

Trends in Ecology and Evolution

Bolder takes all? The behavioural dimension of biogeography

--Manuscript Draft--

Manuscript Number:	TREE-D-15-00270R2
Article Type:	Opinion
Keywords:	historical biogeography, animal personality, behavioural polymorphism, dispersal, colonization, range expansion
Corresponding Author:	Claudio Carere, Ph.D Biology of Behaviour University of Tuscia Viterbo, Italy ITALY
First Author:	Daniele Canestrelli, PhD Animal Ecology
Order of Authors:	Daniele Canestrelli, PhD Animal Ecology
	Roberta Bisconti, PhD Animal Ecology
	Claudio Carere, Ph.D Biology of Behaviour
Abstract:	Animal personality can be seen as behavioural polymorphism that could play a direct and active role in driving evolutionary pathways. Here, we argue that consistent individual differences in key personality traits affecting dispersal and other density-dependent processes provided substantial contributions to moulding biogeographic patterns. Building upon opportunities recently opened by genomics and other novel approaches, we explore the hypothesis that Pleistocene range expansions, island colonisations, and other historical biogeographic processes could have been promoted by non-random samples of behavioural types of the founder populations. We provide context and testable hypotheses, based on case studies, that could bring new implications to our understanding of the processes shaping spatial and temporal patterns of variation in animal biodiversity.

TRENDS BOX

- Animal personality can influence dispersal processes. Evidence is emerging that personality traits can affect departure, distance covered, transience/settlement success, as well as density-dependent processes related to both natal and novel habitats.
- Non-random spatial distributions of the behavioural types that affect dispersal suggest in several instances that dispersers (i.e. colonisers, founders) could be a non-random sample of behavioural types from the source population.
- Recent advances in studying the heritability of animal personality indicate that the contribution of additive genetic variance to personality variation is substantial.
- The potential contribution of behavioural polymorphism to key historical biogeographic processes is a substantially unexplored research area

Bolder takes all? The behavioural dimension of biogeography

Daniele Canestrelli¹, Roberta Bisconti¹, Claudio Carere^{1,2}

¹Department of Ecological and Biological Science, University of Tuscia, 01100 Viterbo, Italy.

²Laboratory of Experimental and Comparative Ethology, University Paris 13, Sorbonne Paris Cité, France.

Corresponding authors: Canestrelli D. (canestrelli@unitus.it); Carere C. (claudiocarere@unitus.it)

Keywords: animal personality, behavioural polymorphism, colonization, dispersal, historical biogeography, range expansion.

Animal personality can be seen as behavioural polymorphism that could play a direct and active role in driving evolutionary pathways. Here, we argue that consistent individual differences in key personality traits affecting dispersal and other density-dependent processes provided substantial contributions to moulding biogeographic patterns. Building upon opportunities recently opened by genomics and other novel approaches, we explore the hypothesis that Pleistocene range expansions, island colonisations, and other historical biogeographic processes could have been promoted by non-random samples of behavioural types of the founder populations. We provide context and testable hypotheses, based on case studies, that could bring new implications to our understanding of the processes shaping spatial and temporal patterns of variation in animal biodiversity.

Animal personality as a pacemaker of evolutionary processes

The role that behaviour plays in actively promoting evolutionary change has long been recognised [1-3]. More recently, the realization that animals possess individual personalities (see Glossary) with a heritable, physiological, and epigenetically regulated basis has deeply impacted several areas of ecology and evolution [4], and has strengthened this view up to the hypothesis that behavioural variation can “act as a ‘pacemaker’ of evolution for non-behavioural traits” through various mechanisms and at different ecological levels [5-7].

Behavioural polymorphisms involving the five most common personality categories of traits described in animals (i.e. boldness-shyness, exploration, activity, aggressiveness, and sociability [8]) have been associated with dispersal propensity and

population structure in several empirical studies and theoretical models. These studies provide fundamental contributions to numerous of research fields including population ecology, contemporary evolution, invasion biology, and climate change biology [9-16]. Surprisingly, how behavioural polymorphisms might have contributed to key past processes structuring biogeographic patterns is a substantially unexplored research ground.

Here we propose a context to study how behavioural polymorphisms within-species could have contributed to moulding current geographic patterns of species distribution and genetic diversity. Our aim is to bridge (historical) biogeography with behavioural biology, as we are positive that this ‘getting closer’ will shed new light on the diversity of processes that have shaped temporal and spatial patterns of variation in animal biodiversity.

Why should biogeographers care about animal personality?

Biogeography is, by definition, the study of the present and past distribution of biological diversity and their causal processes. Many new perspectives and technical advances have deeply reshuffled historical biogeography in the last decades, to become ‘prototypic of integrative science’ [17-22]. Accordingly, research around long-recognised key processes in biogeography, such as dispersal, has also changed its ‘physiognomy’.

Dispersal (including departure, transience, and settlement) is a central process in the entire range of disciplines dealing with ecology, evolution, and conservation of biodiversity [23]. Since its inception, historical biogeographic investigation has been mostly concerned with extrinsic factors (geology, climate, or ecological), which

influence the likelihood of dispersal between habitats (e.g. barriers and corridors) in relation to the organism's dispersal abilities (i.e. dispersal modes and distance covered) [24]. However, dispersal is a strongly conditional process [25,26], which directly relates to lineage range variation over time [27]. Whilst biogeography research has largely integrated instances where dispersal is context dependent (e.g. relative to changing environmental conditions and demographic parameters [28,29]) and non-random (depending on individual variables such as sex [e.g. 30]), the emphasis here is on personality-dependent dispersal [31-33].

In Table 1, we list a set of predictions of behavioural polymorphism in key personality traits leading to non-random dispersal, based on empirical studies. Notably, in many cases dispersal propensity is not best predicted by behavioural polymorphisms alone, but by their interaction with socio-ecological factors related to the natal and novel habitat [32]. These factors can include foraging, competition, risk of predation, risk of inbreeding, and partner availability—most of which have been associated with behavioural polymorphisms, are relevant in both natal and novel habitats, and are density-dependent. Thus, behavioural polymorphism could have influenced all the steps (departure, transience, and settlement) of past dispersal events, ultimately affecting a number of historical processes that are iconic research grounds for historical biogeography, including range variations in response to Quaternary environmental changes and island colonisations.

Toward an integration of animal personality and biogeographic research

From a historical biogeographic perspective, dispersal events of special interest are diffusion and long-distance dispersal, due to their immediate link to contiguous range

expansions and colonisations [22,24]. Recent technological progress has allowed extensive documentation of genetic and biogeochemical imprints of these long-controversial events [19,22,34], and deep reappraisal of their role in the shaping of biogeographic patterns. In fact, diffusion and long-distance dispersal were once considered as rare, somewhat incidental (particularly long-distance dispersal), and as the outcome of interactions between an organism's unconditional dispersal capabilities and rare historical events (e.g. geological, climatic, ecological). Instead, due to recent advances, they are now best depicted as the (rare, successful) outcome of the complex, conditional, continuous, and ubiquitous dispersal process [31,33]. Since Dobzhansky and Wright's [35] landmark research on *Drosophila* flies, there is now compelling evidence that individuals dispersing 'extremely' long distances are widespread in animal populations, albeit often at very low frequency [9]. Therefore, long-distance and non-random dispersal appear integral rather than incidental in animal populations. Further, their underlying mechanisms need to be fully disclosed for a thorough understanding of the processes ultimately leading to the geographic patterns of biological diversity and their changes over time.

Evidence of behavioural polymorphism-dependent dispersal, its interactions with density -dependent and -independent processes, and its contribution to the dynamic spatial structure of populations, clearly invites an integration of the behavioural polymorphism into the historical biogeographic research agenda. Nevertheless, merging inputs from two such apparently disparate fields is undoubtedly challenging. However, we believe that efforts in this direction should focus on: 1) exploiting the whole range of opportunities opened by genomics to explore behavioural polymorphisms in space and time, and 2) investigating and integrating empirical evidence of personality-dependent

dispersal, both across multiple spatial and temporal scales. Although still scant, research contributions are now emerging along these avenues.

A number of excellent reviews and perspectives have been published addressing the potential opportunities genomic approaches provide to the study of both biogeography and the genetic architecture of complex traits, including animal personality [36-42]. Here we emphasize that these approaches can promote the integration of animal personality research into the study of the mechanisms underlying organism distribution. Indeed, using genomic approaches, three fundamental and previously hardly accessible steps toward this integration can be addressed: i) unveiling the genetic architecture of animal personality, ii) studying the geographic variation of genetic diversity at genes that are associated with behavioural polymorphism, and the contribution of various types of selection to this variation, and iii) investigating how biotic and abiotic environmental features modulate their expression patterns. The diversity and flexibility of genomic techniques (e.g. in terms of number of individuals and genes analysed) allow scaling for each experimental phase based on features of the study organism, the specific research questions, and (to some extent) the analytical resources of each lab. Noteworthy, in addition to continuous improvements of genomics technologies, bioinformatics tools for population genomics, phylogenomics, and (comparative) phylogeographic analysis methods are also improving [41-46], allowing researchers to go deeper into the study of non-neutral genetic variation and its role in driving spatial and temporal patterns of diversity.

Our emphasis here on genomic approaches is mostly based on the huge opportunities offered by this rapidly developing research area at increasingly accessible costs.

Nonetheless, it is worth mentioning that other potentially useful approaches, assuming the ‘phenotypic gambit’, have received support by major achievements in the study of heritability of personality traits [36,37,47]. Heritability is a key issue when studying the evolutionary dynamics of personality, and recent studies show that a substantive portion of personality variation is heritable [36,37,47]. These findings give general support for the phenotypic gambit [37], and indicate that ‘first-line’ insights concerning evolutionary dynamics can also be drawn from phenotypic estimates (but see [39]).

In Box 1, we present two case studies showing the implication of the behavioural polymorphism in shaping biogeographic patterns through behavioural polymorphism-dependent dispersal. In these examples, either by analysing geographic patterns of genetic variation, or by (implicitly) assuming the phenotypic gambit, the authors showed that novelty-seeking behavioural traits (including boldness, exploration, risk taking, and reactivity to novel stressors) were implicated in a recent island colonisation by the common frog *Rana temporaria*, and in the range expansion of our own species out-of-Africa.

A crucial point in these dynamics is that not all individuals within a population successfully pass through the stages of an expansion/colonisation process. Since only a subset of individuals manages to overcome any stage successfully, these processes could constitute a ‘selective filter’ on behavioural polymorphisms [14]. So, historical demographic processes not only could have been affected by behavioural polymorphism, but also the genetic and phenotypic individual composition of the populations could have as well. Support for this scenario also comes from the non-random spatial distribution of personality traits across the range of expanding

populations. For example, among house sparrow populations in Kenya, a greater propensity toward exploration and neophilia was found at the expanding range edge [48,49]. Moreover, theoretical models including spatial selection, spatial sorting, and analysing the dynamics of both equilibrium and non-equilibrium populations of an expanding lineage, predict non-random spatial distributions of traits favouring dispersal abilities (including personality traits), and suggest that their (genetic) imprints might persist long after the completion of a range expansion process [50-52]. Interestingly, growing evidence from the study of successful invaders support these predictions, as nicely exemplified by the case of the cane toad *Rhinella marina* in Australia [see 53,54 and references therein].

From this picture, the hypothesis of a ‘dispersal prone personality’ might be generated, with more active explorers, bold, and less social individuals appearing as those with a higher propensity to disperse, to disperse longer, and therefore with a higher probability to contribute to range expansions (or other forms of long-distance movement [55]; see Table 1) and to the personality make-up of newly established populations. Noteworthy, if ‘founders’ were such a non-random behavioural sample of the source population, behavioural polymorphisms would have played a role even in some putatively neutral and density-dependent processes generating and sustaining uneven patterns of geographic distribution of genetic diversity within species, such as progressive founder events at the leading front of post-glacial range expansions, (sequential) island colonisations, and high-density blocking [29].

However, in several situations the influences of the behavioural polymorphism on the spatial population structure and dynamics that ultimately primed large-scale range

changes might have been significantly more complex than predicted by this scenario. For example, some personality traits can be advantageous during some but not all of the phases of an expansion process. This point is vividly exemplified by long-term studies of the western bluebird [27,56]. In this species, high aggression is coupled with a high dispersal tendency allowing for colonisation waves of new habitats and displacements of its native competitor, the mountain bluebird. However, colonisation waves need to introduce a range of behavioural traits to allow actual population increase in new areas over time. The occurrence of successive dispersal waves of individuals with different personality types has also been suggested by studies of invasive species [11]. In addition, to explain the success of many invasions (departure and transience are often assisted phases, which potentially relax their link to individual phenotypes; but see [14,57]), it has been proposed that successful invaders have high levels of behavioural polymorphism within the invasion pool, which allow for both the establishment and reinforcement of new populations in subsequent phases [13].

Bridging the perspectives, methods, and results of two traditionally disparate research fields of biogeography and behavioural biology will be challenging in many respects, but we anticipate that new insights and testable hypotheses will emerge. In Box 2, we attempt to exemplify this by looking at the mitochondrial genome (which is iconic to phylogeographic investigation) through both biogeographic and behavioural points of view, and exploring a potential implication of such a ‘contamination’.

Concluding remarks

Trait-based approaches allowing a direct link between ecological and evolutionary

processes with biogeographic patterns have proven powerful to ‘opening the black-box of biogeographic processes’ [58]. However, previous research has focused mostly on morphological characters. Here, we have considered how behavioural traits (which might also influence morphological trait changes [6]) are involved in the processes promoting range variation over time, since these processes have direct and outstanding importance for historical biogeographic research. Previous reviews [e.g. 5,59] suggested a number of different ecological and evolutionary implications of the behavioural polymorphism, affecting life history, disease dynamics, social evolution, evolvability, speciation, species interactions, community structure, and ecosystem processes, each potentially affecting biogeographic patterns. Importantly, robust hypothesis testing, hampered until recently by the lack of suitable methods, is becoming increasingly affordable.

While we rooted our arguments on the opportunities opened by genomic approaches in the study of heritability, the genetic architecture of animal personality, and their spatial and temporal variation, it is worth noting that advances in several other fields will likely prove essential in building and testing hypotheses. Bio-logging technologies, for example, are revolutionizing the study of ecology, physiology, and behaviour of wild animal populations (including cryptic and wide-ranging species), which allow researchers to develop and test entirely new theories in these fields [60]. A careful integration of personality research methods, bio-logging technologies and genomic approaches, could plausibly provide the utmost power of resolution in a wide range of spatial and temporal scales, along the ecological-evolutionary continuum. These integrations will prove essential to move steps forward (Box 3) toward the effective bridging of the behavioural and biogeographic sciences, that we aimed to

promote here.

Acknowledgement We are grateful to Paul Craze, Dave Jenkins and Kees van Oers for their very helpful and constructive comments on earlier versions of this manuscript. We thank Kelsey Horvath and Editage for their English revisions. RB was supported by a post-doctoral grant from the Italian Ministry of Education, University and Research (PRIN project 2012FRHYRA). CC is supported by the European Commission (H2020-MSCA-IF-2014-659106).

References

1. Waddington, C.H. (1959) Evolutionary systems – animal and human. *Nature* 183, 1634-1638
2. Wyles, J.S. *et al.* (1983) Birds, behavior and anatomical evolution. *Proc. Natl. Acad. Sci. USA* 80, 4394-4397
3. Bateson, P. (1988) The active role of behaviour in evolution. In *Process and metaphors in evolution* (Ho, M. W. and Fox, S. eds), pp. 191-207, Wiley
4. Carere, C. and Maestripieri, D. eds. (2013) *Animal personalities. Behavior, physiology, and evolution*, The University of Chicago Press
5. Wolf, M. and Weissing, F.J. (2012) Animal personalities: consequences for ecology and evolution. *Trends Ecol. Evol.* 27, 452-461
6. Zuk, M. *et al.* (2014) The role of behaviour in the establishment of novel traits. *Anim. Behav.* 92, 333-344
7. Pruitt, J.N. and Modlmeier, A.P. (2015) Animal personality in a foundation species drives community divergence and collapse in the wild. *J. Anim. Ecol.* 84,

248 1461-1468

249 8. Réale, D. *et al.* (2007) Integrating animal temperament within ecology and
 250 evolution. *Biol. Rev.* 82, 291-318

251 9. Fraser, D.F. *et al.* (2001) Explaining leptokurtic movement distributions:
 252 intrapopulation variation in boldness and exploration. *Am. Nat.* 158, 124-135

253 10. Dingemanse, N.J. *et al.* (2003) Natal dispersal and personalities in great tits
 254 (*Parus major*). *Proc. Roy. Soc. B* 270, 741-747

255 11. Cote, J. *et al.* (2010) Personality traits and dispersal tendency in the invasive
 256 mosquitofish (*Gambusia affinis*). *Proc. Roy. Soc. B* 277, 1571-1579

257 12. Cote, J. *et al.* (2014) Personality traits and spatial ecology in non-human
 258 animals. In *Geographical Psychology* (Rentfrow, P.J. ed), pp. 89-112,
 259 Washington, DC: American Psychological Association

260 13. Fogarty, S. *et al.* (2011) Social personality polymorphism and the spread of
 261 invasive species: a model. *Am. Nat.* 177, 273-287

262 14. Chapple, D.G. *et al.* (2012) Can behavioral and personality traits influence the
 263 success of unintentional species introductions? *Trends Ecol. Evol.* 27, 57-64

264 15. Sih, A. *et al.* (2012) Ecological implications of behavioural syndromes. *Ecol.*
 265 *Lett.* 15, 278-289

266 16. van Oortmerssen, G.A. and Busser, J. (1989) Studies in wild house mice 3:
 267 disruptive selection on aggression as a possible force in evolution. In *House*
 268 *mice aggression: a model for understanding the evolution of social behaviour*
 269 (Brain P.F. *et al.* eds), pp. 87-118, Harwood Academic Publishers

270 17. Donoghue, M.J. and Moore, B.R. (2003) Toward an integrative historical
 271 biogeography. *Integr. Comp. Biol.* 43, 261-270

18. Avise, J.C. *et al.* (1987) Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. *Ann. Rev. Ecol. Syst.* 18, 489–522
19. Riddle, B.R. *et al.* (2008) The role of molecular genetics in sculpting the future of integrative biogeography. *Prog. Phys. Geog.* 32, 173–202
20. Wiens, J.J. and Donoghue, M.J. (2004) Historical biogeography, ecology and species richness. *Trends Ecol. Evol.* 19, 639–644
21. Ricklefs, R.E. and Jenkins, D.G. (2011) Biogeography and ecology: towards the integration of two disciplines. *Phil. Trans. Roy. Soc. B* 366, 2438–2448
22. Lomolino, M.V. *et al.* (2010) *Biogeography Fourth edition*, Sinauer Associates Inc
23. Clobert, J. *et al.* (2012) *Dispersal ecology and evolution*, Oxford Univ. Press
24. Wilkinson, D.M. (2011) Dispersal: biogeography. In: *eLS*. John Wiley & Sons, Ltd: Chichester. DOI: 10.1002/9780470015902.a0003237.pub2
25. Bowler, D.E. and Benton, T.G. (2005) Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biol. Rev.* 80, 205–225
26. Pocock, M.J.O. *et al.* (2005) Dispersal in house mice. *Biol. J. Linnean. Soc.* 84, 565–583
27. Duckworth, R.A. (2008) Adaptive dispersal strategies and the dynamics of range expansion. *Am. Nat.* 172, S4–S17
28. Hewitt, G.M. (2000) The genetic legacy of the Quaternary ice ages. *Nature* 405, 907–913

29. Waters, J.M. *et al.* (2013) Founder takes all: density-dependent processes structure biodiversity. *Trends Ecol. Evol.* 28, 78–85
30. Prugnolle, F. and De Meeûs, T. (2002) Inferring sex-biased dispersal from population genetic tools: a review. *Heredity* 88, 161-165
31. Edelaar, P. and Bolnick, D. I. (2012) Non-random gene flow: an underappreciated force in evolution and ecology. *Trends Ecol. Evol.* 27, 659–665
32. Cote J., *et al.* (2010) Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Phil. Trans. Roy. Soc. B* 365, 4065-4076
33. Lowe, W.H. and McPeck, M.A. (2014) Is dispersal neutral? *Trends Ecol. Evol.* 29, 444–450
34. Waters, J.M. *et al.* (2013) Biogeography off the tracks. *Syst. Biol.* 62, 494-498
35. Dobzhansky, T. and Wright, S. (1943) Genetics of natural populations. X. Dispersion rates in *Drosophila pseudoobscura*. *Genetics* 28, 304–340
36. van Oers, K. and Sinn, D. L. (2013) Quantitative and molecular genetics of animal personality. In *Animal Personalities. Behavior, Physiology, and Evolution* (Carere, C. and Maestripieri, D. eds.), pp. 149-200, The University of Chicago Press
37. van Oers, K. and Sinn, D. L. (2011) Toward a basis for the phenotypic gambit: advances in the evolutionary genetics of animal personality. In *From genes to animal behavior, primatology monographs*. (Inoue-Murayama, M. *et al.* eds), pp. 165–183, Springer

38. van Oers, K. and Mueller, J.C. (2010) Evolutionary genomics of animal personality. *Phil. Trans. Roy. Soc. B* 365, 3991–4000
39. Rittschof, C.C. and Robinson, G.E. (2014) Genomics: moving behavioural ecology beyond the phenotypic gambit. *Anim. Behav.* 92, 263–270
40. Rocha, L.A. *et al.* (2013) Massively parallel DNA sequencing: the new frontier in biogeography. *Front. Biogeogr.* 5, 67–77
41. McCormack, J.E. *et al.* (2013) Applications of next-generation sequencing to phylogeography and phylogenetics. *Mol. Phylogenetic. Evolut.* 66, 526–538
42. Jensen, H. *et al.* (2014) Molecular quantitative genetics. In *Quantitative genetics in the wild* (Charmantier, A. *et al.* eds), pp. 209–227, Oxford University Press
43. Ellegren, H. (2014) Genome sequencing and population genomics in non-model organisms. *Trends Ecol. Evol.* 29, 51–63
44. Pompanon, F. and Bonin, A., eds (2012) *Data production and analysis in population genomics: methods and protocols*, Humana Press
45. Goolsby, E.W. (2015) Phylogenetic comparative methods for evaluating the evolutionary history of function-valued traits. *Syst. Biol.* 64, 568–578
46. Lemmon, E. M. and Lemmon, A. R. (2013) High-Throughput genomic data in systematics and phylogenetics. *Annu. Rev. Ecol. Evol. Syst.* 44, 99–121
47. Dochtermann, N.A. *et al.* (2015) The contribution of additive genetic variation to personality variation: heritability of personality. *Proc. R. Soc. B* 282, 2014–2201
48. Liebl, A.L. and Martin, L. B. (2014) Living on the edge: range edge birds consume novel foods sooner than established ones. *Behav. Ecol.* 25, 1089–1096

49. Liebl, A.L. and Martin, L.B. (2012) Exploratory behaviour and stressor hyperresponsiveness facilitate range expansion of an introduced songbird. *Proc. R. Soc. B*, 279, 4375–4381
50. Phillips, B.L. *et al.* (2010) Life-history evolution in range-shifting populations. *Ecology* 91, 1617–1627
51. Shine, R. *et al.* (2011) An evolutionary process that assembles phenotypes through space rather than through time. *Proc. Natl. Acad. Sci. USA* 108, 5708–5711
52. Cobben, M.M.P. *et al.* (2015) Spatial sorting and range shifts: consequences for evolutionary potential and genetic signature of a dispersal trait. *J. Theor. Biol.* 373, 92–99
53. Lindström, T. *et al.* (2013) Rapid shifts in dispersal behavior on an expanding range edge. *Proc. Natl. Acad. Sci. USA* 110, 13452–13456
54. Brown, G.P. *et al.* (2014) The straight and narrow path: the evolution of straight-line dispersal at a cane toad invasion front. *Proc. R. Soc. B* 281, 20141385
55. Liedvogel, M. *et al.* (2011) The genetics of migration on the move. *Trends Ecol. Evol.* 26, 561–569
56. Duckworth, R.A. and Badyaev, A.V. (2007) Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. *Proc. Natl. Acad. Sci. USA* 104, 15017–15022
57. Carrete, M. *et al.* (2012) Don't neglect pre-establishment individual selection in deliberate introductions. *Trends Ecol. Evol.* 27, 67–68
58. Dawson, M.N. *et al.* (2013) An horizon scan of biogeography. *Front Biogeogr.* 5, 130–157

59. Ingley, S.J. and Johnson, J.B. (2014) Animal personality as a driver of reproductive isolation. *Trends Ecol. Evol.* 29, 369-371
60. Wilmers, C.C. *et al.* (2015) The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. *Ecology* 96, 1741-1753
61. Bonte, D. *et al.* (2012) Costs of dispersal. *Biol. Rev.* 87, 290-312
62. Brodin, T. *et al.* (2013) Personality trait differences between mainland and island populations in the common frog (*Rana temporaria*). *Behav. Ecol. Sociobiol.* 67, 135-143
63. Coyne, S.P. *et al.* (2015) Dopamine D4 receptor genotype variation in free-ranging rhesus macaques and its association with juvenile behavior. *Behav. Brain Res.* 292, 50-55
64. Mueller, J.C. *et al.* (2014) Behaviour-related *DRD4* polymorphisms in invasive bird populations. *Mol. Ecol.* 23, 2876–2885
65. Chen, C. *et al.* (1999) Population migration and the variation of dopamine D4 receptor (*DRD4*) allele frequencies around the globe. *Evol. Hum. Behav.* 20, 309–324
66. Matthews, L.J. and Butler, P.M. (2011) Novelty-seeking *DRD4* polymorphisms are associated with human migration distance out-of-Africa after controlling for neutral population gene structure. *Am. J. Phys. Anthropol.* 145, 382-389
67. Toews, D.P.L. and Brelsford, A. (2012) The biogeography of mitochondrial and nuclear discordance in animals. *Mol. Ecol.* 21, 3907-3930
68. Currat, M. *et al.* (2008) The hidden side of invasions: massive introgression by local genes. *Evolution* 62, 1908–1920

69. Løvlie, H. *et al.* (2014) The influence of mitonuclear genetic variation on personality in seed beetles. *Proc. R. Soc. B* 281, 20141039.
70. Šichová, K. *et al.* (2014) On personality, energy metabolism and mtDNA introgression in bank voles. *Anim. Behav.* 92, 229–237
71. Krackow, S. (2003) Motivational and heritable determinants of dispersal latency in wild male house mice (*Mus musculus musculus*). *Ethology* 109, 671–689
72. Edelsparre, A.H. *et al.* (2014) Alleles underlying larval foraging behaviour influence adult dispersal in nature. *Ecol. Lett.* 17, 333–339
73. O’Riain, M.J. *et al.* (1996) A dispersive morph in the naked mole-rat. *Nature* 380, 619–621
74. Cote, J. *et al.* (2013) Personality-dependent dispersal cancelled under predation risk. *Proc. Roy. Soc. B* 280, 2013–2349
75. Howell, S. *et al.* (2007) Serotonergic influences on life-history outcomes in free-ranging male rhesus macaques. *Am. J. Primat.* 69, 851–865
76. Dingemanse, N.J. and de Goede, P. (2004) The relationship between dominance and exploratory behaviour is context-dependent in wild great tits. *Behav. Ecol.* 15, 1023–1030
77. Blumstein, D.T. *et al.* (2009) A test of the social cohesion hypothesis: interactive female marmots remain at home. *Proc. Roy. Soc. B* 276, 3007–3012
78. Cote, J. and Clobert, J. (2007) Social personalities influence natal dispersal in a lizard. *Proc. R. Soc. Lond. B Biol. Sci.* 274, 383–390
79. Cote, J. *et al.* (2011) Personality-dependent dispersal in the invasive mosquitofish: group composition matters. *Proc. Roy. Soc. B* 278, 1670–1678

Figure legends

Box 1. Figure I (A) Mean personality trait values in tadpoles and froglets of the common frog from island populations in Sweden compared to source populations from the mainland (modified from [62]). Boldness was measured as the difference between maximum time (s) allowed to exit a refuge, and the latency time; exploration tendency was measured as the amount of area explored in a given time after exiting the refuge. Error bars denote standard errors. (B) Relationship between the summed frequency of high NS alleles at the DRD4 exon3 in human populations, and migration distance out-of-Africa, after controlling for population structure (modified from [66]).

Box 2. Figure I A schematic representation of the hypothesis put forward in this box. For simplicity, potentially interacting processes are ignored.

BOX 1. Animal personality and historical biogeographic patterns

Evidence is emerging (albeit still in short supply), that animal personality could influence several biogeographic patterns through their effect on the dispersal process (Table 1), including island colonisations and Pleistocene range expansions.

Island colonisations. Although there are many potential benefits to successfully colonising new habitats, dispersal also carries a variety of costs and a high risk of failure for individuals [61]. Accordingly, dispersal propensity (and distance covered) has often been linked to personality traits favouring ‘risk taking’, such as boldness and more exploratory behaviour [9]. In a recent study [62], these personality traits have been compared between island and neighbouring mainland populations of the common frog *Rana temporaria* in Sweden. Tadpoles and froglets (i.e. the more dispersing life-stages) from insular populations were consistently bolder and more exploratory (Figure IA). The authors explored alternative explanations for this pattern, such as effect of other potential factors (e.g. different predator environments), and they concluded that colonisers were not a random sample of the founder population, but a subset of the founder population that was bolder and more exploratory than the average random frog.

Pleistocene range expansions. Once we understand the genetic underpinnings of personality traits, the study of geographic variation at the underlying genes can provide insights into the implication of these traits during the formation of biogeographic patterns. In the human population, there is a well-established correlation between

polymorphisms at the dopamine receptor D4 (DRD4), levels of neuronal reactivity, and personality traits related to novelty seeking (NS), which include boldness and exploratory behaviour. Notably, this correlation is also emerging from studies in other species (e.g. [63,64]). Studies [65,66] have demonstrated a substantial correlation between the frequency of alleles linked to high NS and the dispersal distance ‘out-of-Africa’ in humans (Figure IB), by analysing the pattern of geographic variation at the DRD4 gene. This event was the major range expansion of our species, which occurred since the Late Pleistocene (~100 000 years ago onward). Importantly, these studies show that the correlation could not be accounted for by neutral genetic processes alone (i.e. genetic drift and admixture), which implies natural selection for high NS during the expansion of populations toward new habitats. As with the above-mentioned study on the common frog, these analyses revealed that migrant individuals were not a random sample of the founder population.

BOX 2. Range expansions, mitonuclear biogeographic discordances, and behavioural polymorphisms

Here we hypothesise that behavioural polymorphism is a factor in the massive introgression of the mitochondrial genome (hereafter mtDNA) from a resident into an expanding species or intraspecific lineage, which is a commonly observed and extensively discussed pattern of nuclear-mitochondrial biogeographic discordance [67].

Geographic pattern and its putative causes

Range expansions can occur toward areas that are either empty from- or already occupied by- a related species or lineage. In the latter case, hybridisation and introgression can follow secondary contact. In this situation, mtDNA introgression has often been observed as strongly asymmetrical, both in quantitative terms (i.e. massive), and in its geographic extent. Moreover, reviews of evidence and spatially explicit simulations indicate that introgression most frequently proceeds from the resident towards the expanding lineage [68].

Several explanations of this pattern have been proposed [67] that encompass sex-biased asymmetries in mating likelihood or offspring production, *Wolbachia* infection in insects, hybrid zone movements, and most frequently adaptive introgression and demographic disparities between the interacting lineages.

mtDNA and animal personality

Recent evidence indicates that mtDNA (especially via mitonuclear epistatic interactions) can affect personality traits such as activity, boldness, and exploration behaviour, which in turn have been linked to dispersal propensity. This has been shown

experimentally, either by manipulating mitonuclear introgression lines in seed beetles [69], or by analysing the personality and physiological differences between pure and introgressed wild-caught individuals of the bank vole from Finland [70].

Potential contribution of personality differences between colonisers and residents

As discussed in the main text, personality (and other) traits favouring dispersal often increase in frequency during a range expansion. When the range expansion stops, and secondary contact occurs, low dispersal genotypes are recruited mostly through (slow) gene flow from the rear [52]. On the other hand, the resident lineage (i.e. not expanding), might harbour both low and high dispersal genotypes. Introgression of low dispersal genotypes (or of genotypes promoting low dispersal phenotypes when in the new nuclear background) from the residents could favour a faster return to equilibrium dispersal rate values among colonisers. Since mtDNA can contribute to personality variation in traits which affect dispersal propensity, we hypothesise that it might contribute to the adaptive landscapes promoting asymmetric introgression patterns between residents and colonisers. The process hypothesised here could interact with other processes (e.g. [68]; i.e. it is not posed as an alternative hypothesis), and it could affect other genomic regions linked to personality trait variation. Interestingly, it could be experimentally tested by using, for example, designs already adopted in studies linking mtDNA and personality variation [69,70].

GLOSSARY

Animal personality: behavioural differences consistent between conspecific individuals across time and context. Statistically, animal personality is the repeatable, non-zero between-individual variance of behaviour.

Behavioural polymorphism: the occurrence of more than one behavioural phenotype within a population.

Bio-logging: the use of miniaturised electronic tags attached to free-ranging animals, that record or remotely relay data about an animal's behaviour, physiology, and environment.

Density-dependent processes: a heterogeneous set of processes that are regulated by demographic density of a population. They include, but are not limited to, Allele effect, competition, predation and, in behavioural ecology, foraging and socio-sexual behaviours. Personality traits influencing exploratory behaviour and dispersal have been frequently observed to be at least partly density-dependent.

Dispersal: the permanent movement of individuals from a natal to a novel habitat, including three steps: departure, transience, and settlement. Dispersal and migration are distinct movement patterns, the latter indicating directional and often cyclical movements between two locations (e.g. a foraging and a breeding area). The two terms, however, are often used interchangeably in evolutionary literature under the meaning of dispersal (e.g. migration out-of-Africa).

Genomics: the study of content, structure, function, and evolution of genomes, by using molecular biology technologies and bioinformatics analytical tools.

525 **Heritability:** the amount of phenotypic variation explained by additive genetic variance
526 (so-called 'narrow-sense' heritability).

527 **Novelty seeking:** an individual's tendency to explore unfamiliar stimuli and
528 environments.

529 **Phenotypic gambit:** the idea that the phenotypic structure of personality reflects its
530 genetic structure, and that details of this genetic structure do not influence the evolution
531 of behaviour substantially.

532

533 **Table 1. Behavioural categories subject to polymorphisms and their predicted**
534 **effects on the dispersal process^{a,b}**

Behavioural categories	Predicted effect		Ref.
	Departure	Transience-Settlement	
<u>Exploration</u> : propensity to explore novel, unfamiliar environments. Assessed by latency to explore, time duration, and activity level in a novel area.	High explorers have a higher propensity to depart.	High explorers have higher transience success and disperse farther. Propensity to explore influences transience/settlement decision. If exploration is positively coupled with aggressiveness, this can help outcompete competitors in the initial settlement phase.	[9,10,32,56,71]
<u>Activity</u> : an individual's level of activity in a familiar environment. Assessed by measuring time spent in locomotion (e.g. walking, hopping, swimming).	More active individuals have a higher propensity to depart.	More active individuals tend to disperse farther.	[72,73]
<u>Boldness</u> : an individual's response towards a risky situation. Assessed e.g. by measuring latency to exit a shelter upon a risky situation (e.g. by simulating predation risk).	Bolder individuals are more likely to depart. This can depend on the degree of perceived risk (e.g. by predation).	Bolder individuals tend to disperse farther.	[9,74]
<u>Aggressiveness</u> : the propensity for aggression towards another individual. Assessed by latency to attack, attack frequency, and time spent in agonistic interactions.	Aggressiveness influences a departure decision, but the relation is hardly predictable owing to contrasting evidence. Usually aggressiveness is positively related to exploration. More aggressive individuals are more likely to depart. (but also) - Less aggressive (e.g. subordinate) individuals are forced to disperse.	High aggressiveness helps to cope with competitors in transient and novel areas, but can become costly as intraspecific density increases.	[8,16, 56,75,76]
<u>Sociability</u> : an individual's non-aggressive response to conspecifics. Assessed by measuring active search/avoidance of conspecifics (or their cues) and social exploration.	More social individuals tend to depart when at low densities. Less social individuals tend to depart at high densities.	Less social individuals tend to disperse at greater distances. Less social individuals cope better with initial low population density. More social individuals cope better at increasing population density.	[73,77-79]

535 ^aSee [8], Fig. 2, for a flow diagram representing possible links between behavioural categories. Syndromes (suites
536 of correlated behaviours) could enhance the overall dispersal success across multiple steps (see main text).

537 ^b Social systems of populations (e.g. eusociality, cooperative breeding) might modify predicted effects, although
538 the study of personality in relation to social systems is still in its infancy.

BOX 3. Outstanding Questions

- What are the genetic and non-genetic underpinnings of personality variation within and among wildlife populations? Despite insightful research with model organisms, there is little data on wild populations. Future research in this area will allow for robust applications of comparative and candidate gene approaches for an increasing number of species, further boosting our comprehensive knowledge.
- How widespread are non-random distribution patterns of behavioural polymorphism and their genetic underpinnings across taxa and geographical contexts? What is the relative contribution of selection, spatial sorting, and stochasticity in driving their formation?
- To what extent do personality-dependent dispersal processes contribute to shaping (meta)population genetic structure? To what extent do they scale up from local to range-wide patterns of non-random variation?
- Does the range distribution of boldness, exploration, and other personality traits co-vary with morphological and physiological traits affecting the range?
- How temporally persistent are the genetic signatures of personality-dependent dispersal processes in structured and non-structured populations?
- How does behavioural polymorphism affect the colonisation-competition tradeoff?
- How do personality traits of colonisers influence the assembly and structure of biological communities in novel habitats?



