



The Early Cretaceous terrestrial ecosystems of the Jehol Biota based on food-web and energy-flow models

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The ancient terrestrial ecosystems of the Lower Cretaceous Yixian Formation and the Jiufotang Formation, consecutive components of the Jehol Group in Northeast China were reconstructed using an energy-flow and food-web model. This model can be used to quantitatively estimate population densities for ancient terrestrial vertebrates based on food webs, net primary productivity, and three categories of energy-transfer efficiency. The results indicate that densities reached 866 individuals km⁻² and 4122 individuals km⁻² in two ecosystems, respectively. The main component of the vertebrate fauna of the Yixian Formation consisted of large herbivorous dinosaurs, while much smaller avians dominated the Jiufotang fauna. The model also indicates a temporal transition in the dinosaur fauna from the Yixian fauna to the Jiufotang fauna in which theropods decreased and ceratopsids became more abundant. We then compared these estimates of biodiversity with the Early Cretaceous Choyr fauna of Mongolia, and Tetori fauna of Japan using Simpson's diversity indices. Those indices, based on biomass, indicate that the biodiversities of the Jehol fauna lay between those of the Choyr and Tetori faunas. This range in biodiversity seems attributable to fundamental differences in vegetation and the environment. © 2014 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2014, **113**, 836–853.

ADDITIONAL KEYWORDS: ecological pyramids – energy intake – Konservat-lagerstätte – metabolic rates – net primary productivity – Yixian and Jiufotang formations.

INTRODUCTION

The Jehol Group of Northeast China has yielded a diverse array of well-preserved fossils of terrestrial vertebrates that have become known as the Jehol fauna. The fossils include the first-discovered feathered dinosaur, *Sinosauropteryx prima*, and thus the group is regarded as a fossil lagerstätte (Chang *et al.*, 2003). Because the Jehol fauna appears to have lived in several, geographically isolated basins, it includes many endemic species, making the Jehol Group and its fossil fauna a particularly suitable material for the

discussion of Early Cretaceous ecosystems. Zhou, Barrett & Hilton (2003) reviewed the Jehol fauna, and Xu & Norell (2006) discussed the ecological features of its non-avian dinosaur. Subsequently, several other studies have examined evolutionary radiation and vertebrate diversity within the Jehol Biota (Zhou, 2006; Zhou & Wang, 2010), the Jehol fish fauna (Zhou, Zhang & Wang, 2010), and the definition and distribution of the Jehol Biota (Pan *et al.*, 2013). However, the interaction between the fauna and the surrounding environment has not been modeled as an ecosystem. Here we propose to reconstruct the terrestrial ecosystems of the Yixian and Jiufotang formations of the Jehol Biota using quantitatively based food-web and energy-flow models. Such ecosystem reconstructions

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can quantify population sizes at each trophic level (Matsukawa *et al.*, 2006). We also discuss the biodiversity of other Early Cretaceous faunas from East Asia.

GEOLOGICAL SETTING

Grabau (1923) initiated studies of the Jehol Series by examining the fossils of fish in strata at Lingyuan city, western Liaoning Province. Afterward, Gu (1962) applied the name 'Jehol Group' to the strata that included volcanic rocks and fossils of clams, shrimp, insect larva and fish. He then named this sequence of sediments the Jehol Biota.

There are now two major opinions on the composition and subdivisions of the Jehol Group:

1. the group comprises, in ascending order, the Yixian, Jiufotang and Fuxin formations (e.g., Jiang & Sha, 2006; Jiang, Sha & Cai, 2007; Sha, 2007; Sha *et al.*, 2007, 2012), or
2. the group comprises the Yixian and Jiufotang formations (Wang & Zhou, 2003) with the more recently described Dabeigou Formation as the lowest level (e.g., Wang & Zhou, 2006; Zhou, 2006; Zhang, Wang & Fang, 2010; Zhou & Wang, 2010).

It may be more appropriate to use the Huajiyang Formation, instead of the Dabeigou Formation, for rocks in northern Hebei Province (Jin *et al.*, 2008; Pan *et al.*, 2013).

The Lower Cretaceous Jehol Group is exposed in western Liaoning and northern Hebei provinces, and the southern portion of Inner Mongolia in Northeast China (Fig. 1). During the deposition of the Jehol Group, numerous active volcanoes surrounded the sedimentary basins (Chang *et al.*, 2003). Their ash falls and sediment from flash floods contributed to anoxic or dysoxic conditions that may have been a critical factor contributing to exceptional preservation of material on the lake bottoms (Fürsich *et al.*, 2007; Hethke *et al.*, 2013).

Pan *et al.* (2013) have proposed a definition of the Jehol Biota that reflects its broader distribution and more varied deposition. In the basins of western Liaoning and adjacent Inner Mongolia and parts of northern Hebei, the Jehol Biota occurs in lacustrine and, only rarely in fluvial sediments, of the Yixian and Jiufotang formations. These have been dated from about 130 Ma to about 120 Ma (Swisher III *et al.*, 1999, 2002; He *et al.*, 2004, 2006b; Zhu *et al.*, 2007; Yang, Li & Jiang, 2007; Chang *et al.*, 2009). In the basin of northern Hebei, the Jehol Biota occurs in both lacustrine and fluvial sediments of the Huajiyang Formation, which have also been dated to about 130 Ma (He *et al.*, 2006a). These radiometric data correspond to late Hauterivian to Aptian (International Commission on Stratigraphy, 2013).

Most fossils of the Jehol Biota come from the Yixian and Jiufotang formations (Pan *et al.*, 2013). The exceptionally preserved Jehol Biota is contained in sedimentary characteristics of a 'Konservat-lagerstätte' (Pan *et al.*, 2013). Pan *et al.* (2013) divided the sedimentary rocks of the Jehol Group into roughly two types: Type A consists of finely laminated sediments, characterized by exceptional preservation of soft tissues, as body outlines, skin casts, wing membranes, scales, integumentary filaments, colour patterns, feathers and furs. Type B consists of massive, tuffaceous, pebbly sandstones, typically yielding larger vertebrate skeletons and a few plant fragments, but no invertebrate material or examples of small, flying vertebrates.

METHODS

To propose a reconstruction for a paleoecosystem it is necessary to understand the structures of its food webs. Trophic dynamics of ecosystems consist of the flow of matter, such as carbon and nitrogen, and the flow of energy, ultimately derived from sunlight. Although matter is re-cycled on a semi-permanent basis within the ecosystem, energy is eventually dissipates heat and is lost to trophic dynamics. This unidirectional flow of energy can be considered a key factor in ecosystems and food-web structures to the extent that Heal & Maclean (1975) suggest that the food-web structure can be modeled generally by energy flow. They estimated secondary productivity by making an ecosystem reconstruction model that is controlled by energy flow, and they attempted validation by comparing estimated data to direct observations from ten tundra, grassland, and forest ecosystems. There was good agreement in their results.

Because their model is given specified values for components that control energy flow to various environments and animals, it can reduce many assumptions inherent in ecosystem reconstruction. In this paper, we adapt the Heal and Maclean model to estimate animal numbers at each trophic level. Although their model includes both a grazing web and a detritus web, the model developed by Matsukawa *et al.* (2006) considers only the grazing food web because it is very difficult to evaluate ancient detritus processing systems from data in the fossil record.

As only plants can convert solar energy into the carbohydrates whose energy is used by other living organisms, ecosystems are controlled by the net primary productivity (NPP) of plants. So an estimate of NPP is indispensable for the reconstruction of an ecosystem. NPP is determined by the types of vegetations. Three categories of transfer efficiency are used in the NPP using process by primary consumer and in further high trophic levels (Begon, Harper & Townsend, 1996). The three categories are consump-

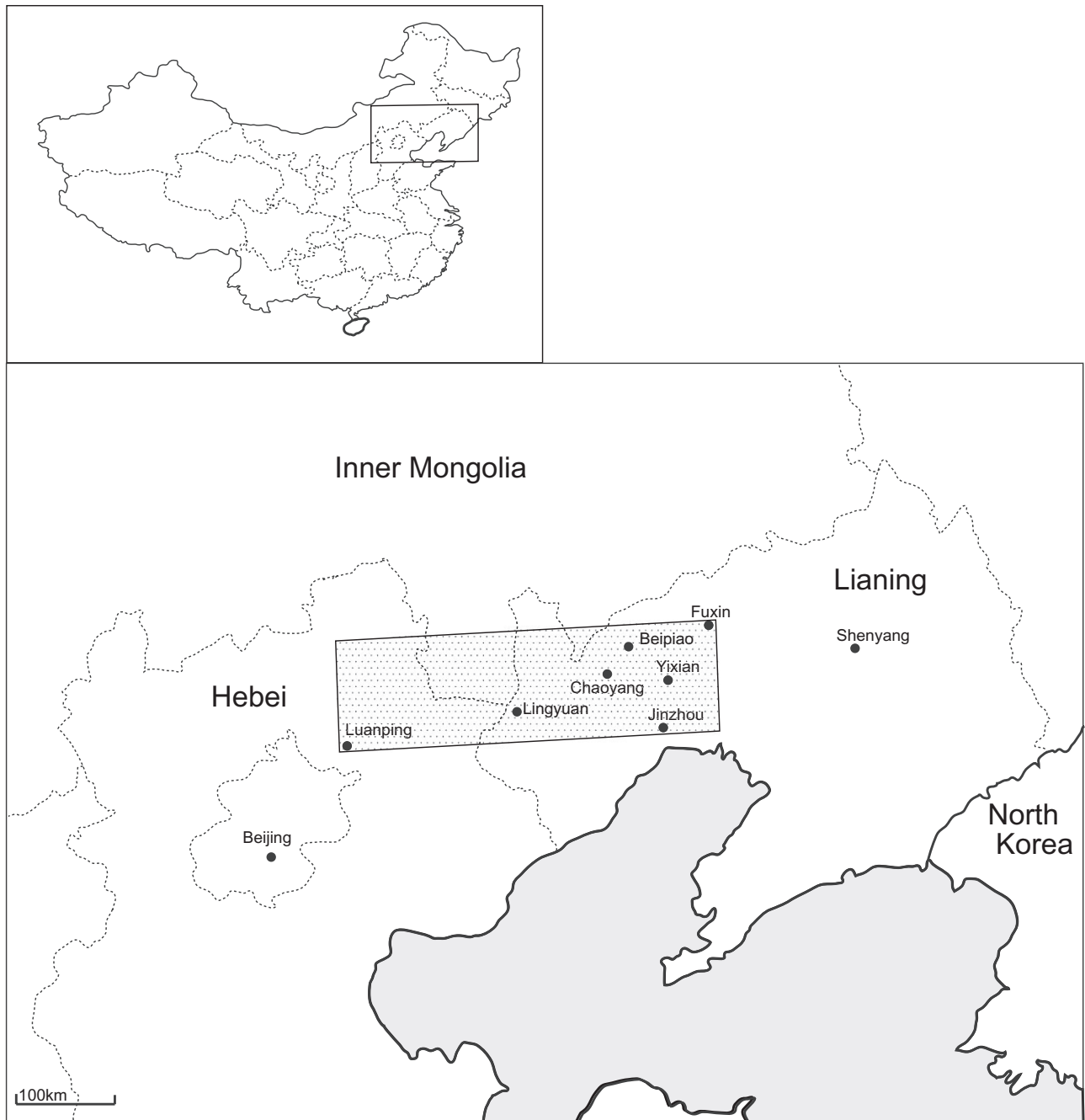


Figure 1. Index map of the investigated area. Dotted area indicates the presumed area of the Jehol ecosystem for reconstruction using food-webs and energy-flow modeling.

tion efficiency, assimilation efficiency, and production efficiency. Transfer efficiencies used in this study are listed in Table 1.

These basic efficiencies vary with types of environment, food habits, and metabolism in animals, and so on. The quantity of energy moving between trophic levels can be calculated by multiplying NPP, or available energy, by estimates of the efficiency levels. The

available energy is distributed to each animal species at a trophic level according to ratios of abundance and energy intake. For example, in a system with two types of animals (*A* and *B*) with population sizes (*a* and *b*), existing at a trophic level with a quantity of energy (*E*), individual energy intakes are *X* and *Y* respectively. Then the energy distributed to *A* (*E_a*) can be calculated by the formula:

Table 1. Transfer efficiencies used in this study. The efficiencies are on the basis of Heal and McLean (1975) and Begon *et al.* (1996)

	%
<hr/>	
Consumption efficiency (CE)	
Herbivores	
Invertebrates	5
Vertebrates (in forest)	5
Carnivores	
Invertebrates on invertebrates	25
Vertebrates on vertebrates	75
Vertebrates on invertebrates	5
Assimilation efficiency (AE)	
Invertebrates	40
Herbivorous vertebrates	50
Carnivorous vertebrates	80
Production efficiency (PE)	
Invertebrates	40
Ectothermic vertebrates	10
Endothermic vertebrates	2

$$Ea = E(aX/(aX + bY))$$

In paleoecosystem reconstruction, frequency and proportions of fossil species are used instead of population counts and species diversity of living animals.

ENERGY INTAKE AND METABOLIC RATES OF ANIMALS

Energy intake is the amount of energy required for continued activity by a living animal and is one of the most important factors for this paleoecosystem reconstruction model in which energy is the limiting factor. Farlow (1976) offers formulas for energy intake by endothermic herbivores, endothermic carnivores, ectothermic herbivores and ectothermic carnivores based on data from caged and free-living animals. The values are reliable because they are derived from animals with a measurable metabolic rate and can be replicated. They are less reliable when applied to extinct animals that may have had different metabolic rates. Therefore Kukihara, Shibata & Matsukawa (2004) created new formulae for energy intake that can systematically be adjusted according to estimates of metabolic rates and activity levels of individual animals.

Matsukawa *et al.* (2006) and Kukihara, Matsukawa & Lockley (2010) began by determining Standard Metabolic Rate (SMR). SMR is the metabolic rate of an inactive animal and is defined as the minimum consumption of oxygen required to sustain an animal's life at a standard temperature and pressure. SMR of mammals can be calculated from animal body mass by the Fowler (1978)'s formula:

$$\text{SMR (kcal day}^{-1}\text{)} = 70 \times W^{0.75}$$

Where W is body mass in kg. This formula is effective for all mammals from small mice to big elephants (Fowler, 1978). The SMR formula of birds except for Passeriformes is:

$$\text{SMR (kcal day}^{-1}\text{)} = 78.3 \times W^{0.723}$$

and for Passeriformes, a group of very small birds, is:

$$\text{SMR (kcal day}^{-1}\text{)} = 129.0 \times W^{0.724}$$

The SMR of reptiles is only 10–20% that of mammals of the same size (Fowler, 1978). Rates higher than SMR are necessary for animals that need to carry out activities, grow, nurse their young, etc. This enhanced rate of consumption is called the Active Metabolic Rate (AMR). AMR can be two to three times the SMR. In this study, we set the SMR of ectotherms at 15% that of endothermic animals and AMR as twice the SMR for all types of animals.

Animals must take in more energy than they require since they cannot assimilate all that they consume. Values of the assimilation efficiency of animals are 0.5 for herbivores and 0.8 for carnivores respectively. Thus formulae of energy intake multiply the AMR by the reciprocal of the assimilation efficiency. For example, the energy intake formula of a herbivorous endotherm is:

$$Ed \text{ (kcal day}^{-1}\text{)} = 2 \times (70 \times W^{0.75}) \times (1/0.5)$$

Where Ed is the daily energy intake.

To ensure that the new formulae were reliable, we compared our results to data derived using Farlow's method (Kukihara *et al.*, 2004). Farlow's analysis was based on plotting actual animal weights and energy intakes on a logarithmic graph and drawing an approximated line (Farlow, 1976). Kukihara *et al.* (2004) plotted the results from the new formulae in the same way and found general agreement according to animal type (Kukihara *et al.*, 2004).

Equations of energy intake per year for four types of animals are shown in Table 4. They are calculated by kJ day^{-1} .

RESTRICTIONS OF THE MODEL

In order to achieve the reconstruction of the Jehol Biota as a paleoecosystem, the following restriction factors for the model are considered:

(1) Duration of Ecosystem through Geological Time

Ecosystem analysis compares living communities based on species and individuals in well-defined units

of time and space, but paleoecosystem reconstruction depends on fossil assemblages deposited over long periods of time. Thus we cannot guarantee that the component species of a fossil assemblage existed in the same time or space. Nor can we be sure of the nature of interactions between fossil species, their range of movement, or their seasonal distribution. Such factors are likely to change through time.

(2) Taphonomic Bias

Thanks to a locally inactive environment in the Cretaceous, fossils from the Jehol Biota display a quality and quantity of preservation that are orders of magnitude better than material from most other formations (Raup & Stanley, 1978). In such an environment, the remains of animals and plants were protected from the normal biologic agents of decay and from many destructive physical and chemical processes.

Diagenetic processes have been restrained to the point where fossils from the Jehol Group appear as detailed images that reflect appearance in life. The undamaged condition of these fossils suggests that there was little or no taphonomical bias.

In a modern examination of taphonomic processes in Amboseri National Park, Kenya, Behrensmeier, Western & Boaz (1979) monitored the activities of a vigorous scavenging community that included vultures, hyenas, jackals, and a large assemblage of insects. The weights of fossil animals from the Jehol Biota are estimated to be less than 20 kg, except for three examples. In Kenya, taphonomic processes cause the loss of about 2–10% of the information on the number of mammals weighing 0.8–20 kg. Losses to the Jehol fauna were probably less than 20%.

EVALUATION OF OUR MODEL

To test our model, Kukiwara *et al.* (2004) and Matsukawa *et al.* (2006) applied it to the Serengeti ecosystem in east Africa, using data from Houston (1979) and Snerson (1986). We calculated error between confirmed and estimated population densities to be a factor 2.8 for herbivores, and 7.8 for carnivores. Such large differences between classes of animal may be related to resource restriction, especially of water; differences in the mobility and activity of individual species; territorial interactions and habitat choices by species. None of those factors are reflected in the fossil record, so it is difficult to resolve such variation in a model. Fortunately the overall error factor appears to be less than eight making it possible to discuss restoring a paleoecosystem with this model, at least in general terms.

RECONSTRUCTION OF PALEOECOSYSTEM

(1) Biota and Food Webs in the Jehol Ecosystem

Diverse vertebrate fossils such as fish, amphibians, turtles, squamates, choristoderes, pterosaurs, dinosaurs, birds, and mammals occur as fossils in the Yixian and Jiufotang formations of the Jehol Group (Chang *et al.*, 2003; Xu & Norell, 2006). Here, we use the fossil record to compare reconstructions of two paleoecosystems. The vertebrate fossil dataset employed was downloaded from the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Science in 2010, and were cited in Chang *et al.* (2003). Vertebrate fossils, other than fish are listed in Tables 2 and 3. Although a few taxa such as *Protopteryx fengningensis* and *Jinfengopteryx elegans* occurred only in the lowest section of the Jehol Group (i.e. Dabeigou or Huajiyang Formation), they have been tentatively included (Table 2).

We presumed that the diet of vertebrate taxa of the Jehol Group (Tables 2 and 3) could be extrapolated from observations of abdominal contents reported from the Jehol fossils (e.g. Dalsätt *et al.*, 2006; Wang & Zhou, 2006; Xing *et al.*, 2012).

(2) Energy Intake and Body Mass in Ancient Animals

Measures of energy intake for animals are a prerequisite for energy-flow modeling (Matsukawa *et al.*, 2006). Here, we estimated the body masses, that drive estimations of energy requirements, in dinosaurs, mammals, and other animals from calculations by Hidaka & Kawamichi (1996), Hidaka *et al.* (1996a, b), Barrett, Martin & Padian (2001), Burnie (2001), Funaki (2002), Chang *et al.* (2003), Hirano *et al.* (2004), Matsui, Hikida & Ota (2004), and Holtz (2007). We interpreted the physiology of amphibians and squamates as ectothermic, and that of birds and mammals as endothermic, similar to that of their modern descendants. We also assumed pterosaurs to be endothermic (Witton, 2013).

Although there have been many discussions about ectothermy and endothermy in non-avian dinosaurs, we used the model of endothermic carnivorous dinosaurs and ectothermic herbivorous dinosaurs following Matsukawa *et al.* (2006). The energy intake for deinonychosaurid carnivorous dinosaurs, including troodontids and dromaeosaurids, was estimated using the equations for modern carnivorous birds. Matsukawa *et al.* (2006) do not show equations for omnivorous animals. Here, we apply an average energy intake of carnivores and herbivores for a given omnivore body mass (Table 4).

Table 2. List of vertebrate taxa and their ecological characters from the Yixian Formation

Taxa / Scientific name	Feeding mode	Specimen count
Amphibians		
<i>Callobatrachus sanyanensis</i>	Omnivore	1
<i>Chunerpeton tianyiensis</i>	Omnivore	1
<i>Jeholotriton paradoxus</i>	Omnivore	2
<i>Laccotriton subsolanus</i>	Omnivore	1
<i>Liaobatrachus grabau</i>	Omnivore	1
<i>Mesophryne beipiaoensis</i>	Omnivore	1
<i>Sinerpetonfengshanensis</i>	Omnivore	1
Turtles		
<i>Manchurochelys</i> sp.	Omnivore	6
Choristoderes		
<i>Hyphalosaurus</i> sp.	Omnivore	2
<i>Monjurosuchus splendens</i>	Omnivore	3
Squamates		
<i>Dalinghosaurus longidigitus</i>	Insectivore	10
<i>Jeholacerta formosa</i>	Insectivore	1
<i>Yaheinosaurus tenuis</i>	Insectivore	4
Pterosaurs		
<i>Dendrorhynchoides curvidentatus</i>	Piscivore	1
<i>Eosipterus yangi</i>	Piscivore	1
<i>Haopterus gracilis</i>	Piscivore	1
<i>Jeholopterus ningchengensis</i>	Insectivore	1
Dinosaurs		
<i>Beipiaosaurus inexpectus</i>	Herbivore	1
<i>Caudipteryx</i> sp.	Herbivore	2
<i>Dilong paradoxus</i>	Carnivore	1
<i>Epidendrosaurus ningchengensis</i>	Carnivore	1
<i>Graciliraptor lujiatunensis</i>	Carnivore	1
<i>Hongshanosaurus hou</i>	Herbivore	2
<i>Huaxiagnathus orientalis</i>	Carnivore	1
<i>Incisivosaurus gauthieri</i>	Herbivore	1
<i>Jeholosaurus shangyuanensis</i>	Herbivore	2
<i>Jinfengopteryx elegans</i>	Carnivore	1
<i>Jinzhouosaurus yangi</i>	Herbivore	1
<i>Liaoceratops yanzigouensis</i>	Herbivore	2
<i>Liaoningosaurus paradoxus</i>	Herbivore	1
<i>Mei long</i>	Carnivore	1
<i>Protarchaeopteryx robusta</i>	Carnivore	1
<i>Psittacosaurus</i> sp.	Herbivore	3
<i>Shenzhouosaurus orientalis</i>	Herbivore	1
<i>Sinocalliopteryx gigas</i>	Carnivore	2
<i>Sinornithosaurus</i> sp.	Carnivore	2
<i>Sinosauropteryx</i> sp.	Carnivore	2
<i>Sinovenator changii</i>	Carnivore	1
<i>Yixianosaurus longimanus</i>	Carnivore	1
Avians		
<i>Changchengornis hengdaoziensis</i>	Omnivore	1
<i>Confuciusornis</i> sp.	Omnivore	8
<i>Eoenantiornis buhleri</i>	Omnivore	1
<i>Jibeinia luanhera</i>	Omnivore	1
<i>Jinzhouornis</i> sp.	Omnivore	2
<i>Liaoningornis longidigitris</i>	Omnivore	1
<i>Liaoxiornis</i> sp.	Omnivore	2
<i>Protopteryx fengningensis</i>	Carnivore	1
Mammals		
<i>Eomaia scansoria</i>	Omnivore	1
<i>Gobiconodon zofiae</i>	Omnivore	1
<i>Jeholodens jenkinsi</i>	Omnivore	1
<i>Repenomamus robustus</i>	Carnivore	1
<i>Sinobaatar lingyuanensis</i>	Herbivore	1
<i>Zhangheotherium quinquecupidens</i>	Omnivore	1

Table 3. List of vertebrate taxa and their ecological characters from the Jiufotang Formation

Taxa / Scientific name	Feeding mode	Specimen count
Amphibians		
<i>Liaoxitriton zhongjiani</i>	Omnivore	34
Choristoderes		
<i>Ikechosaurus gaoi</i>	Omnivore	1
Pterosaurs		
<i>Chaoyangopterus zhang</i>	Piscivore	1
<i>Liaoningopterus gui</i>	Piscivore	1
<i>Sinopterus dongi</i>	Frugivore	1
Dinosaurs		
<i>Microraptor</i> sp.	Carnivore	2
<i>Psittacosaurus</i> sp.	Herbivore	2
Avians		
<i>Boluochia zhengi</i>	Omnivore	1
<i>Cathayornis</i> sp.	Omnivore	8
<i>Chaoyangia beishanensis</i>	Omnivore	1
<i>Cuspirostrisornis hou</i>	Omnivore	1
<i>Eocathayornis walkeri</i>	Omnivore	1
<i>Gansus yumenensis</i>	Omnivore	1
<i>Jeholornis prima</i>	Omnivore	3
<i>Largirostrornis sexdentornis</i>	Omnivore	1
<i>Longchengornis sanyanensis</i>	Omnivore	1
<i>Longipteryx chaoyangensis</i>	Omnivore	1
<i>Otogornis genghisi</i>	Omnivore	1
<i>Sapeornis chaoyangensis</i>	Omnivore	3
<i>Sinornis santensis</i>	Omnivore	1
<i>Songlingornis linghensis</i>	Omnivore	1
<i>Yanornis martini</i>	Omnivore	4
<i>Yixianornis grabau</i>	Omnivore	1

Table 4. Equations of energy intake for ancient animals used this study. Modified from Matsukawa *et al.* (2006). Ed: energy intake (kJ day⁻¹), W: body mass (kg)

Animal types	Unit	Formula
Endothermic herbivorous animals	kJ/day	Ed = 1176 × W ^{0.75}
Endothermic carnivorous animals	kJ/day	Ed = 735 × W ^{0.75}
Endothermic omnivorous animals	kJ/day	Ed = 955.5 × W ^{0.75}
Ectothermic herbivorous animals	kJ/day	Ed = 176.4 × W ^{0.75}
Ectothermic carnivorous animals	kJ/day	Ed = 110.3 × W ^{0.75}
Ectothermic omnivorous animals	kJ/day	Ed = 143.3 × W ^{0.75}
Omnivorous birds	kJ/day	Ed = 1068.8 × W ^{0.723}

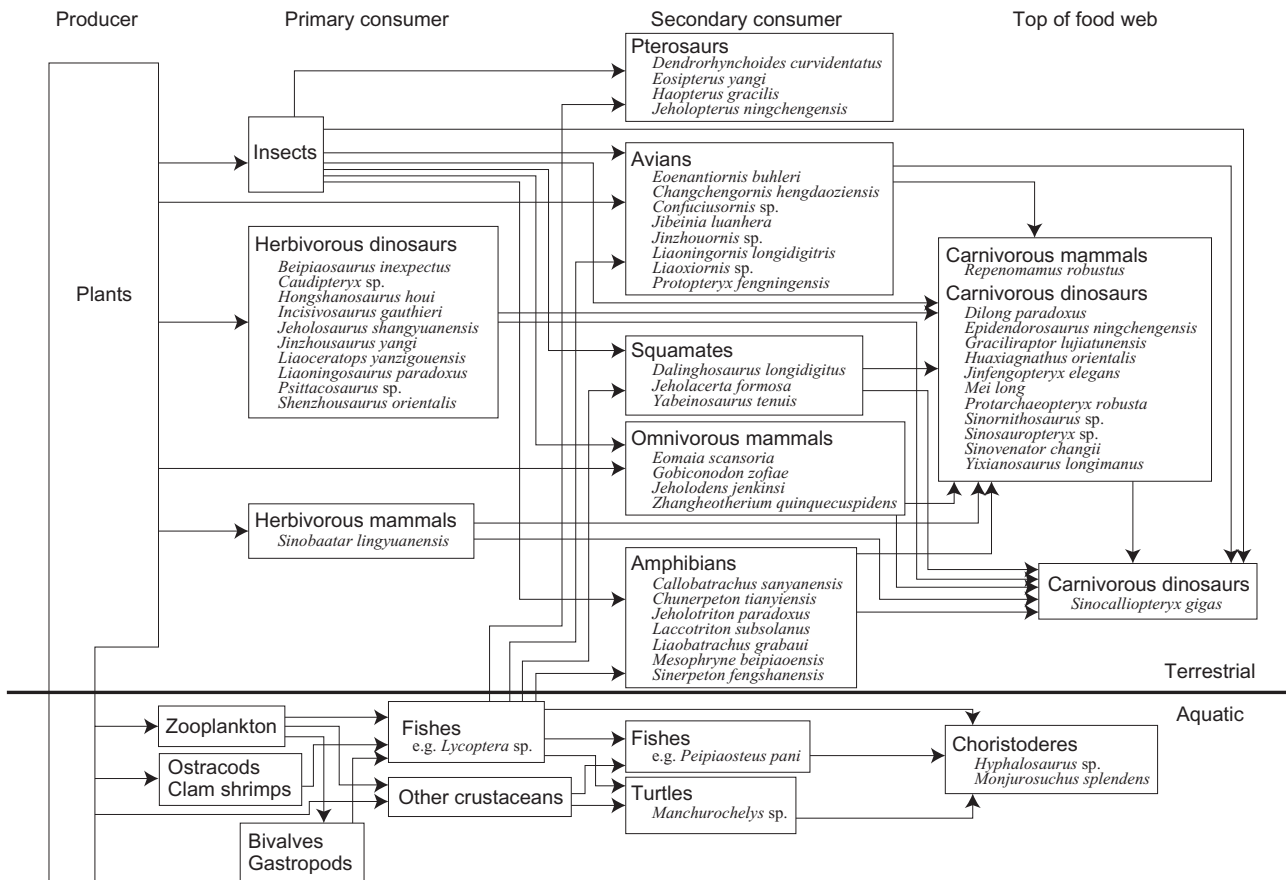


Figure 2. Early Cretaceous food-web model based on taxa occurrences from the Yixian Formation of the Jehol Group.

(3) Geographical Setting

To estimate energy requirements and population sizes of animals, we assume a total area for the reconstructed paleoecosystem based on the distribution of the related sedimentary strata. The Yixian Formation in the Liaoning Province extends from the eastern side of Fuxin to the western side of Lingyuan east and west (Jiang & Sha, 2007). The Jiufotang Formation outcrops are distributed east-west from western side of Fuxin to the western side of Lingyuan east and west. The total area covered by the Jehol ecosystem was approximately 38 000 km², covering Fuxin, western Liaoning Province and Luanping, northern Hebei Province.

The reconstructed food webs (Figs 2, 3) include terrestrial and aquatic herbivores (the trophic level directly dependent on plant biomass). Much of the Jehol Group is interpreted as having a lacustrine origin (Chang *et al.*, 2003) but the detailed paleogeography is not fully understood, and the relative importance of terrestrial and aquatic habitats cannot be determined with confidence. Therefore, in this paper, only values for the terrestrial energy flow

are calculated and the terrestrial vertebrate community is emphasized. Because the productivity of fish populations cannot be estimated, we also excluded the fish-eating pterosaurs except for *Jeholopterus ningchengensis* and *Sinopterus dongi*, that appear to have been insectivorous and frugivorous, respectively (Wang & Zhou, 2006).

(4) Net Primary Productivity

The Jehol Group yields diverse plant fossils such as bryophytes, lycopods, sphenopsids, filicopsids, ginkgos, czezanowskialeans, conifers, bennettites, gnetales, and angiosperms. The dominant plant taxa in the Yixian Formation are conifers, including evergreen trees of the genus *Schizolepis*, which appear to have comprised more than 90% of the terrestrial vegetation (Chang *et al.*, 2003). The ginkgos that occurred in the Jehol Group are also gymnosperms but are seasonally deciduous like angiosperms (Chang *et al.*, 2003). Kimura (1987) divided East Asian flora of the Late Jurassic to Early Cretaceous into three types: Tetori, Ryoseki, and mixed. The Jehol flora is the mixed type, suggesting a

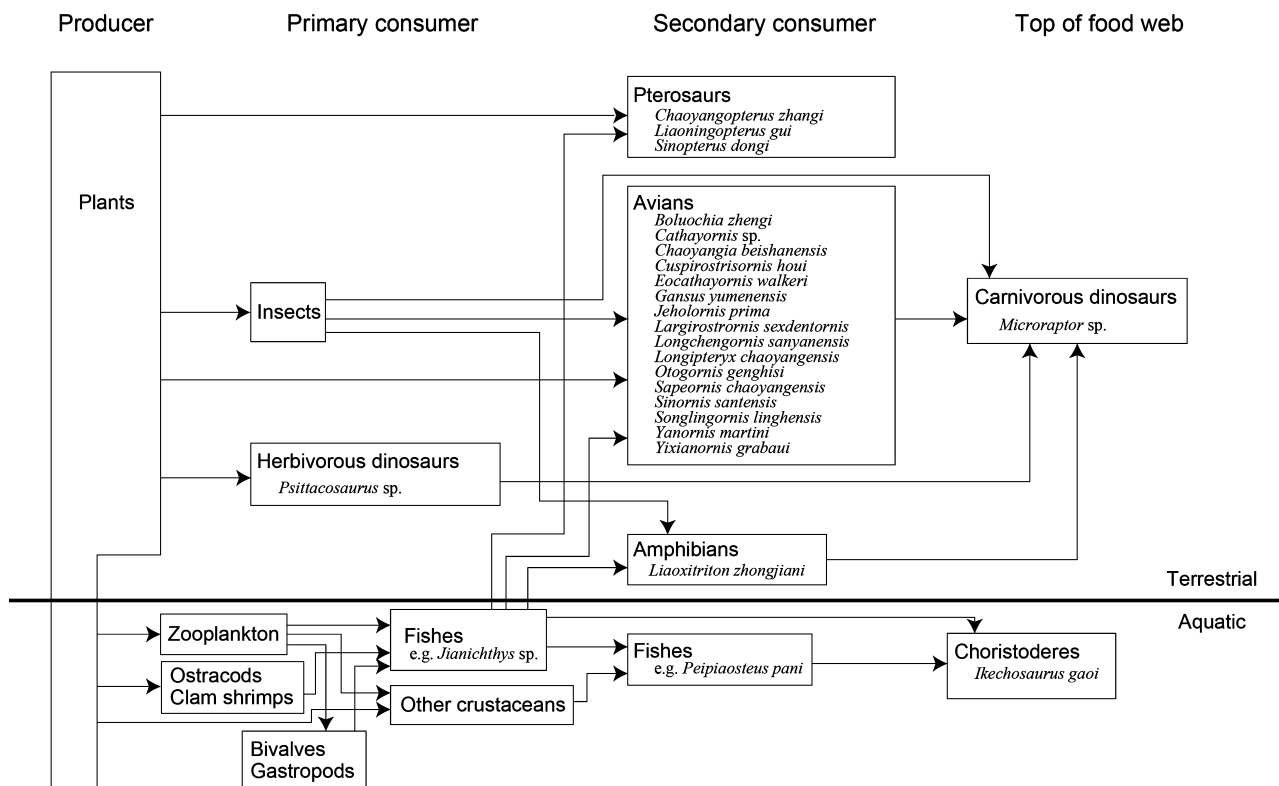


Figure 3. Early Cretaceous food-web model based on taxa occurrences from the Jiufotang Formation of the Jehol Group.

warm-temperate and arid/semi-arid climate (Kimura, 1987; Saiki & Wang, 2003). This concurs with the inference of Barrett & Hilton (2006) that climates fluctuated between arid/semi-arid and more mesic conditions. We have tentatively assumed a 9 : 1 ratio for evergreen over deciduous forest.

Mean NPP of the present temperate evergreen forest and temperate deciduous forest are estimated as $1300 \text{ gm}^{-2} \text{ year}^{-1}$ and $1200 \text{ gm}^{-2} \text{ year}^{-1}$, respectively (Whittaker, 1975), and these values have been applied to our reconstruction of the paleoecosystem. The values were converted to $23\,205 \text{ kJ m}^{-2} \text{ year}^{-1}$ and $21\,420 \text{ kJ m}^{-2} \text{ year}^{-1}$ because the calorific transfer efficiency of plant dry matter is 17.8 kJ g^{-1} in terrestrial plants (Whittaker, 1975). The actual rate of production in the study area was estimated by multiplying the mean NPP and estimated land areas. Production by the evergreen forest was estimated at approximately $7.9 \times 10^{14} \text{ kJ year}^{-1}$ by multiplying the mean NPP ($23\,205 \text{ kJ m}^{-2} \text{ year}^{-1}$) by $3.42 \times 10^{10} \text{ m}^2$ or 90% of the study area. Production by the deciduous forest was estimated at approximately $8.1 \times 10^{13} \text{ kJ year}^{-1}$ by multiplying the mean NPP ($21\,420 \text{ kJ m}^{-2} \text{ year}^{-1}$) by $3.8 \times 10^9 \text{ m}^2$ or 10% of the study area. Total production in the study area is approximately $8.75 \times 10^{14} \text{ kJ year}^{-1}$.

(5) Energy-flow Calculations

In the Yixian terrestrial ecosystem, we estimate that herbivorous vertebrates and insects consumed about $4.38 \times 10^{13} \text{ kJ year}^{-1}$ of the production of plants, based on a 5% consumption efficiency (Begon *et al.*, 1996).

In the Yixian herbivorous vertebrate community, the ratio of energy for *Jinzhouosaurus yangi* is approximately 0.252. Thus, *J. yangi* required ca $1.1 \times 10^{13} \text{ kJ year}^{-1}$. The productivity of *J. yangi* was estimated as ca $5.5 \times 10^{11} \text{ kJ year}^{-1}$ by multiplying *J. yangi*' intake (ca $1.1 \times 10^{13} \text{ kJ year}^{-1}$) and the assimilation efficiency (0.5) and production efficiency (0.1) (Begon *et al.*, 1996). The productivity is also used for carnivores at higher trophic level. Because mean consumption efficiency of vertebrates feeding on herbivorous vertebrates is 0.75 (Begon *et al.*, 1996), carnivores obtained about $4.1 \times 10^{11} \text{ kJ year}^{-1}$ by preying on *J. yangi*.

By similar calculations, based on the food-web model, we can estimate total annual energy intake for each taxon. Dividing the energy intake for a taxon by that for an individual, provides estimates of population sizes. For instance, the population for *J. yangi* was calculated to be near 1.0×10^6 by dividing the energy intake for a group of *J. yangi*. (about

1.1×10^{13} kJ year⁻¹) by that for an individual (ca 1.1×10^7 kJ year⁻¹). The population density of *J. yangi* was calculated at about 27.4 per 1 km² by dividing the population size (about 1.0×10^6) by the estimated area size (38 000 km²). Finally, biomass of *J. yangi* was estimated at about 24 695 kg* km⁻² by multiplying the population density (about 27.4 individuals km⁻²) and estimated mean body mass (900 kg).

RESULTS

The food-web models of both the Yixian and Jiufotang terrestrial ecosystems indicate the presence of four trophic levels; a producer, a primary consumer, a secondary consumer, and the top of the food web (Figs 2, 3). Calculations of energy flow have estimated population size, population density, productivity, and biomass for each terrestrial taxon in the Yixian and Jiufotang ecosystems (Tables 5 and 6). The ecological pyramids based on productivity, population density, and biomass of each trophic level has been also made (Figs 4, and 5).

For the Yixian terrestrial ecosystem, the population density of the vertebrates was estimated at 866 individuals km⁻² with the dominant taxa being herbivo-

rous dinosaurs (50.7%) and avians (33.7%) (Fig. 6). In contrast, the population density of the Jiufotang terrestrial ecosystem were calculated at 4122 individuals 1 km⁻² dominated by avians (83.9%) and herbivorous dinosaurs (9.0%) (Fig. 7). Carnivorous dinosaurs were estimated to have been a minor component of the Yixian and Jiufotang terrestrial vertebrate faunas (2.3% and 0.5% respectively). Some ecological pyramids of the Jehol ecosystem are unusually top heavy, such as those of the Yixian terrestrial ecosystem based on productivity and biomass, and those of the Jiufotang terrestrial ecosystem based on population density (Figs 4, and 5).

DISCUSSION

COMPARISON BETWEEN THE YIXIAN AND JIUFOTANG TERRESTRIAL FAUNAS

The reconstructed paleoecosystems and estimated population densities of the terrestrial vertebrates provide information about spatial and temporal variations of the faunal composition. In the Yixian terrestrial vertebrate fauna, avians are a secondary group accounting for 33.7% of the terrestrial vertebrate fauna (Fig. 6). In contrast, avians are the most

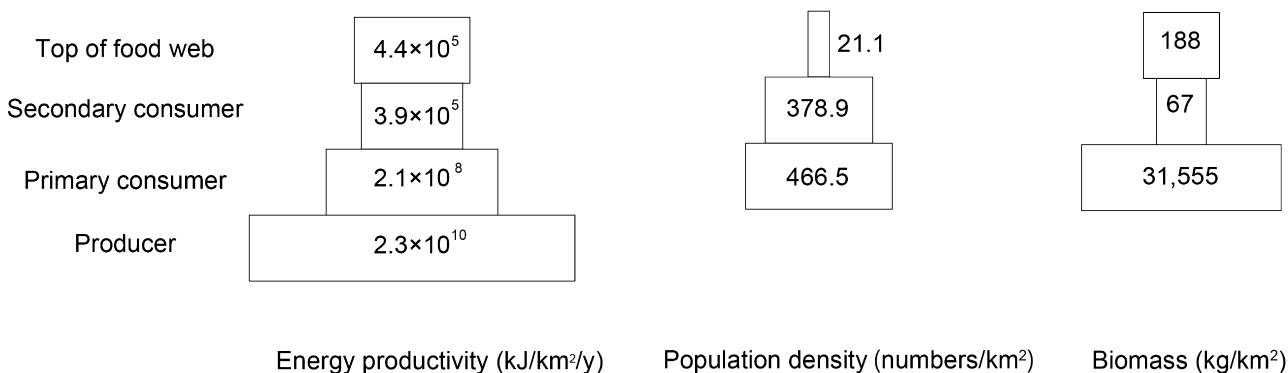


Figure 4. Ecological pyramids of the Yixian terrestrial ecosystem based on productivities, population densities, and biomass of each trophic level.

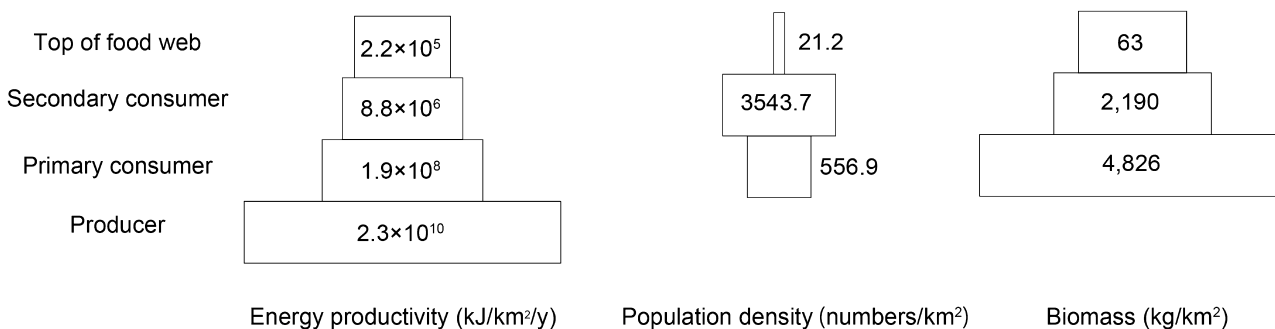


Figure 5. Ecological pyramids of the Jiufotang terrestrial ecosystem based on productivities, population densities, and biomass of each trophic level.

Table 5. Results of the energy-flow modeling of the Yixian terrestrial ecosystem

Taxa / Scientific name	Feeding mode	Specimen count	Body mass (kg)	Required energy of individuals (kJ/year)	Energy distributed for each species (kJ/year)	Energy productivity for each species (kJ/year)	Estimated population	Population density (/km ²)	Biomass (kg/km ²)
Amphibians									
<i>Callobatrachus sanyanensis</i>	Omnivore	1	0.06	4 878	70 200 752	5 616 060	28 780	0.8	0.05
<i>Chunerpeton tianyiensis</i>	Omnivore	1	0.02	1 725	24 819 714	1 985 577	28 780	0.8	0.01
<i>Jeholiriton paradoxus</i>	Omnivore	2	0.01	1 273	36 623 372	2 929 870	57 559	1.5	0.02
<i>Laccotriton subsolanus</i>	Omnivore	1	0	381	5 476 471	438 118	28 780	0.8	0.002
<i>Liaobatrachus grabau</i>	Omnivore	1	0.05	4 255	61 228 812	4 898 305	28 780	0.8	0.04
<i>Mesophryne beipiaoensis</i>	Omnivore	1	0.05	4 255	61 228 812	4 898 305	28 780	0.8	0.04
<i>Sinerpeton fengshanensis</i>	Omnivore	1	0	381	5 476 471	438 118	28 780	0.8	0.002
Squamates									
<i>Dalinghosaurus longidigitus</i>	Insectivore	10	0.5	23 928	6 886 298 225	550 903 858	287 797	7.6	3.8
<i>Jeholacerta formosa</i>	Insectivore	1	0.5	23 928	688 629 823	55 090 386	28 780	0.8	0.4
<i>Yabeinosaurus tenuis</i>	Insectivore	4	0.5	23 928	2 754 519 290	220 361 543	115 119	3.0	1.5
Pterosaurs									
<i>Jeholopterus ningchengensis</i>	Insectivore	1	2	451 183	12 984 928 459	207 758 855	28 780	0.8	1.5
Dinosaurs									
<i>Beipiaosaurus inexpectus</i>	Herbivore	1	90	12 542 441	13 077 758 614 178	130 777 586 142	1 042 680	27.4	2,469.5
<i>Caudipteryx</i> sp.	Herbivore	2	5	1 435 250	2 993 015 278 826	29 930 152 788	2 085 361	54.9	274.4
<i>Dilong paradoxus</i>	Carnivore	1	20	2 537 188	126 623 352 363	2 025 973 638	49 907	1.3	26.3
<i>Epidendrosaurus ningchengensis</i>	Carnivore	1	3	611 535	30 519 839 937	488 317 439	49 907	1.3	3.9
<i>Graciliraptor lujiatunensis</i>	Carnivore	1	5	960 725	47 946 879 309	767 150 069	49 907	1.3	6.6
<i>Hongshanosaurus houi</i>	Herbivore	2	6	246 834	514 737 877 520	25 736 893 876	2 085 361	54.9	329.3
<i>Huaxiagnathus orientalis</i>	Carnivore	1	20	2 537 188	126 623 352 363	2 025 973 638	49 907	1.3	26.3
<i>Incisivosaurus gauthieri</i>	Herbivore	1	5	1 435 250	1 496 507 639 413	14 965 076 394	1 042 680	27.4	137.2
<i>Jeholosaurus shangyuanensis</i>	Herbivore	2	2	108 284	225 811 048 029	11 290 552 401	2 085 361	54.9	109.8
<i>Jimfengopteryx elegans</i>	Carnivore	1	1	300 085	14 976 317 294	239 621 077	49 907	1.3	1.3
<i>Jinzhousaurus yangi</i>	Herbivore	1	900	1 0 579 699	11 031 246 164 425	551 562 308 221	1 042 680	27.4	24 695.1
<i>Liaoceratops yanzigouensis</i>	Herbivore	2	10	362 069	755 044 745 629	37 752 237 281	2 085 361	54.9	548.8
<i>Liaoningosaurus paradoxus</i>	Herbivore	1	3	146 768	153 032 486 577	7 651 624 329	1 042 680	27.4	82.3

Table 5. Continued

Taxa / Scientific name	Feeding mode	Specimen count	Body mass (kg)	Required energy of individuals (kJ/year)	Energy distributed for each species (kJ/year)	Energy productivity for each species (kJ/year)	Estimated population	Population density (/km ²)	Biomass (kg/km ²)	
<i>Mei long</i>	Carnivore	1	1	300 085	14 976 317 294	239 621 077	49 907	1.3	1.3	
<i>Protarchaeopteryx robusta</i>	Carnivore	1	3	611 535	30 519 839 937	488 317 439	49 907	1.3	3.9	
<i>Psittacosaurus</i> sp.	Herbivore	3	12	415 124	1 298 523 708 006	64 926 185 400	3 128 041	82.3	987.8	
<i>Shenzhousaurus orientalis</i>	Herbivore	1	70	10 387 803	10 831 159 839 756	108 311 598 398	1 042 680	27.4	1920.7	
<i>Sinocallopteryx gigas</i>	Carnivore	2	20	2 537 188	262 135 612 948	4 051 947 276	103 317	2.7	54.4	
<i>Sinornithosaurus</i> sp.	Carnivore	2	6	1 096 093	109 405 305 279	1 750 484 884	99 814	2.6	15.8	
<i>Sinosauropteryx</i> sp.	Carnivore	2	9	1 393 998	139 140 381 027	2 226 246 096	99 814	2.6	23.6	
<i>Sinovenator changii</i>	Carnivore	1	2	495 323	24 720 071 324	395 521 141	49 907	1.3	2.6	
<i>Yixianosaurus longimanus</i>	Carnivore	1	10	1 508 621	75 290 695 778	1 204 651 132	49 907	1.3	13.1	
Avians										
<i>Changchengornis hengdaoziensis</i>	Omnivore	1	0.25	143 185	93 459 603 886	944 105 648	652 719	17.2	4.3	
<i>Confuciusornis</i> sp.	Omnivore	8	0.25	143 185	747 676 831 085	7 552 845 184	5 221 749	137.4	34.4	
<i>Eoenantiornis buhleri</i>	Omnivore	1	0.05	44 724	29 192 320 796	294 893 556	652 719	17.2	0.9	
<i>Jibeinia luanhera</i>	Omnivore	1	0.25	143 185	93 459 603 886	944 105 648	652 719	17.2	4.3	
<i>Jimzhouornis</i> sp.	Omnivore	2	0.2	121 852	159 069 894 216	1 606 884 465	1 305 437	34.4	6.9	
<i>Liaoningornis longidigitris</i>	Omnivore	1	0.1	73 822	48 185 160 480	486 754 494	652 719	17.2	1.7	
<i>Liaoxiornis</i> sp.	Omnivore	2	0.05	44 724	58 384 641 592	589 787 112	1 305 437	34.4	1.7	
<i>Protopteryx fengningensis</i>	Omnivore	1	0.1	73 822	48 185 160 480	486 754 494	652 719	17.2	1.7	
Mammals										
<i>Eomaia scansoria</i>	Omnivore	1	0.03	21 927	14 312 140 606	144 577 680.8	652 719	17.2	0.4	
<i>Gobiconodon zoffae</i>	Omnivore	1	0.1	62 018.8	40 480 846 703	408 927 434.1	652 719	17.2	1.7	
<i>Jeholodens jenkinsi</i>	Omnivore	1	0.02	18 548	12 106 596 956	122 297 828	652 719	17.2	0.3	
<i>Repenomamus robustus</i>	Carnivore	1	7	1 500 884	57 618 883 768	921 902 140	49 907	1.3	9.2	
<i>Sinobaatar lingyuanensis</i>	Herbivore	1	0.03	26 987	28 138 856 288	281 388 563	1 042 680	27.4	0.7	
<i>Zhangtheotherium quinquecupidens</i>	Omnivore	1	0.05	36 876.6	24 070 055 460	243 149 707.1	652 719	17.2	0.9	

Table 6. Results of the energy-flow modeling of the Jiufotang terrestrial ecosystem

Taxa/Scientific name	Feeding mode	Specimen count	Body mass (kg)	Required energy of individuals (kJ/year)	Energy distributed for each species (kJ/year)	Energy productivity for each species (kJ/year)	Estimated population	Population density (/km ²)	Biomass (kg/km ²)
Amphibians									
<i>Liaoxitriton zhongjitani</i>	Omnivore	34	0.01	1 273	2 107 879 561	168 630 365	3 312 869	87.2	0.9
Pterosaurs									
<i>Sinopterus dongi</i>	frugivore	1	2	721 893	5 092 094 074 201	50 920 940 742	7 053 810	185.6	371.3
Dinosaurs									
<i>Microraptor</i> sp.	Carnivore	2	3	664 053	533 857 376 151	8 541 718 018	803 938	21.2	63.5
<i>Psittacosaurus</i> sp.	Herbivore	2	12	415 124	5 856 405 110 791	292 820 255 540	14 107 619	371.3	4455.0
Avians									
<i>Boluochia zhengi</i>	Omnivore	1	0.25	143 185	626 904 833 375	6 301 244 282	4 378 282	115.2	28.8
<i>Cathayornis</i> sp.	Omnivore	8	0.25	143 185	5 015 238 666 999	50 409 954 253	35 026 255	921.7	230.4
<i>Chaoyangia beishanensis</i>	Omnivore	1	0.1	73 822	323 214 616 217	3 248 745 493	4 378 282	115.2	11.5
<i>Cuspirostrisornis houi</i>	Omnivore	1	1	390 110	1 708 012 292 440	17 167 841 302	4 378 282	115.2	115.2
<i>Eoathayornis walkeri</i>	Omnivore	1	0.25	143 185	626 904 833 375	6 301 244 282	4 378 282	115.2	28.8
<i>Gansus yumenensis</i>	Omnivore	1	0.25	143 185	626 904 833 375	6 301 244 282	4 378 282	115.2	28.8
<i>Jeholornis prima</i>	Omnivore	3	2	643 920	8 457 790 696 540	85 012 273 673	13 134 846	345.7	691.3
<i>Largirostrornis sexdentornis</i>	Omnivore	1	1	390 110	1 708 012 292 440	17 167 841 302	4 378 282	115.2	115.2
<i>Longchengornis sanyanensis</i>	Omnivore	1	0.25	143 185	626 904 833 375	6 301 244 282	4 378 282	115.2	28.8
<i>Longipteryx chaoyangensis</i>	Omnivore	1	0.25	143 185	626 904 833 375	6 301 244 282	4 378 282	115.2	28.8
<i>Otogornis genghisi</i>	Omnivore	1	0.25	143 185	626 904 833 375	6 301 244 282	4 378 282	115.2	28.8
<i>Sapeornis chaoyangensis</i>	Omnivore	3	2	643 920	8 457 790 696 540	85 012 273 673	13 134 846	345.7	691.3
<i>Sinornis santensis</i>	Omnivore	1	0.25	143 185	626 904 833 375	6 301 244 282	4 378 282	115.2	28.8
<i>Songlingornis linghensis</i>	Omnivore	1	0.05	44 724	195 815 156 961	1 968 208 047	4 378 282	115.2	5.8
<i>Yanornis martini</i>	Omnivore	4	0.25	143 185	2 507 619 333 499	25 204 977 126	17 513 127	460.9	115.2
<i>Yixianornis grabaui</i>	Omnivore	1	0.1	73 822	323 214 616 217	3 248 745 493	4 378 282	115.2	11.5

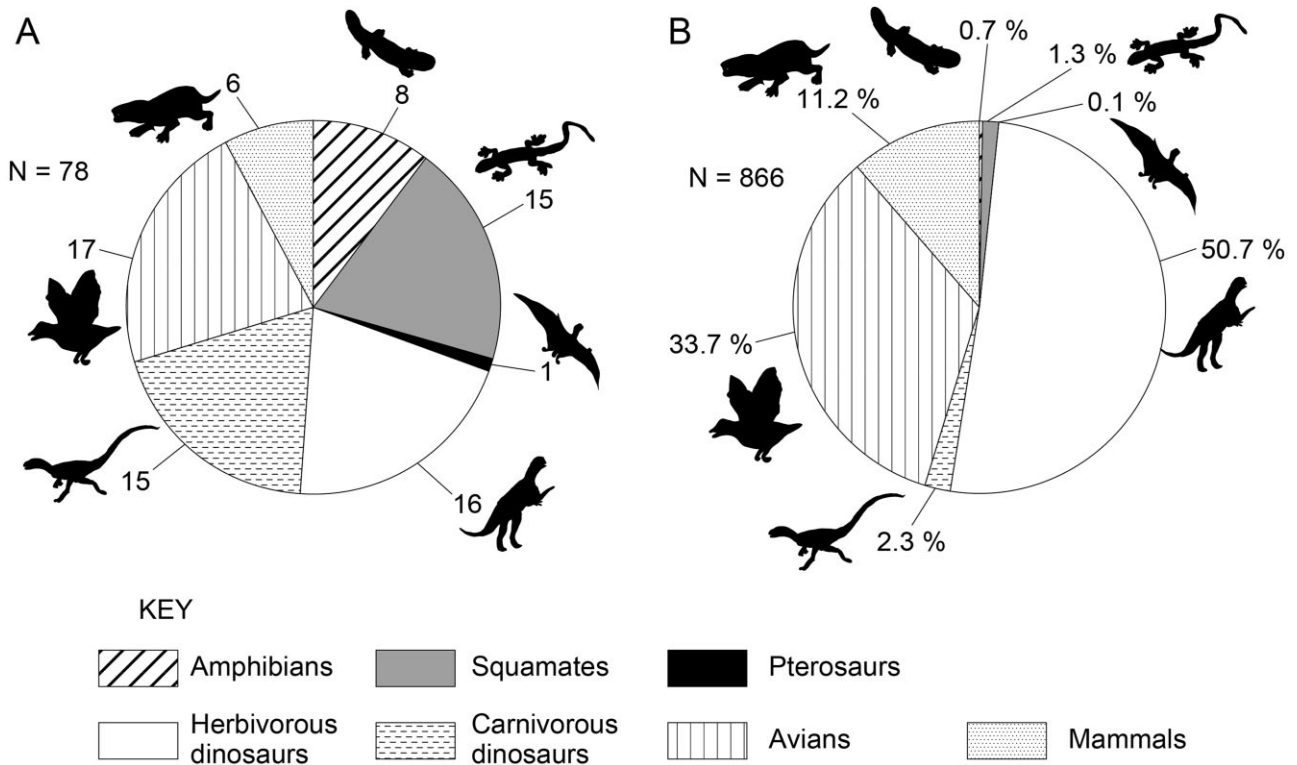


Figure 6. Ratio of the Yixian terrestrial vertebrate fauna on the basis of actual fossil data (A) and estimated population densities (B).

dominant group in the Jiufotang fauna, accounting for 83.9% of the terrestrial vertebrate fauna (Fig. 7). The density of avians in the Jehol terrestrial ecosystem does not contradict fossil data: the Yixian Formation yields eight genera and 17 individuals of avians while the Jiufotang Formation 16 genera and 30 individuals (Table 2).

Estimated population densities also suggests variation in relative abundance for herbivorous and carnivorous dinosaurs in the two areas (Fig. 8). Theropod dinosaurs comprise an estimated 34.2% of the dinosaur community in the Yixian ecosystem, but only 5.4% in the Jiufotang ecosystem. In contrast, ceratopsids comprise 41.9% and 94.6% in the two communities, respectively. These changes in vertebrate fauna during the deposition of the Yixian Formation through the Jiufotang Formation possibly reflect temporal faunal transitions.

ECOLOGICAL PYRAMIDS

Ecological pyramids usually form a typical bottom-heavy shape. However, pyramids of the Jehol ecosystem include some top-heavy shapes (Figs 4, 5). This is because the animals at the top of the food web, were carnivorous dinosaurs that preyed on primary consumers such as herbivorous dinosaurs rather than secondary consumers such as avians and squamates. The

smaller population density of herbivorous dinosaurs in the Jiufotang ecosystem reflects large body masses and energy intakes. The primary consumers in both ecosystems must also have included a variety of insects but it is impossible to assess their importance.

POTENTIAL FOR FOSSIL PRESERVATION

Energy-flow modeling becomes a useful tool to evaluate the degree of completeness of fossil assemblages. The analyses provide estimates of energy flow and animal population densities at each trophic level. Therefore, the proportion of animals that belong to different trophic levels may vary when applying assessments based on estimated population density rather than actual fossil data. In the both Yixian and Jiufotang vertebrate faunas, the population density estimates show that a smaller proportion of theropods were included in the dinosaur communities than is suggested by the fossil data (Fig. 8). In the Yixian terrestrial ecosystem, theropods account for only 34.2% of the estimated dinosaur numbers, but their fossil frequency suggests a value of 64.5%. Perhaps theropods preferred open, near-shore habitats, such as lake margins, that offered a higher preservation potential than upland habitats occupied by ornithomids, ceratopsids, ankylosaurids, and other herbivorous dinosaurs.

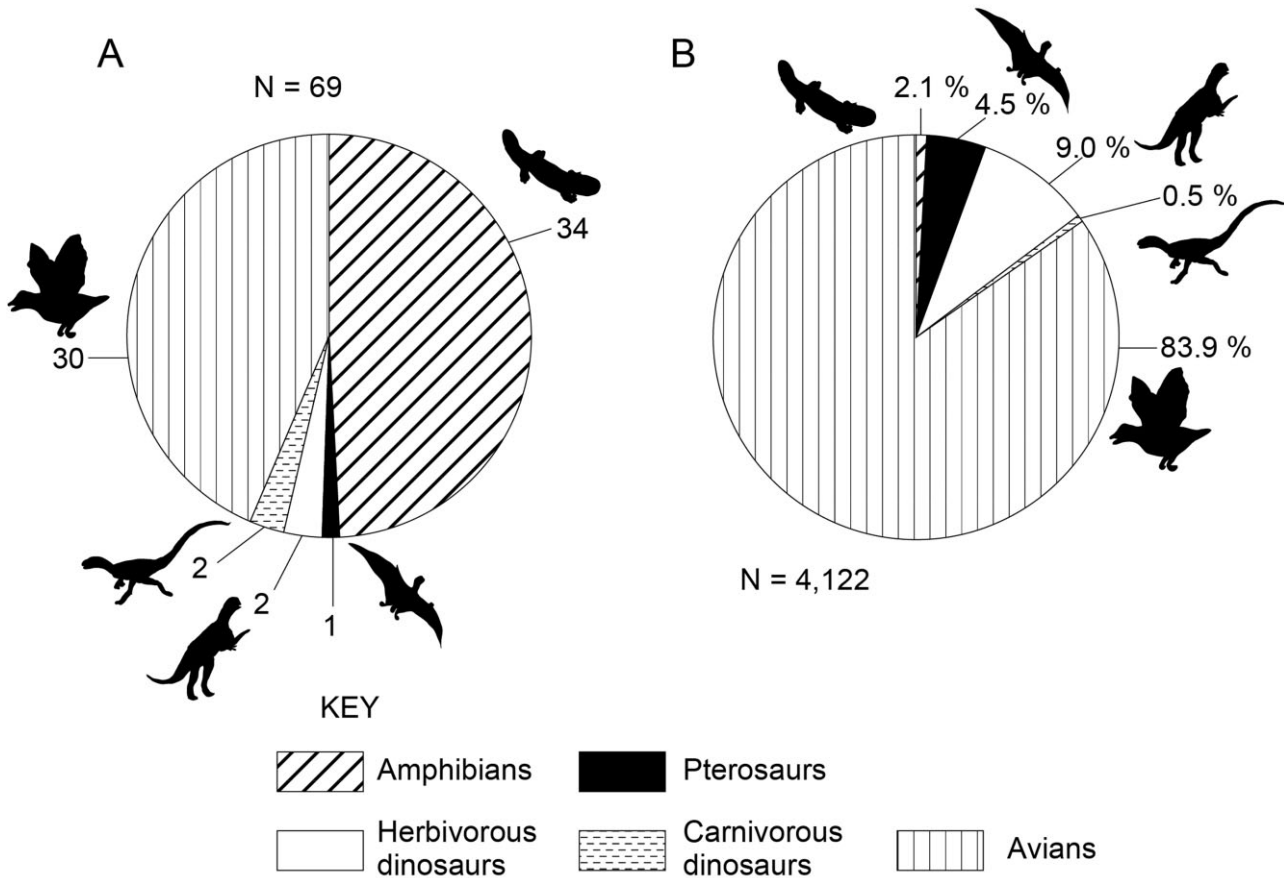


Figure 7. Ratio of the Jiufotang terrestrial vertebrate fauna on the basis of actual fossil data (A) and estimated population densities (B).

BIODIVERSITY

Diversity refers to the taxonomic richness of a community. Here, Simpson's diversity indices (Begon *et al.*, 1996), which take into account both abundance patterns and species richness, have been estimated on the basis of fossil data, estimated population density, and estimated biomass to compare the biodiversity of the Yixian and Jiufotang faunas (Table 7). The result suggest that the diversity of the Yixian communities (based on fossil data and estimated population density) was larger than that of Jiufotang. In contrast, diversity indices based on biomass show a more diverse Jiufotang community (Table 7). This implies that the existence of heavy herbivorous dinosaurs such as *Jinzhouosaurus yangi* in the Yixian terrestrial ecosystem decreased overall diversity. In other words, the majority of biomass in the Yixian terrestrial vertebrate fauna was contained within large herbivorous dinosaurs. In spite of this result, diverse fossil taxa have been discovered from the Yixian Formation.

In earlier studies, Matsukawa *et al.* (2006) reconstructed the Early Cretaceous terrestrial ecosystems

in the Choyr basin, southeastern Mongolia, and Tetori basin, inner zone of southwest Japan, and estimated Simpson's diversity indices for each terrestrial vertebrate community on the basis of estimated population size, biomass, and actual fossil data of vertebrate taxa (Table 7) so that the biodiversity of the Choyr, Tetori, and Jehol faunas could be compared. Vertebrate species richness in the Choyr and Tetori fauna was smaller than in the Yixian and Jiufotang faunas. Similarly, the diversity indices based on estimated population size and fossil data indicate greater diversity among vertebrates of the Yixian fauna compared to the Choyr or Tetori faunas while values for the Jiufotang fauna are similar to the Tetori fauna.

In contrast, among the diversity indices based on biomass, the most diverse community is that of Tetori (Simpson's Diversity Index: $D = 2.46$), slightly lower in Jiufotang ($D = 2.38$), and much lower in Yixian ($D = 1.63$). The diversity index of the Choyr vertebrate community is the smallest ($D = 1.07$).

The relatively small diversity index of the Yixian fauna, due to dominance of heavy herbivorous

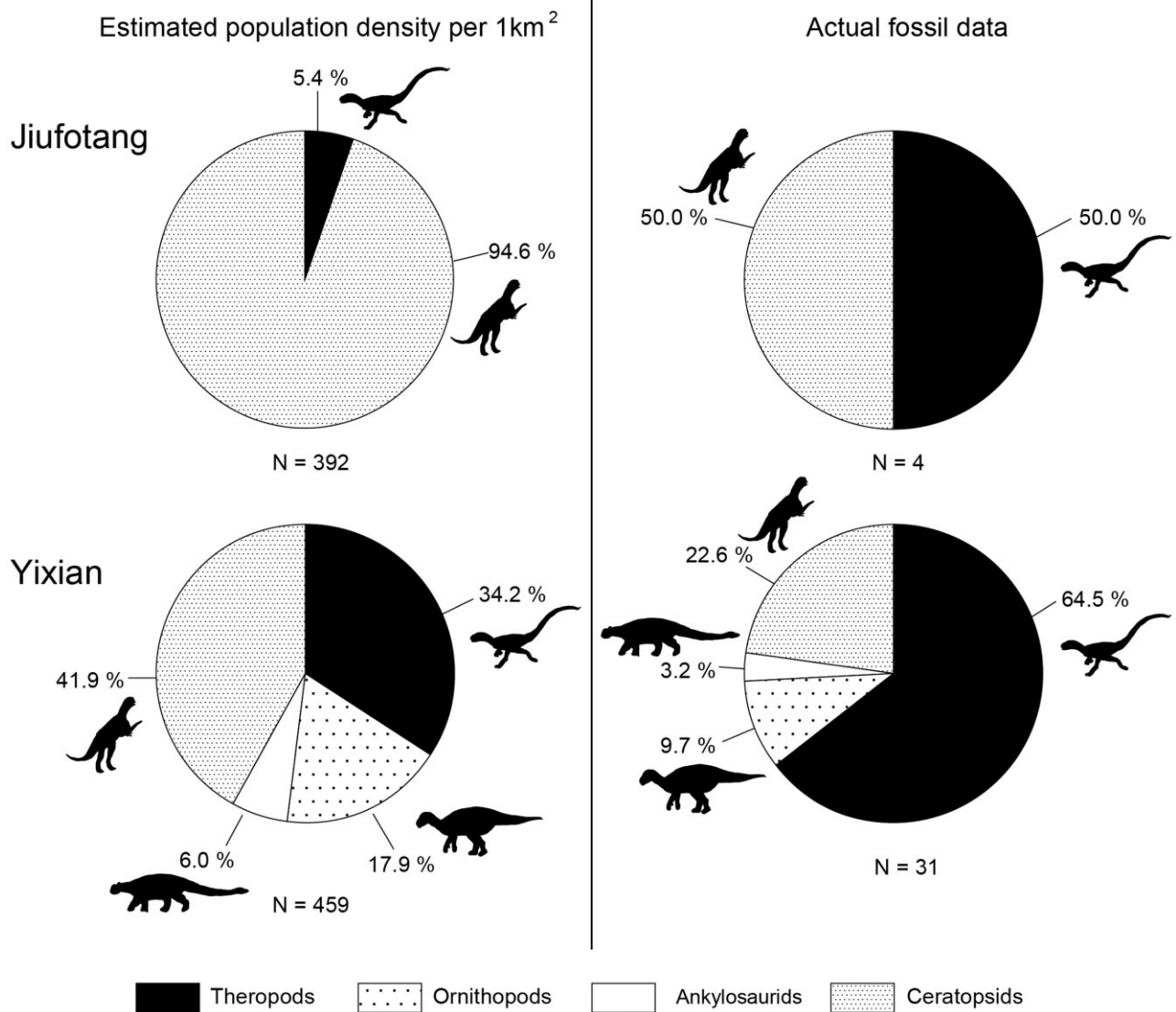


Figure 8. Comparison of estimated population densities and actual fossil data of dinosaurs in the Yixian and Jiufotang terrestrial vertebrate communities.

dinosaurs such as ornithopods, imply that diversity indices based on biomass decreased from the coastal area towards inland areas in the Early Cretaceous ecosystems of East Asia. Such a difference in biodiversity seems to reflect a difference in environments within the paleoecosystems. In these Early Cretaceous ecosystems, the highly diverse Tetori ecosystem lay in a mostly coastal area covered, by temperate evergreen forests or temperate deciduous forests. In contrast, the less diverse Choyr ecosystem lay in an inland basin that featured temperate steppes. The Jehol basin was located between these two and was also covered with the temperate evergreen and deciduous forests. Such a conclusion cannot be

derived solely from fossil data, and thus, food-web and energy-flow modeling may offer an effective tool to compare the biodiversity of long-extinct ecosystems in terms of both abundance patterns and species richness.

CONCLUSIONS

1. Paleoecosystems were reconstructed using a food-web and energy-flow model on the basis of data from the Lower Cretaceous Yixian and Jiufotang formations, in the ascending order of the Jehol Group of Northeast China. The reconstructions were used to make quantitative estimates of

Table 7. Simpson's diversity indices of the Yixian, Jiufotang, Choyr, and Tetori terrestrial vertebrate faunas based on estimated population densities, biomass, and actual fossil data. Data of the Choyr and Tetori ecosystems are from Matsukawa *et al.* (2006)

	Terrestrial ecosystem	Species richness	Simpson's diversity index		
			Estimated population size	Biomass	Specimen count
This study	Yixian	47	15.86	1.63	23.22
	Jiufotang	20	10.36	2.38	3.73
Matsukawa <i>et al.</i> (2006)	Choyr	7	3.11	1.07	3.40
	Tetori	16	3.82	2.46	3.76

$$D = \frac{1}{\sum_{i=1}^S P_i^2}$$

D: Simpson's diversity index

S: species richness

P_i: populational abundance of the species *i*

population densities and biomasses of the terrestrial vertebrate communities.

- Population densities of the terrestrial vertebrates were estimated as 866 individuals km⁻² and 4122 individuals km⁻² in the Yixian and Jiufotang terrestrial ecosystems, respectively. The Yixian terrestrial vertebrate fauna was dominated by herbivorous dinosaurs. In contrast, avians dominated the Jiufotang terrestrial vertebrate fauna. Furthermore, relative abundance of herbivorous dinosaurs within the terrestrial vertebrate fauna of the Yixian ecosystem was estimated to have been larger than in the Jiufotang ecosystem in the dinosaur fauna. These changes in vertebrate fauna seem to reflect temporal faunal transitions.
- Estimates of diversity indices based on biomass are larger for the Yixian and Jiufotang terrestrial vertebrate faunas on than for the Early Cretaceous faunas of the Choyr ecosystem, Mongolia, but, are smaller than the Early Cretaceous Tetori ecosystem, Japan. The difference in biodiversity was possibly caused by the differences in vegetation and environment in these ecosystems.

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