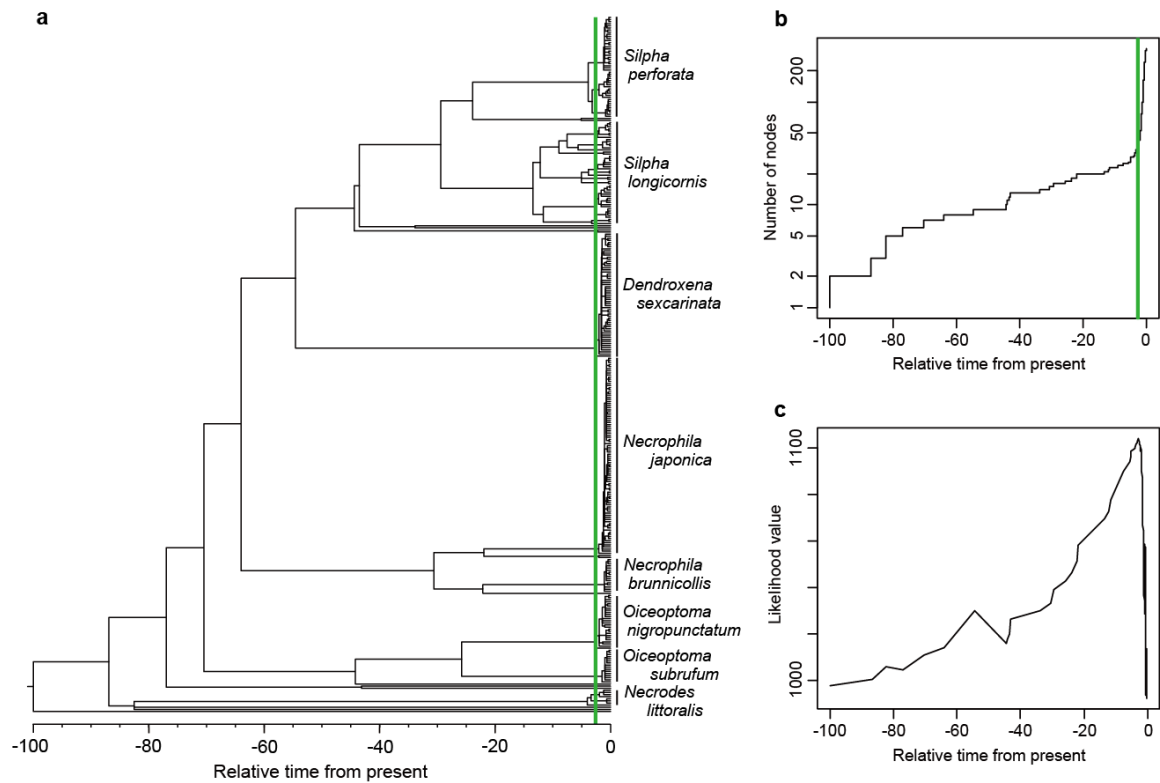


Supplementary Figure S2 | Relationship between the present habitat discontinuity and the genetic differentiation of the *COI-II* gene. The genetic differentiation is expressed as the proportion of molecular variance among populations in the analysis of molecular variances. Blue, red, and purple circles indicate flight-capable, flightless, and dimorphic species, respectively.



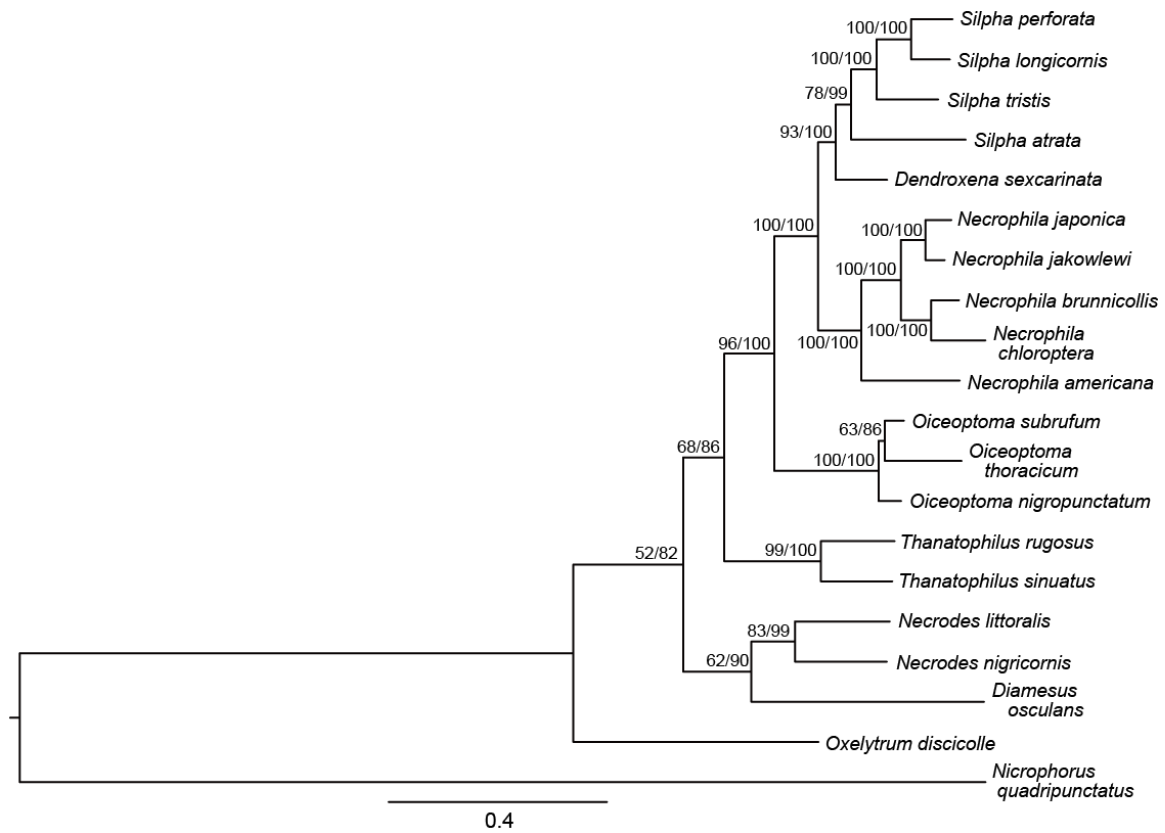
Supplementary Figure S3 | Maximum likelihood (ML) tree of all *COI-II* haplotypes.

Numbers on the branches for different species represent the ML bootstrap percentage. The scale bar is based on the number of substitutions per site.



Supplementary Figure S4 | Results of the single-threshold model using the GMYC

approach. (a) Ultrametric tree transformed from the ML tree of all *COI-II* haplotypes. The time of the root node in Silphinae was arbitrarily set at 100. The threshold time estimated from the single-threshold model is shown by a green line (threshold time: 2.72). **(b)** Relationship between the relative time from the present and the number of nodes. The threshold time estimated from the single-threshold model is shown by a green line. **(c)** Relationship between the relative time from the present and the likelihood value of threshold time.



Supplementary Figure S5 | Maximum likelihood (ML) tree based on the *COI-II*, *16S*, *28S*, *Wg*, and *Pepck* genes. The values at the nodes represent the ML bootstrap percentage/Bayesian posterior probability. The scale bar is based on the number of substitutions per site.

Supplementary Table S1 | GenBank accession numbers of the *COI-II* gene sequences used in this study.

Species	Accession number	Sample used for species tree
<i>Oxelytrum discicolle</i>	AB606431	AB606431
<i>Diamesus osculans</i>	AB606432	AB606432
<i>Necrodes littoralis</i>	AB606438-AB606445	AB606442
<i>Necrodes nigricornis</i>	AB606433	AB606433
<i>Thanatophilus rugosus</i>	AB606434	AB606434
<i>Thanatophilus sinuatus</i>	AB606435	AB606435
<i>Oiceoptoma nigropunctatum</i>	AB606446-AB606471	AB606447
<i>Oiceoptoma subrufum</i>	AB606472-AB606487	AB606472
<i>Oiceoptoma thoracicum</i>	AB606436	AB606436
<i>Necrophila chloroptera</i>	AB606437	AB606437
<i>Necrophila brunnicollis</i>	AB376113, AB606488-AB606502	AB606488
<i>Necrophila jakowlewi</i>	AB606503, AB606504	AB606504
<i>Necrophila japonica</i>	AB376112, AB376114, AB606505-AB606596	AB606575
<i>Dendroxena sexcarinata</i>	AB376110, AB376117, AB606597-AB606653	AB606612
<i>Silpha atrata</i>	AB376111, AB606654	AB376111
<i>Silpha tristis</i>	AB376109	AB376109
<i>Silpha perforata</i>	AB376167-AB376209, AB438997, AB606655-AB606658	AB376185
<i>Silpha longicornis</i>	AB376119-AB376166, AB606659	AB376161
<i>Silpha koreana</i>	AB376116	—
<i>Silpha businskyorum</i>	AB376104, AB376105	—
<i>Nicrophorus quadripunctatus</i>	AB606660, AB606661	AB606661

Supplementary Table S2 | GenBank accession numbers of the *PepCK* and *Wg* gene sequences used for AMOVA.

Species name	Accession number	
	<i>PepCK</i>	<i>Wg</i>
<i>Necrodes littoralis</i>	AB285599, AB668649-AB668656	AB285631, AB668811-AB668813
<i>Oiceoptoma nigropunctatum</i>	AB285603, AB668657-AB668689	AB285635, AB668814-AB668848
<i>Oiceoptoma subrufum</i>	AB285600, AB668602-AB668608	AB285632, AB668613-AB668620
<i>Necrophila brunnicollis</i>	AB285613, AB668599-AB668601	AB285645, AB668609-AB668612
<i>Necrophila japonica</i>	AB285602, AB668690-AB668748	AB285634, AB668849-AB668881
<i>Dendroxena sexcarinata</i>	AB285598, AB668621-AB668648	AB285630, AB668772-AB668810
<i>Silpha perforata</i>	AB285597, AB668749-AB668754	AB285629, AB668882-AB668904
<i>Silpha longicornis</i>	AB285601, AB285608, AB668755-AB668771	AB285633, AB285640, AB668905-AB668939

Supplementary Table S3 | The contribution of each environmental variable to the estimated distribution areas. The area under the receiver operating curve (AUC) values are also shown.

Species	No. of sites	AUC values	Proportion of contribution (%)										
			Annual mean temperature	Temperature seasonality	Minimum temperature of coldest month	Mean temperature of coldest month	Maximum temperature of warmest month	Mean temperature of warmest month	Annual mean precipitation	Precipitation seasonality	Precipitation of driest month	Precipitation of wettest month	Maximum snow depth
<i>D. sexcarinata</i>	105	0.80	0.0	2.0	9.0	0.9	63.5	12.1	0.5	4.3	3.1	4.2	0.4
<i>O. subrufum</i>	97	0.83	0.0	2.4	0.3	0.0	57.0	0.9	2.0	1.5	1.6	18.5	15.7
<i>O. nigropunctatum</i>	159	0.80	4.7	9.5	11.1	7.5	12.8	9.2	17.0	3.5	0.7	7.3	16.8
<i>N. littoralis</i>	193	0.75	2.7	20.0	16.4	2.2	0.4	2.8	17.5	6.3	3.3	6.2	22.1
<i>N. brunnicollis</i>	115	0.77	2.8	10.4	2.2	1.9	5.9	0.1	2.3	5.3	3.4	17.2	48.5
<i>N. japonica</i>	379	0.77	10.5	14.1	2.4	16.3	19.2	2.3	4.7	9.6	2.2	9.6	9.1
<i>S. longicornis</i>	169	0.92	18.7	15.7	1.5	9.4	18.9	8.3	1.6	6.1	1.2	15.2	3.4
<i>S. perforata</i>	114	0.93	3.0	5.3	0.4	1.2	67.1	0.9	8.0	1.7	1.2	7.1	4.0

Supplementary Table S4 | The data used in the meta-analysis of the relationship between flight ability and genetic differentiation in beetles.

Family Species	Gene	Flight ability	Percent of molecular variance among populations	Sampling range (km)	Study region
Carabidae					
<i>Coptolabrus smaragdinus</i> ⁵¹	<i>COI</i>	flightless	91.70	300	South Korea
<i>Coptolabrus jankowski</i> ⁵¹	<i>COI</i>	flightless	75.70	300	South Korea
<i>Leptocarabus koreanus</i> ⁵²	<i>COI</i>	flightless	47.64	300	South Korea
<i>Leptocarabus seishinensis</i> ⁵²	<i>COI</i>	flightless	79.16	300	South Korea
<i>Leptocarabus semiopacus</i> ⁵²	<i>COI</i>	flightless	37.73	300	South Korea
Cerambycidae					
<i>Acrocinus longimanus</i> ⁵³	<i>COI</i>	flight-capable	54.30	2400	Panama, Trinidad
<i>Semanotus japonicus</i> ⁵⁴	<i>COI-II</i>	flight-capable	43.47	1000	Japan
Chrysomelidae					
<i>Plateumaris constricticollis</i> ⁵⁵	<i>COI</i>	flight-capable	98.00	1400	Japan
<i>Plateumaris sericea</i> ⁵⁵	<i>COI</i>	flight-capable	90.00	1600	Japan
<i>Plateumaris shirahatai</i> ⁵⁵	<i>COI</i>	flight-capable	97.00	1200	Japan
<i>Plateumaris weisei</i> ⁵⁵	<i>COI</i>	flight-capable	88.00	300	Japan
Coccinellidae					
<i>Henosepilachna pustulosa</i> , <i>H. niponica</i> and <i>H. yasutomii</i> ^{56*}	<i>COI</i>	flight-capable	64.00	300, 1000, 700	Japan
Curculionidae					
<i>Curculio camelliae</i> ⁵⁷	<i>COI</i>	flight-capable	76.40	1100	Japan
<i>Dendroctonus pseudotsugae</i> ⁵⁸	<i>COI</i>	flight-capable	19.84	3300	America, Mexico
<i>Dendroctonus ponderosae</i> ⁵⁹	<i>COI-II</i>	flight-capable	35.04	2300	North America
<i>Porthetes hispidus</i> ⁶⁰	<i>COI</i>	flight-capable	16.00	200	South Africa

<i>Tomicus destruens</i> ⁶¹	<i>COI-II</i>	flight-capable	17.68	900	France
<i>Tomicus destruens</i> ⁶²	<i>COI-II</i>	flight-capable	65.04	4000	Mediterranean basin
<i>Tomicus piniperda</i> ⁶¹	<i>COI-II</i>	flight-capable	13.92	800	France
<i>Xylosandrus crassiusculus</i> ⁶³	<i>COI</i>	polymorphic	90.33	2600	Japan
<i>Xylosandrus germanus</i> ⁶⁴	<i>COI</i>	flight-capable	69.59	1600	Japan
<i>Polydrusus inustus</i> ⁶⁵	<i>COII-NDI</i>	flightless	77.20	700	central Europe
<i>Centricnemus leucogrammus</i> ⁶⁵	<i>COII-NDI</i>	flightless	75.50	800	central Europe
Dytiscidae					
<i>Nebrioporus ceresyi</i> ⁶⁶	<i>COI</i>	flight-capable	78.22	3800	Mediterranean basin
<i>Paroster macrosturtensis</i> ⁶⁷	<i>COI</i>	flightless	55.70	3	Australia
<i>Paroster microsturtensis</i> ⁶⁷	<i>COI</i>	flightless	70.00	3	Australia
<i>Paroster mesosturtensis</i> ⁶⁷	<i>COI</i>	flightless	40.60	3	Australia
Histeridae					
<i>Hypocaccus lucidulus</i> ⁶⁸	<i>COI</i>	flight-capable	10.00	400	California
Hydraenidae					
<i>Ochthebius glaber</i> ⁶⁶	<i>COI</i>	flight-capable	89.34	500	Mediterranean basin
<i>Ochthebius notabilis</i> ⁶⁶	<i>COI</i>	flight-capable	62.51	1100	Mediterranean basin
Hydrophilidae					
<i>Cercyon fimbriatus</i> ⁶⁸	<i>COI</i>	flight-capable	1.00	600	California
Leiiodidae					
<i>Agryrtodes labralis</i> ⁶⁹	<i>COI</i>	flight-capable	34.59	800	New Zealand
Lucanidae					
<i>Lucanus formosanus</i> ⁷⁰	<i>COI</i>	flight-capable	-0.30	300	Taiwan
Pythidae					
<i>Pytho abieticola</i> ⁷¹	<i>COI</i>	flight-capable	61.23	6000	Eurasia

<i>Pytho depressus</i> ⁷¹	<i>COI</i>	flight-capable	42.33	6000	Eurasia
<i>Pytho kolwensis</i> ⁷¹	<i>COI</i>	flight-capable	48.82	6000	Eurasia
Scarabaeidae					
<i>Antitrogus parvulus</i> ⁷²	<i>COII</i>	flight-capable	70.80	50	Australia
<i>Temnoplectron reyi</i> and <i>T. politulum</i> ^{73*}	<i>COI</i>	flight-capable	36.86	100, 200	Australia
<i>Temnoplectron subvolitans</i> and <i>T. aeneopiceum</i> ^{73*}	<i>COI</i>	polymorphic	73.80	100, 200	Australia
Staphylinidae					
<i>Sepedophilus castaneus</i> ⁷⁴	<i>COI</i>	flightless	86.47	500	California
Tenebrionidae					
<i>Coelus ciliatus</i> ⁷⁵	<i>COI</i>	flightless	90.00	800	California
<i>Dichomma dardanum</i> ²⁷	<i>COI</i>	flightless	94.00	400	Aegean archipelago
<i>Eutagenia</i> sp. 'sand' ²⁷	<i>COI</i>	flightless	73.00	300	Aegean archipelago
<i>Eutagenia</i> sp. 'soil' ²⁷	<i>COI</i>	flightless	94.00	300	Aegean archipelago
<i>Micrositus orbicularis</i> ²⁷	<i>COI</i>	flightless	86.00	200	Aegean archipelago
<i>Opatroides punctulatus</i> ²⁷	<i>COI</i>	flight-capable	61.00	300	Aegean archipelago
<i>Pimelia sparsa</i> ⁷⁶	<i>COII</i>	flightless	41.80	50	Gran Canaria
<i>Zophosis punctata</i> ²⁷	<i>COI</i>	flightless	88.00	600	Aegean archipelago

*Two or three species were combined in the AMOVA in these references. Therefore, we removed the molecular variance among species and recalculated the proportion of variance among populations within combined species for our meta-analysis.

Supplementary Methods

Sampling

We collected eight species of Silphinae (*Dendroxena sexcarinata*, *Oiceoptoma subrufum*, *Oiceoptoma nigropunctatum*, *Necrodes littoralis*, *Necrophila brunnicollis*, *Necrophila japonica*, *Silpha perforata*, and *Silpha longicornis*) over a wide geographical area in the Japanese archipelago, namely Hokkaido, Honshu, Shikoku, Kyushu, and their adjacent islands (Supplementary Figure S1). The genus *Silpha* is totally wingless, and the above two species colonized Japan via landbridges during the Pleistocene¹⁸. Furthermore, 12 silphine species were included in the phylogenetic analysis of Silphinae: *Oxelytrum discicolle*, *Diamesus osculans*, *Necrodes nigricornis*, *Thanatophilus rugosus*, *Thanatophilus sinuatus*, *Oiceoptoma thoracicum*, *Necrophila chloroptera*, *Necrophila jakowlewi*, *Silpha atrata*, *Silpha tristis*, *Silpha koreana*, and *Silpha businskyorum*. *Nicrophorus quadripunctatus*, which is in the sister subfamily Nicrophorinae, was used as the outgroup. All specimens were identified by HI and MN. Taxonomic treatments followed references^{48,77,78}. Specimens used for DNA analyses are all preserved as vouchers in Department of Entomology, Forestry and Forest Products Institute, Tsukuba, Japan, and to be deposited in the Kyoto University Museum.

Sequencing

Methods for DNA sequencing were identical to those in previous papers^{16,18}. The following primers were used for PCR amplification and direct sequencing: mitochondrial *COI-II* gene (842 bp): COS2183N (forward), 5'-CAR CAY YTA TTY TGR TTY TTY GG-3'⁷⁹;

C1-J-2195 (forward), 5'-TTG ATT TTT TGG TCA TCC AGA AGT-3'⁸⁰; 1J2441 (forward), 5'-CCA ACA GGA ATT AAA ATT TTT AGA TGA TTA GC-3'⁸⁰; COA3107S (reverse), 5'-TCY ATY ARA GGK GAR GCW CTR TCT TG-3'¹⁸; COA3186E (reverse), 5'-ATT AAG TAT CCG ACT AAA ACA G-3'⁵⁰; COA3374 (reverse), 5'-TAT CAT TGA TGX CCA ATA GTT TT-3'¹⁸; 2N3661 (reverse), 5'-CCA CAA ATT TCT GAA CAT TGA CCA-3'⁸⁰; phosphoenolpyruvate carboxykinase gene (*PepCK*; 398 bp): Peps (forward), 5'-GGA GAT GAT ATY GCT TGG ATG-3'¹⁶; Pepa (reverse), 5'-GCW GCA GCR GTA GCT TCA CT-3'¹⁶; *wingless* gene (*Wg*; 386 bp): LEPWG1 (forward), 5'-GAR TGY AAR TGY CAY GGY ATG TCT GG-3'⁸¹; ModLEPWG2 (reverse), 5'-ACT ICG CAR CAC CAR TGG AAT GTR CA-3'⁸¹; Wgsils (forward), 5'-TGG ATG CGT TTR CCA CCR TT-3'¹⁶; Wgsila (reverse), 5'-TTG CAC CGY TCG ACG ACG AC-3'¹⁶; WgsilF2 (forward), 5'-AGT GTC ATG GTA TGT CTG GCT CGT GTA CAG-3' (this study); WgsilR2 (reverse), 5'-CGT TCG ACG ACG ACC ACT TCT TGT GT-3' (this study). Data generated in previous papers^{16, 18} were also used.

Estimated distribution areas

Species distributions in the Japanese archipelago were estimated using the program Maxent ver. 3.2.19³³. We obtained 11 environmental variables from the 1-km-mesh meteorological data of the area for 1971–2000⁸²: annual mean temperature, temperature seasonality (coefficients of the variation in the monthly mean temperatures), minimum temperature of the coldest month, mean temperature of the coldest month, maximum temperature of the warmest month, mean temperature of the warmest month, annual precipitation, precipitation

in the driest month, precipitation in the wettest month, precipitation seasonality (coefficients of the variation in monthly precipitations), and maximum snow depth. The data associated with the presence of species after the 1970s were constructed based on specimens deposited at the Osaka Museum of Natural History and Wakayama City Museum, literature (Supplementary References), and unpublished data by HI and MN. An index of model performance, the area under the receiver operating curve (AUC), ranged from 0.75 to 0.93 for each species (Supplementary Table S3). AUC uses values between 0 and 1, where scores closer to 1 indicate a better performance of the model. Generally, models with AUC values greater than 0.75 are considered appropriate⁸³.

Species distributions during the Last Glacial Maximum (LGM; 20,000 ya) were also estimated based on previous paleoclimatic data²¹. The temperature during the LGM was assumed to be 11°C lower than the present temperature and the area was assumed to have experienced 1100/2100 times more precipitation than at present. The maximum snow depth during the LGM was estimated from temperature and precipitation using the following formula⁸⁴⁻⁸⁶:

$$\text{Snow depth in a month} = \text{Precipitation for the month} \times (1 - P_{\text{rain}})/\rho + \text{Snow depth of the previous month} - \text{Monthly snow melt},$$

where P_{rain} is the proportion of rain in the total precipitation and ρ is the snow density. P_{rain} was determined using the monthly mean temperature (T), the threshold temperature where 50% snowfall occurs (T_T), and the temperature range at which both solid and liquid

precipitation occur (T_R):

$$P_{\text{rain}} = 5 \times [(T - T_T)/(1.4 \times T_R)]^3 + 6.76 \times [(T - T_T)/(1.4 \times T_R)]^2 + 3.19 \times [(T - T_T)/(1.4 \times T_R)] + 0.5 \text{ if } T \leq T_T \text{ and } P_{\text{rain}} \geq 0;$$
$$P_{\text{rain}} = 5 \times [(T - T_T)/(1.4 \times T_R)]^3 - 6.76 \times [(T - T_T)/(1.4 \times T_R)]^2 + 3.19 \times [(T - T_T)/(1.4 \times T_R)] + 0.5 \text{ if } T \geq T_T \text{ and } P_{\text{rain}} \leq 0.$$

Monthly snow melt was determined as the daily snow melt \times 30, where

Daily snow melt = 1 if T ($^{\circ}\text{C}$) $<$ 0;

Daily snow melt = $2 \times T^{1.44} + 1$ if T ($^{\circ}\text{C}$) \geq 0.

T_T , T_R , and ρ were set to 2.8°C , 13.0°C , and 0.3 g/cm^3 , respectively. We calculated the snow depth in December, January, February, and March. The highest snow depth of these months was used as the maximum snow depth. Snow depth of the previous month was set to 0 in December. Sea level at the LGM was assumed to be 120 m lower than at present²².

Phylogenetic tree reconstruction for estimating the number of potential species

We constructed the maximum likelihood (ML) phylogeny of all COI-II haplotypes using the likelihood ratchet method and Phylogears2 ver. 2.0³⁵ with TreeFinder, October version³⁶. We used three constraints for the tree search following the phylogeny based on five gene sequences (Supplementary Figure S5): the sister relationship of *Oxelytrum discicolle* to all other silphine species, the sister relationship of *Diamesus* and *Necrodes*, and the monophyly

of *Necrodes* species. The confidence level at each node in the ML analysis was assessed by 100 bootstrap replicates without any constraints (Supplementary Figure S3).

We converted the ML tree, of which the outgroup species (*Nicrophorus quadripunctatus*) was pruned, into an ultrametric form using the penalized likelihood method³⁸ implemented in r8s ver. 1.7³⁹. First, cross-validation was performed to select the appropriate smoothing parameter between 1 and 1000 (algorithm = TN). Second, a penalized likelihood search was conducted using the result of the cross-validation analysis (penalty = add, smoothing = 32). The time of the root node in the Silphinae was arbitrarily set to 100. Polytomies in the tree were randomly bifurcated using TreeEdit ver. 1.0a10⁸⁷.

Speciation and extinction rate in flight-capable and flightless lineages

We constructed the ML phylogeny of Silphinae using the *COI-II*, *16S*, *28S*, *Wg*, and *Pepck* gene regions by a likelihood ratchet method and Phylogears2 ver. 2.0³⁵ with TreeFinder, October version³⁶. The confidence level at each node in the ML analysis was assessed by 100 bootstrap replicates. Bayesian inference was also performed using MrBayes ver. 3.1^{88,89} for the phylogenetic analysis with the same models of sequence evolution as in the ML analysis. Gaps were treated as a separate presence/absence character using simple indel coding⁹⁰, and these coded gap characters (16S: 11 characters; 28S: 49 characters) were included in the Bayesian inference as restriction characters (coding = variable). The search was run for 2,000,000 generations and sampled every 100 generations. The first 5000 trees were discarded as burn-in. Trees constructed by ML and Bayesian inference showed the same topology and were congruent with the tree constructed in a previous study¹⁶ (Supplementary

Figure S5).

We converted the ML tree, of which the outgroup species (*Nicrophorus quadripunctatus*) was pruned into an ultrametric form using a penalized likelihood method implemented in r8s. Cross-validation was performed to select the appropriate smoothing parameter between 1 and 10,000 (algorithm = TN), and a penalized likelihood search was performed using the result of the cross-validation analysis (penalty = add, smoothing = 10,000). The time of the root node in Silphinae was arbitrarily set to 100.

We calculated the speciation and extinction rates using a binary-state speciation and extinction (BiSSE) model⁴⁴. The BiSSE model estimates the speciation and extinction rates in each binary state using a ML inference. In this analysis, we used genera of Silphinae as OTUs of a phylogenetic tree and assigned the numbers of nominal species and different character states (flight-capable, flightless, unknown) in each clade to each OTU. Silphinae comprises 12 genera and 109 species^{48,49}. Of these, four genera were not available for the present phylogenetic analysis and were treated as follows in the BiSSE analysis. (1) The phylogenetic position of *Heterotemna* (3 species) was unknown, and hence it was excluded from the analysis; (2) *Heterosilpha* (2 species) was included in the *Necrophila* clade because these genera were sister groups in the previous molecular phylogenetic analysis⁹¹; the flight ability of *Heterosilpha* was set as unknown; (3) *Ptomaphila* (3 species) was included in the *Oxyletrum* clade because of their inferred sister-group relationship^{92,93}. *Ptomaphila* was considered to be flight-capable based on its ecology⁹²; (4) *Aclypea* (13 species) was included in the *Silpha* clade because *Aclypea* is considered to belong to the *Silpha* lineage⁹¹. *Aclypea* was treated as flightless based on its ecology^{94,95}. In addition, we treated the single

dimorphic species (*Necrophila japonica*) as flight-capable because flight-capability has been maintained in this species and no speciation event had occurred after the evolution of dimorphism. The data set used for the BiSSE analysis contained 8 clades and 106 species, of which 36 were flightless, 68 were flight-capable, and 2 were of unknown flight-capability. Note that even when *Aclypea* was treated as of unknown flight-capability, the speciation rate was higher with the flightless state (0.269) than with the flight-capable state (0.091).

Supplementary References

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