

Figure 2 Comparison of ϵ_W to Cr/Ti ratio. **a**, Covariation between ϵ_W and Cr/Ti ratio (note that the x axis is on a logarithmic scale). All metasediment data points from this study (filled squares) define a tight ($r^2 = 0.919$) logarithmic fit (solid line). The fit extends to average enstatite chondrites¹⁰ (open circle), the carbonaceous chondrite Allende^{7,13} (open diamond), and close to average iron meteorite⁹ (solid diamond). Elemental abundance data from refs 17 and 22. Iron meteorites were assigned a Ti abundance of 2 p.p.m., based on the observation¹⁷ that troilite inclusions contain about 10 p.p.m. Ti. **b**, Comparison of metasediment data (solid squares with error bars connected by dashed line representing logarithmic fit) with model mixing hyperbolae. One hyperbola (open diamonds) was calculated between a hypothetical chondrite endmember (data sources as in **a**) and a terrestrial endmember using Cr and Ti concentration data from the IGB metapelite with the lowest known Cr/Ti ratio (0.002) and the lowest observed W content of 100 p.p.b. This endmember represents the Hadean crust, and was assigned an ϵ_W of zero. The second hyperbola (filled diamonds) was calculated between a hypothetical iron meteorite endmember (data sources as in **a**) and the terrestrial endmember. In this case, the terrestrial endmember was assigned a relatively high W content of 3,000 p.p.b.

not show the appropriate hyperbolic relationship (Fig. 2b) predicted by mixing of unmodified terrestrial and meteorite debris. We propose that weathering of meteoritic debris caused preferential liberation of certain elements, depending on the stability of the host minerals in the Hadean atmosphere and hydrosphere. For example, most Cr in iron-meteorite is hosted by troilite (FeS), whereas all W is found in the FeNi metal phase¹⁷. Although W isotopes cannot be used to directly identify the nature of the meteoritic impactors, our data nevertheless provide evidence for the oldest impact event(s) so far discovered on Earth, lending support to interpretation of slightly increased Ir concentrations in some IGB lithologies¹⁸.

Most of the studied metasediments contain particles of carbon. In particular, sample SM/GR/01/01a is from the same outcrop where Rosing¹⁹ described discrete graphite microparticles with isotopically light C ($\delta^{13}\text{C}$ approximately -19‰), which he interpreted as biogenic. However, in view of the present evidence for extraterrestrial W in this sample, the possibility needs to be considered that the graphite represents insoluble carbon particles from carbonaceous chondrites, with $\delta^{13}\text{C}$ of about -18‰ (ref. 20). □

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The authors declare that they have no competing financial interests.

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A long-tailed, seed-eating bird from the Early Cretaceous of China

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The lacustrine deposits of the Yixian and Jiufotang Formations in the Early Cretaceous Jehol Group in the western Liaoning area of northeast China are well known for preserving feathered dinosaurs, primitive birds and mammals^{1–3}. Here we report a large basal bird, *Jeholornis prima* gen. et sp. nov., from the Jiufotang

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Formation. This bird is distinctively different from other known birds of the Early Cretaceous period in retaining a long skeletal tail with unexpected elongated prezygopophyses and chevrons, resembling that of dromaeosaurids^{4–6}, providing a further link between birds and non-avian theropods^{7–8}. Despite its basal position in early avian evolution, the advanced features of the pectoral girdle and the carpal trochlea of the carpometacarpus of *Jeholornis* indicate the capability of powerful flight. The dozens of beautifully preserved ovules of unknown plant taxa in the stomach represents direct evidence for seed-eating adaptation in birds of the Mesozoic era.

Aves L., 1758

Jeholornis prima gen. et sp. nov.

Holotype. IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China) collection number V13274, a nearly completely articulated skeleton.

Etymology. The generic name is derived from the holotype-bearing

'Jehol Group', which contains the Jehol biota. The specific name refers to its primitive appearance in the tail.

Locality and horizon. Dapingfang, Chaoyang City, western Liaoning, China; Jiufotang Formation, middle Early Cretaceous. Associated vertebrate fossils include feathered dromaeosaurs⁹ and several primitive birds such as the ornithurine *Yanornis*¹⁰, *Confuciusornis*², the newly reported *Sapeornis*¹¹ and abundant enantiornithines¹².

Diagnosis. A large bird with the following derived characters: lachrymal with two vertical and elongated pneumatic fossae; mandibles robust with well ossified symphysis; first phalanx of the third manual digit twice as long as the second phalanx, which together form a bow-shaped structure; 20 caudal vertebrae behind the transition point; lateral trabecula of the sternum with a rounded fenestra at the distal end; ratio of forelimb (humerus plus ulna plus carpometacarpus) to hindlimb (femur plus tibiotarsus plus tarso-metatarsus) of about 1.2.

Description. *Jeholornis* is a large bird, represented by a partially articulated skull and nearly complete postcranial bones (Fig. 1). The holotype comprises five slabs. Their associations are unambigu-



Figure 1 Complete holotype of *Jeholornis prima* gen. et sp. nov. (IVPP V13274).

a, Skeleton. **b**, Caudal vertebrae. **c**, Line drawing of the caudal vertebrae. ch, chevron; co, coracoid; cv, cervical vertebra; dv, dorsal vertebra; fe, femur; fi, fibula; fu, furcula; ga, gastralia; hu, humerus; hy, hyoid bone; il, ilium; is, ischium; ma, mandible; mcIII, metacarpal III; ov, ovule; pr, prezygopophysis; pu, pubis; ra, radius; sc, scapula; sk, skull; st, sternum; sv, sacral vertebra; ta, tail; ti, tibia; tm, tarsometatarsus; tp, transverse process; ul, ulna; un, unguals; 1–22, caudal vertebrae 1–22.

metacarpal III; ov, ovule; pr, prezygopophysis; pu, pubis; ra, radius; sc, scapula; sk, skull; st, sternum; sv, sacral vertebra; ta, tail; ti, tibia; tm, tarsometatarsus; tp, transverse process; ul, ulna; un, unguals; 1–22, caudal vertebrae 1–22.

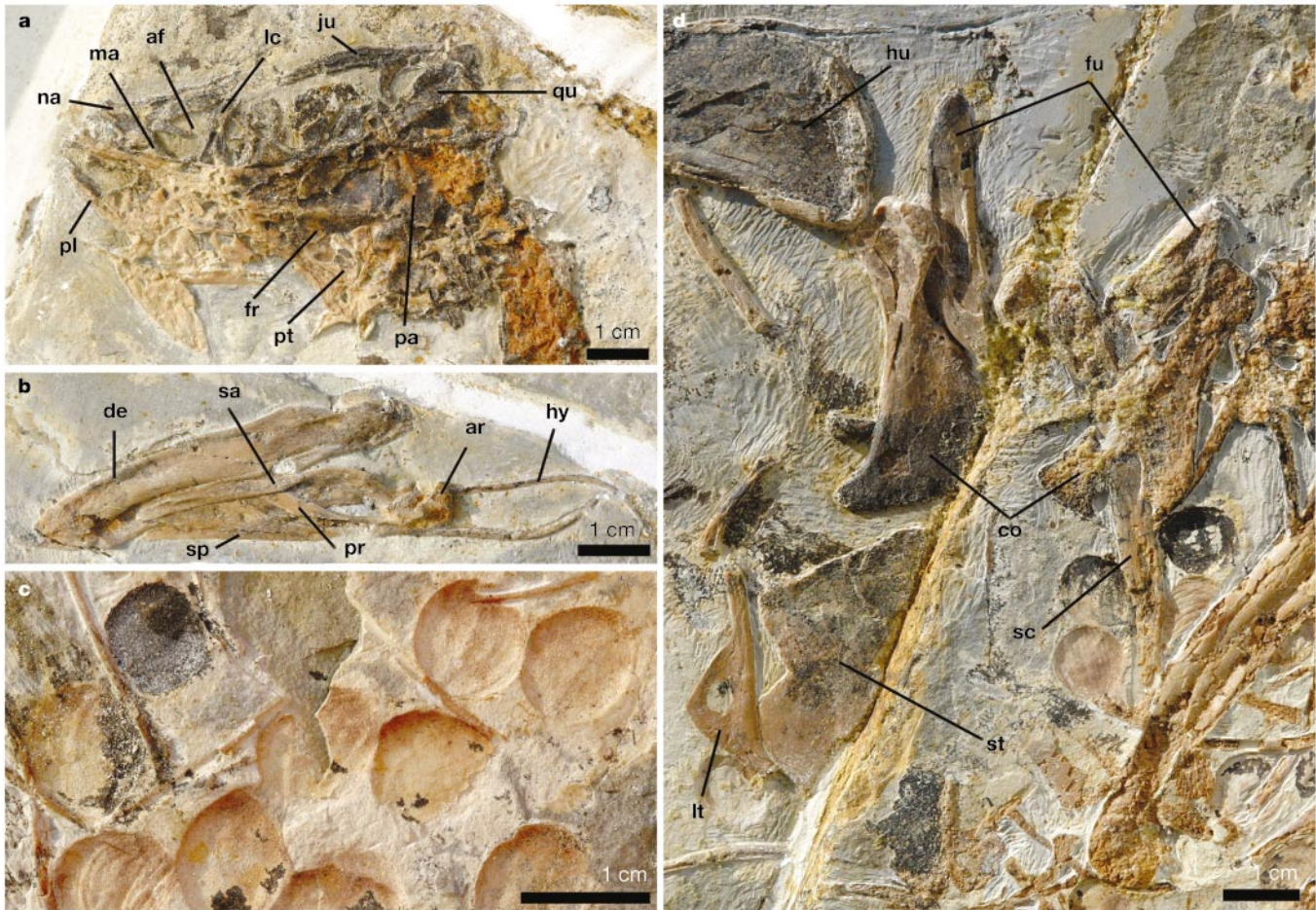


Figure 2 Holotype of *Jeholornis prima* gen. et sp. nov. (IVPP V13274). **a**, Skull. **b**, Mandibles. **c**, Ovules. **d**, Pectoral girdle and sternum. af, antorbital fenestra; ar, articular; de, dentary; fr, frontal; ju, jugal; lc, lachrymal; lt, lateral trabecula of the sternum; ma, maxilla; na, nasal; pa, parietal; pl, palatine; pr, prearticular; pt, pterygoid; qu, quadrate; sa, surangular; sp, splenial. See Fig. 1 for other abbreviations.

ously supported by, among other evidence, the presence of at least one skeletal element on two neighbouring slabs. For example, the association of the two principal slabs—that is, one slab with the skull and the other slab containing the most caudals—is supported by the distribution of a pubis, an ischium and two tibiae on both slabs. Furthermore, all of the slabs that include parts comprising the whole tail have been prepared completely by a professional technician under our supervision in the laboratory. Therefore, the possibility of a composite specimen for the holotype can be ruled out.

The maxilla is reduced and does not bear any teeth. There is a large antorbital fenestra. The lachrymal is ‘T’-shaped with two elongated pneumatic fossae vertically distributed (Fig. 2a). The jugal is rod-shaped; it has a long, slender and posteriorly curved postorbital process similar to that of *Sinornithosaurus*¹³. The isolated mandibles are robust and they are well fused at the rostral end.

There are three very small conical teeth on the left mandible. Of note, the teeth of the Late Cretaceous *Gobipteryx* are also reduced together with the development of a fused mandibular symphysis. Two well-developed hyoid bones are long, slender and curved (Fig. 2b).

The cervical vertebrae are robust, and there are at least ten cervicals. There are 22 caudals that are nearly completely articulated in preservation. The last sacral has an expanded transverse process at the distal end and it is articulated with the first caudal. The two proximal caudals are short, with well-developed transverse processes. The second caudal has a rod-shaped chevron, with a forked caudal end. There are 20 elongated caudal vertebrae behind the transition point, with distinctively elongated prezygopophyses and chevrons (Fig. 1b, c). The prezygopophyses of the posterior caudal vertebrae extend to more than one-third the length of the preceding caudals. The horizontally distributed chevrons of the last 20 caudals

Table 1 Comparison of *J. prima* gen. et sp. nov. (IVPP V13274) with other primitive birds and theropods

Selected element	<i>Jeholornis prima</i> (IVPP V13274)	<i>Sapeornis chaoyangensis</i> (IVPP V12698)	<i>Archaeopteryx bavarica</i> (Solnhofen specimen)	<i>Confuciusornis sanctus</i> (IVPP V11619)	<i>Sinornithosaurus millenii</i> (IVPP V12811)	<i>Microraptor zhaoianus</i> (IVPP V12330)
Humerus	110 (r)	127 (l)	83	52 (r)	134 (r)	—
Ulna	109 (r)	133 (l)	72*	47 (r)	110 (r)	35 (r)
Metacarpal II	47 (r)	57 (l)	34†	27 (r)	63 (r)	—
Pubis	64 (r)	85 (l)	59	47 (r)	116 (l)	—
Femur	75 (r)	80 (l)	70*	47 (l)	148* (l)	53 (l)
Tibiotarsus/tibia	88 (r)	83 (l)	90	54 (l)	—	68 (l)
Metatarsal III	47 (r)	44 (l)	48	25 (l)	93	34 (l)

Measurements are in millimetres. l, left side; r, right side.

*Estimated values.

†Preserved length.

are all connected at their forked extremities. The last caudal tapers distally and is medio-laterally compressed. The gastralia are long, slender and rod-like.

The scapula and coracoid are not fused. The scapula is curved and tapers caudally, as in advanced birds. The coracoid is strut-like, with a well-developed lateral process. It is more elongated than in both *Archaeopteryx*^{14,15} and *Sapeornis*, but is shorter and more robust than in more advanced birds such as enantiornithines¹⁶. Most of the medial margin of the coracoid is convex as in *Archaeopteryx* and *Confuciusornis*^{17,18}. The furcula is robust, shaped like a boomerang, and is generally similar to those in *Archaeopteryx*, *Confuciusornis* and some dromaeosaurids. The sternum is short; the lateral trabecula is unfused with the main body of the sternum, with a rounded fenestra near the caudal end (Fig. 2d).

The ratio of the forelimb (humerus plus ulna plus carpometacarpus) to hindlimb (femur plus tibiotarsus plus tarsometatarsus) is about 1.2, which is much larger than in *Archaeopteryx* (less than 1); however, *Sapeornis*¹¹ and the enantiornithine *Longipteryx*¹² have forelimbs that are relatively longer among early birds (Table 1).

The humerus has a large deltoid crest, and the ventral tubercle is not well developed. The radius is slightly shorter than the humerus, as in *Archaeopteryx* and *Confuciusornis*. The manus nearly equals the humerus and ulna in length (Fig. 1a). The carpometacarpus is fused at the proximal end, with a well-developed carpal trochlea. The third metacarpal is bow-shaped and is tightly attached to the second metacarpal at the distal end. The ulnare has a well-developed metacarpal incision. There are three large and curved unguals in the hand. Unlike *Archaeopteryx*, *Confuciusornis* and *Protopteryx*¹⁹, the first phalanx of the first digit does not extend to the distal end of the second metacarpal, which is similar to that of *Sapeornis*¹¹ and more advanced enantiornithines and ornithurine birds¹⁰. The third digit comprises four phalanges as in *Archaeopteryx* and *Confuciusornis*. The second phalanx of the third digit is less than half the size of the first phalanx. It is noteworthy that new materials of *Sapeornis* show that it has only two reduced phalanges, contrary to previous reconstruction.

The pelvis is most similar to that of *Archaeopteryx* with respect to the position of the pubis relative to the ilium; the pubes are less caudally retroverted than in some dromaeosaurs²⁰. The pubic symphysis appears to be short. The pubic foot is spoon-shaped as in *Archaeopteryx* and some enantiornithines, but is different from

that of *Confuciusornis*. The ischium has a marked strut-like proximal dorsal process as in *Sapeornis*, *Confuciusornis* and enantiornithines (Fig. 3a). A less-well-developed process is present in *Archaeopteryx* and non-avian theropods such as *Sinornithosaurus* and *Unenlagia*²¹.

The femur has a deep and narrow popliteal fossa at the distal end. The ankle is generally similar to that of *Archaeopteryx*, *Rahonavis*²² and non-avian theropods such as *Sinornithosaurus* in having an unfused calcaneum and an astragalus with an ascending process (Fig. 3b–e). The calcaneum is narrow, nearly rounded, and about one-fifth the width of the astragalus. It seems that the character of the astragalus (that is, a large ascending process) of non-avian theropods is hardly modified in the most basal birds, and the pretibial bone is most probably a new trait that only appeared in a later stage of avian evolution²³.

The tarsometatarsus is fused at the proximal end, as in all known birds. The fifth metatarsal is present as in *Archaeopteryx*, *Confuciusornis* and *Sapeornis*. The hallux is reversed as in all birds, but is unknown in any non-avian theropods. The unguals of the foot are large and curved, as in most basal birds. The hypertrophied second ungual is similar to that of *Archaeopteryx* and *Rahonavis*²², and is also reminiscent of the situation of dromaeosaurids and troodontids^{6,20,22}. The second phalanx of the second digit is longer than the first phalanx, as in *Microraptor* and nearly all basal birds.

Although feathers have been found to be associated with various birds and dromaeosaurs from the same locality, they have not been preserved with the holotype of *Jeholornis*.

In the stomach position of *Jeholornis*, over 50 ovules are preserved (Fig. 1a). These are mainly rounded and average 8–10 mm in width and length (Fig. 2c). Similar ovules have been reported by palaeobotanists elsewhere, and are referred to the genus *Carpolithus*; however, they belong to an unknown plant group²⁴.

Except for *Sapeornis*, which has a short tail and a pygostyle, and derives from the same area and horizon, *Jeholornis* is the largest bird known from the Early Cretaceous. Both genera are also larger than the Late Jurassic *Archaeopteryx* (Table 1). Except for *Archaeopteryx* and *Rahonavis*, *Jeholornis* is the only known bird with a long caudal series (Fig. 1). The tail is longer than the hindlimb; however, in the largest *Archaeopteryx*, the tail is shorter than the hindlimb¹⁵. The chevrons are also better developed and more elongated in *Jeholornis* than in *Archaeopteryx*. There are 20 caudals behind the transition point in *Jeholornis*, and there are less than 20 in *Archaeopteryx*^{15,25}. The presence of such a primitive skeletal tail largely resembling that of dromaeosaurids provides further evidence supporting the relationship between birds and dromaeosaurids (Fig. 4). The

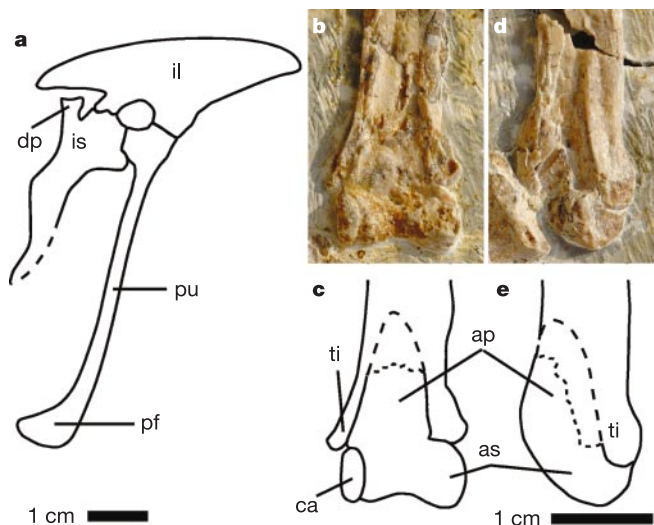


Figure 3 Pelvic girdle and tibia, calcaneum and astragalus of *Jeholornis prima* gen. et sp. nov. (IVPP V13274). **a**, Reconstruction of the pelvic girdle (right) in lateral view. **b–e**, Distal end of the tibia and its relationship with the calcaneum and astragalus (**b, c**, right, in cranial view; **d, e**, left, in cranio-lateral view). ap, ascending process of the astragalus; as, astragalus; ca, calcaneum; dp, dorsal process of the ischium; pf, pubic foot. See Fig. 1 for other abbreviations.

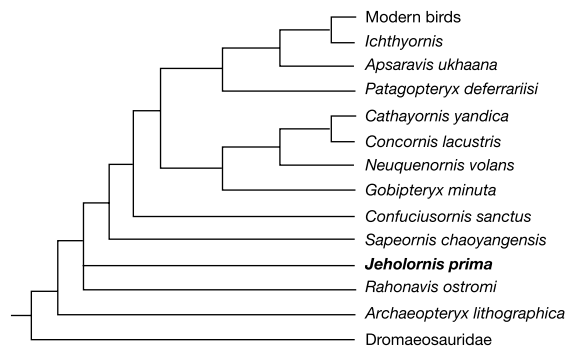


Figure 4 Cladogram showing phylogenetic relationships between *Jeholornis prima* and other major groups of birds. We used the PAUP 4.0 beta 10 method for phylogenetic analysis. We followed the same method as in ref. 28 by using 201 characters and analysing 18 taxa, with Dromaeosauridae as an outgroup. We also revised the data matrix from ref. 28. Four most parsimonious trees were obtained. Consistency index = 0.72; retention index = 0.83; tree length = 339. The cladogram is simplified from the congruent tree (see Supplementary Information).

derived features of the pectoral girdle of *Jeholornis* such as a strut-like coracoid and the well-developed carpal trochlea of the carpo-metacarpus, suggest the capability of powerful flight.

One of the most significant features of *Jeholornis* is the preservation of dozens of ovules in the stomach (Fig. 2c). Although hundreds of excellently preserved Mesozoic birds such as *Confuciusornis* have been discovered, our knowledge about their diet has been at best speculative. *Jeholornis* represents direct evidence for seed-eating adaptations in Mesozoic birds. The ovules, referable to the generic name *Carpolithus*²⁴, cannot be positively included into any of the chief plant groups (J. Hilton and Q. Leng, personal communication). It is difficult to determine whether, in life, *Jeholornis* ate cones on a tree, ovules from intact cones, or ovules shed from their cones. The intact nature of the ovules, however, may indicate that the bird ate them whole, to be digested in the gizzard, rather than breaking them up to eat them in small pieces (J. Hilton, personal communication). The large number of seemingly undigested ovules in the specimen probably indicates a large crop. Furthermore, the robust mandibles with fused mandibular symphysis, reduced teeth and well-developed hyoid bones seem to lend further support for the seed-eating habit of *Jeholornis*.

Jeholornis certainly possessed an arboreal capability, as evidenced by its reversed hallux, long and strongly curved pedal unguals, and toe proportions (Fig. 1a). However, as in other basal birds such as *Archaeopteryx* and *Confuciusornis*, there is no evidence to discount the possibility that *Jeholornis* spent some time on the ground^{26,27}. Therefore, without further evidence, it is difficult to conclude whether *Jeholornis* fed on ovules from cones on trees, or on the ground. This discovery, together with many others in recent years, suggests that by the Early Cretaceous, early birds had not only diverged significantly in morphology, size and ecology^{11,28}, but had also differentiated with respect to feeding adaptation. □

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Competing interests statement

The authors declare that they have no competing financial interests.

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Mechanisms of long-distance dispersal of seeds by wind

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Long-distance dispersal (LDD) is central to species expansion following climate change, re-colonization of disturbed areas and control of pests^{1–8}. The current paradigm is that the frequency and spatial extent of LDD events are extremely difficult to predict^{9–12}. Here we show that mechanistic models coupling seed release and aerodynamics with turbulent transport processes provide accurate probabilistic descriptions of LDD of seeds by wind. The proposed model reliably predicts the vertical distribution of dispersed seeds of five tree species observed along a 45-m high tower in an eastern US deciduous forest. Simulations show that uplifting above the forest canopy is necessary and sufficient for LDD, hence, they provide the means to define LDD quantitatively rather than arbitrarily. Seed uplifting probability thus sets an upper bound on the probability of long-distance colonization. Uplifted yellow poplar seeds are on average lighter than seeds at the forest floor, but also include the heaviest seeds. Because uplifting probabilities are appreciable (as much as 1–5%), and tree seed crops are commonly massive, some LDD events will establish individuals that can critically affect plant dynamics on large scales.