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Evolutionary biology

Wormholes record species history in space and time

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Genetic and fossil data often lack the spatial and temporal precision for tracing the recent biogeographic history of species. Data with finer resolution are needed for studying distributional changes during modern human history. Here, I show that printed wormholes in rare books and artwork are trace fossils of wood-boring species with unusually accurate locations and dates. Analyses of wormholes printed in western Europe since the fifteenth century document the detailed biogeographic history of two putative species of invasive wood-boring beetles. Their distributions now overlap broadly, as an outcome of twentieth century globalization. However, the wormhole record revealed, unexpectedly, that their original ranges were contiguous and formed a stable line across central Europe, apparently a result of competition. Extension of the wormhole record, globally, will probably reveal other species and evolutionary insights. These data also provide evidence for historians in determining the place of origin or movement of a woodblock, book, document or art print.

1. Introduction

Printed wormholes in woodblock prints (woodcuts) have recorded the activity of wood-boring insects for centuries, long before species were described and museum collections were assembled, and are an untapped source for studying distributional changes through time. The woodcut was the primary form of book illustration between the early fifteenth and early nineteenth centuries because carved woodblocks have raised relief, such as metal type, and could be integrated easily in the hand-operated book printing press [1]. During this period, at least seven million different books (different titles) were produced [2], with a large fraction containing woodcuts, and many with printed wormholes. There were also separately issued woodcuts, as in maps and art prints. Altogether, millions of different woodcuts have been printed over the centuries, providing a rich source of data for the wormhole record.

In Europe, the tree species most commonly used by blockcutters were box, pear and apple [3]. Their wood is fine-grained, even-textured and small-pored, which provided a smooth surface for cutting. For economic reasons, blocks were typically carved shortly before their use and were retained if future editions of a book were planned, even if slightly damaged by cracks and wormholes. Damage occurring on the raised relief, unless extensive, was printed and appeared as white, uninked areas (figure 1). Rarely, historians have used the number of printed wormholes to determine the order of editions [4], but otherwise have not studied them.

2. Material and methods

European woodcuts were examined for the presence of printed wormholes. An effort was made to sample broadly, both geographically and temporally (see the electronic supplementary material). Printed wormholes were rare (less than 1%) in first edition woodcuts but were common in later editions and in popular literature where illustrations were frequently reprinted (e.g. Dutch *centsprenten*, English *chapbooks*, French *bilbliotheque bleue* and *imagerie populaire*, German *volksbücher*, Italian *stampe popolari* and Spanish *pliegos sueltos*). Measurements (±0.01 mm) were made on original prints, reproductions and digital images

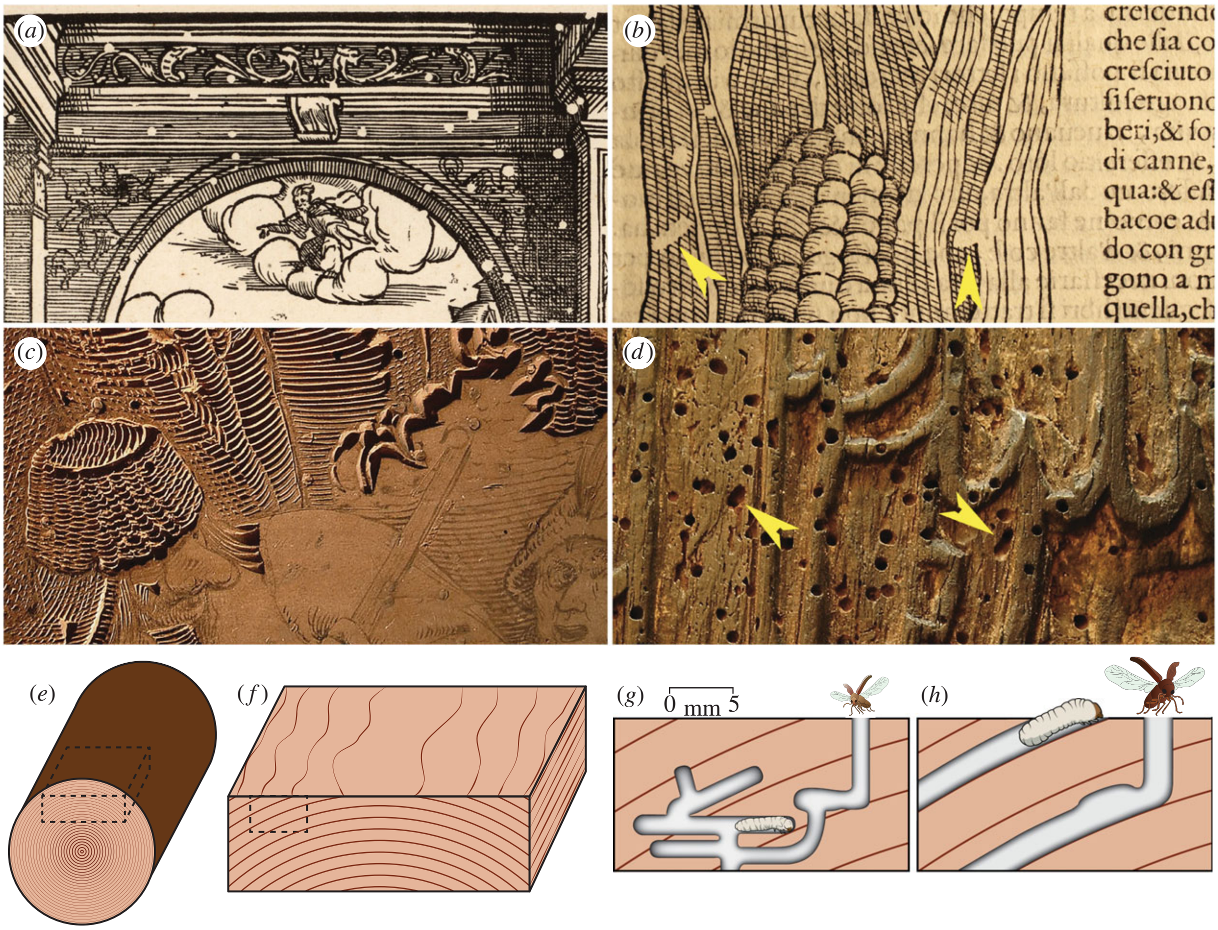

Figure 1. Details of European prints (*a*, northern; *b*, southern) showing printed wormholes, and woodblocks (*c*, northern; *d*, southern) showing actual wormholes (scale, 1 : 1). (*a*) Netherlandish woodcut art print *de Rijke Man* (1541) by Anthoniszoon (Rijksmuseum). (*b*) Italian woodcut (1606) by Ramusio (Library of Congress). (*c*) Netherlandish woodblock *The wedding of Mopsus and Nisa* (1566) by Bruegel (Metropolitan Museum of Art). (*d*) *Bois Protat* (1370–1380) from Saône-et-Loire, France (Bibliothèque national de France). Yellow arrows indicate wormhole tracks. Diagrams showing (*e*) position of typical woodblock (110 mm wide) in log from hardwood tree, (*f*) cross section showing grain, and the position of tunnels produced by (*g*) northern and (*h*) southern woodborers. The wood-boring larvae are shown in tunnels, and adults are shown emerging from flight holes (wormholes) following pupation.

(adjusted for scale). Surviving woodblocks in museums, and the prints themselves, often have real wormholes but they were not used because the dates and locations of those wormholes are usually poorly constrained. For later editions, the date recorded for a printed wormhole was a range between that edition and the first edition (if known). When reproductions or digital images of woodcuts were used, care was taken to distinguish and avoid wormholes in the original paper, evidenced by the presence of a hole at the corresponding location on the reverse side (e.g. previous or next page of a book), a tonal difference in the hole compared with the surrounding uninked area of the print, or a white hole in an otherwise uninked but coloured portion of the print. Images of different impressions of the same print were sometimes available and this provided additional evidence. Later editions of prints were used if they were printed in the same city as the first edition. The likely species responsible for the wormholes were identified by hole size and shape, wood preference and species habits (see the electronic supplementary material).

3. Results

Two different sizes of printed wormholes were observed (figure 1*a*,*b*). Actual wormholes (undated) in surviving woodblocks (figure 1*c*,*d*) also fell into two size classes. The round holes are characteristic 'exit holes' of beetles, made when adults emerge from pupation and leave the wood to reproduce and die during a short interval (one or a few weeks), whereas tracks (wormhole lines) in the southern prints and blocks were possibly caused by larvae following the grain (figure 1*e*–*h*; see the electronic supplementary material). The widths of 3263 printed wormholes and lengths of 318 tracks were measured in 473 woodcuts spanning five centuries, 1462–1899 (figure 2*a*). In woodcuts from northern cities, holes were small and round, averaging 1.43 mm in width (0.9–2.2 mm, range; $n = 2072$), although one wormhole from London was a track, 1.43×3.35 mm. By contrast, woodcuts from southern cities had larger, round, holes averaging 2.30 mm (0.93–4.7 mm; $n = 1191$) and, on the same woodcuts, 2–22 mm tracks (average, 6.2 mm in length) of similar width, often meandering, and averaging 2.44 mm in width (1.3–4.0 mm; $n = 317$). Seventeen per cent of the southern printed wormholes were tracks. The 95% CI of the mean (± 2 s.e.) for the northern wormholes was 1.41–1.44 mm, and for the southern wormholes (mean = 2.33; $n = 1508$) it was 2.31–2.35 mm. The 95% population interval (± 2 s.d.) for the northern wormholes was 0.85–2 mm, and for the southern wormholes it was 1.41–3.25 mm. Average wormhole diameter showed consistency within each of the two geographical regions (figure 2*a*) suggesting that each corresponded to the distribution of a single species. Old, plugged wormholes ($n = 515$) were measured in one unusually well-preserved sixteenth century

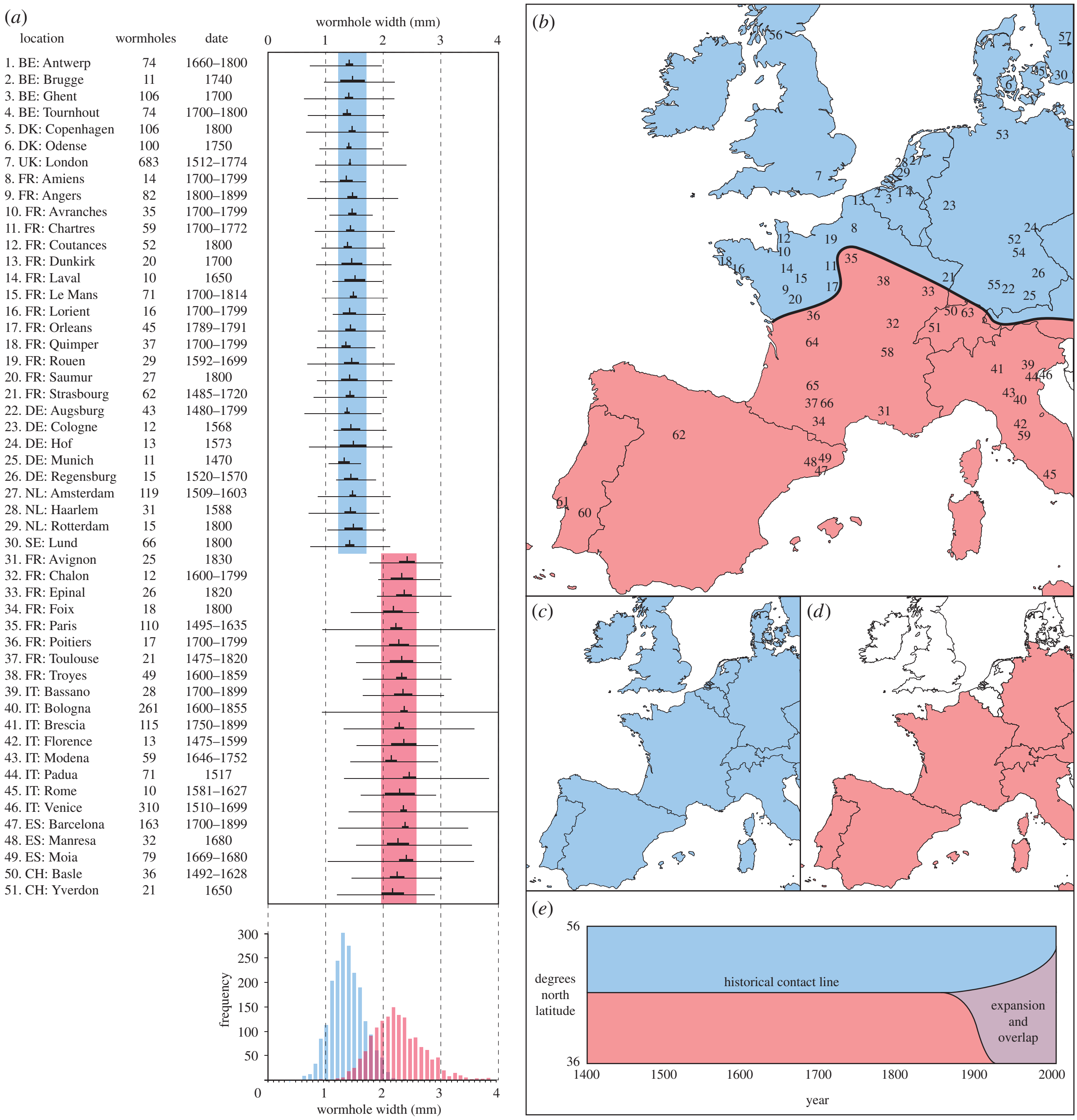

Figure 2. Wormhole measurements and distributions. (*a*) Widths of wormholes summarized for cities in western Europe, showing mean (vertical tick mark), 95% CI of the mean (thick line), range (narrow line) and histogram below. Colours denote northern (blue) and southern (red) species of wood-boring beetle, and circumscribe the confidence intervals of each species. (*b*) Historical distributions determined by the wormhole record, 1462–1899. Numbers are cities where wormholes were printed; additional locations 52–63 have lower sample sizes (less than 10 wormholes) or only wormhole track evidence (see the electronic supplementary material). Thick line is the historical contact line separating the two species. (*c*) Current distribution of *Anobium punctatum* by country [5]. (*d*) Current distribution of *Oligomerus ptilinoides* by country [5]. (*e*) Summary diagram showing stability of historical distributions and contact line, followed by recent expansion and overlap of ranges.

Dutch woodblock made by Bruegel [6] and averaged 1.44 mm, consistent with the northern type.

The species most probably responsible for printed wormholes from northern Europe is the common furniture beetle, *Anobium punctatum*. It is the most frequently encountered wood-borer of drywood objects, such as furniture, produces exit holes of the same size (1–2 mm), and is known to attack the wood of box, pear and apple, among other species [7]. Until now, the historical distribution (pre-twentieth century) of this species was virtually unknown (see the electronic supplementary material). It has been considered a native of temperate Europe [7] and is known from archaeological sites dating to 12 000 years ago [8], although it is now widely distributed in the Mediterranean Basin, the Americas, South Africa, Australia and New Zealand [5]. The species most probably responsible for printed wormholes from southern Europe is the Mediterranean furniture beetle, *Oligomerus ptilinoides*. It is also known to attack dry hardwoods and produce exit holes of approximately the same size as in prints from southern Europe (1.3–3 mm) and to have caused extensive damage to furniture and works of art throughout that region since at least the end of the nineteenth century [9–12]. It occurs now in central, southern and southeastern Europe; North Africa and the Near East [13], although there is no detailed information on the historical distribution of this species (see the electronic supplementary material). Other species of wood-borers can be ruled out based on their preference for damp or rotting wood, softwoods or hardwoods with larger pores (see the electronic supplementary material). Nonetheless, the species identifications presented here are, necessarily, based on indirect evidence.

Wormholes record detailed historical distributions of these two species for the first time (figure 2*b*). The ranges show remarkable contiguity, with no evidence that the species co-occurred over four centuries (1462–1899), either at the same time period or across time periods. This stands in contrast to their current ranges, based on museum records, showing broad overlap (figure 2*c*,*d*). The shape of the historical line of contact (figure 2*b*), curving southwards as it approaches the cooler and more humid west coast of France, is consistent with the current 20°C isotherm for July. Given the sensitivity of *A. punctatum* to low humidity and high temperatures [14,15], this may indicate that the wormhole boundary line across Europe reflects a natural species contact which was, at least partly, influenced by climate. Nonetheless, because climate has changed during the time period considered here, and because the two species replace each other locally even in areas where they broadly overlap now [16], and feed on the same type of wood, local competition may explain the contiguous nature of the historical wormhole line.

4. Discussion

The results show that printed wormholes are trace fossils that can be species-specific, especially considering a population with a mean, variance and wormhole shape (figure 2*a*). Although most woodblocks were carved near where they were printed, the printed wormholes also record evidence of woodblock travel. For example, the blocks for Mattioli's Renaissance botanical (*Commentarii*) [17] were printed throughout Europe (e.g. Italy, Germany and France) in many editions over two centuries accumulating wormholes from both species, and tracks from the southern species. As would be expected from a mixed species sample, the mean wormhole width (1.74 mm, $n = 52$) was intermediate and different ($p < 0.001$) from those of the northern and southern species.

The spread of at least *A. punctatum* apparently occurred in the late nineteenth or early twentieth centuries (figure 2*e*), because it was well established on the Iberian peninsula by the mid-twentieth century [16]. This timeframe is consistent with globalization as the explanation for the current overlapping distributions of these two species. Greatly increased trade and commerce would have moved infested wood products between the two historical ranges, and the improved indoor environments of new buildings and houses would have provided suitable habitats for colonization.

Much of the wormhole record remains to be explored. Woodcuts on paper date from about 1400 in Europe [3] but they appeared much earlier, in the eighth century, in Asia [18]. The ongoing imaging of books and art prints [2], and comparative data from living species, will permit greater exploration and databasing of the record. DNA sequence data, if obtainable from old wormholes in surviving woodblocks, could corroborate or refute species identifications. Knowledge of the wormhole record will allow biologists to trace the recent biogeographic history of species, including invasives of economic importance [19], and historians to evaluate the place of origin and movement of a woodblock, book, document or art print.

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