Density-dependent effect affecting elephant seed-dispersed tree recruitment (Irvingia gabonensis) in Congo Forest

David Beaune, Loïc Bollache, Barbara Fruth, Gottfried Hohmann, François Bretagnolle

Density-dependent effect affecting elephant seed-dispersed tree recruitment (*Irvingia gabonensis*) in Congo Forest

David Beaune,[1,2,] Loïc Bollache, [2] Barbara Fruth,[1] Gottfried Hohmann[1] and François Bretagnolle [2]*

[1] Max Planck Institute for Evolutionary Anthropology, Department of Primatology, Deutscher Platz 6, Germany
[2] Laboratoire Biogéosciences, UMR CNRS 6282, Université de Bourgogne, 6 bd Gabriel, 21000 Dijon, France
* corresponding author email: david.beaune@gmail.com

Introduction

Several tree species are known to be important for local wildlife, rural communities (White & Abernethy 1997) and even the 'Western world'. However, little is known about the ecology of these species, and a biodiversity crisis could change the population survival. Among these, the bush mango (*Irvingia gabonensis*), widespread in West and Central Africa, is of major importance for rural communities (Atangana et al. 2001; Leakey et al. 2005). Recently, the plant is used as a slimming supplement in the Western world. Elephants are widely recognized as the most important *Irvingia* seed dispersers in Africa (Theuerkauf et al. 2000; Nchanji & Plumptre 2003; Morgan & Lee 2007). In this study we focus on *I. gabonensis* as the example to illustrate seed fate without dispersion, and thus density-dependence effect affecting tree recruitment.

We investigated this megafaunal tree population's ability to survive without elephants in the evergreen lowland rainforest of the Max-Planck research site, LuiKotale, on the south-western fringe of Salonga National Park (NP), Democratic Republic of the Congo (DRC). In and around Salonga NP elephants (*Loxondota cyclotis*) have been severely poached for decades (Van Krunkelsven et al. 2000; Blake et al. 2007;), and poaching has increased with increasing post-war availability of automatic weapons (AK47) and ammunition. The current nationwide elephant population is said to have declined by as much as two-thirds to that of the 1990s, and the remainder is said to survive in fragmented subpopulations (Alers et al. 1992). Throughout 10 years of continuous presence at the research site at LuiKotale, pressure on the species became evident when carcasses from massacres were documented.

Overall, we aimed to assess the ability of the *I. gabonensis* tree community at LuiKotale to reproduce without elephant dispersal. If megafaunal trees depend on elephants for seed dispersal, one would expect no alternative seed dispersers and thus a high mortality of seedlings and poles due to the density-dependent effect (Paine et al. 2012).

Methods

Study site

The LuiKotale research site is located within the equatorial rainforest 2°47′ S–20°21′ E, at the south-western fringe of Salonga NP (DRC), in the same continuous forest block (Fig. 1). This park,

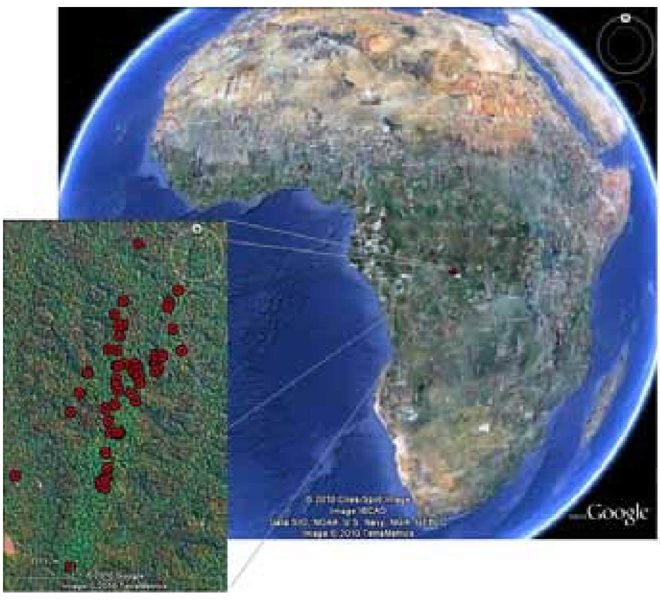

Figure 1. Sampling area, red spots representing adult trees.

classified as a World Heritage Site, is the largest protected rainforest area in Africa and the second largest protected rainforest in the world (33,346 km²) (Grossmann et al. 2008). The study site is a primary evergreen tropical lowland rainforest ancestrally owned and used by Lompole village, 17 km away. The site covers > 60 km² with a network trail of 76 km. Since 2001, all exploitation within the site ceased, to allow research (Hohmann & Fruth 2003).The climate is equatorial with abundant rainfall (> 2000 mm/yr), a small dry season in February and a larger one between May and August. Mean temperature at LuiKotale ranges between 21 °C and 28 °C, with a minimum of 17 °C and a maximum of 38 °C (2007–2010). Five major vegetation types were distinguished: 1) mixed tropical forest on *terra firme,* 2) monodominant forest dominated by *Monopetalanthus* sp., 3) monodominant primary forest dominated by *Gilbertiodendron dewevrei,* 4) temporarily inundated mixed forest, and 5) permanently inundated mixed forest. Dry habitats (1–3) dominate site cover, with 73% heterogeneous and 6% homogenous in composition. Wet habitats (4 + 5) represent 17% and 4% of the cover respectively (Mohneke & Fruth 2008).

To investigate the density-dependent effect on seed survival of this elephant-dependent tree, we focused on all adult trees of *Irvingia gabonensis* inventoried since 2007 that produced ripe fruits during the survey from January 2010 to June 2011. (A database of the LuiKotale research site geo-references all feeding trees within the observed range of bonobo, *Pan paniscus*, communities.)

We counted 1) seeds 2) seedlings 3) saplings and 4) poles in the fruit-fall zone of each individual and judged the state of each of the four stages of growth, assessing pathogens and folivores by visual inspection (absence/presence of traces).

Results

We investigated 54 adult trees of *I. gabonensis* (83.1 cm ± SE. 0.7 diameter at breast height) producing ripe fruit. Figure 2 shows the presence and state of 1) seeds, 2) seedlings, 3) saplings, and 4) poles.

Seeds

Seeds were present within all fruit-fall zones. Seeds revealed a loss rate of 54% ± SE 3 due to seed predation, and among the unopened seeds 76% ± 4 were rotten or showed signs of pathogen attacks. Red river hogs (*Potamochoerus porcus*) in herds of two to six animals were found responsible for predating on large quantities of seeds, cracking the endocarps (Beaune et al. 2012).

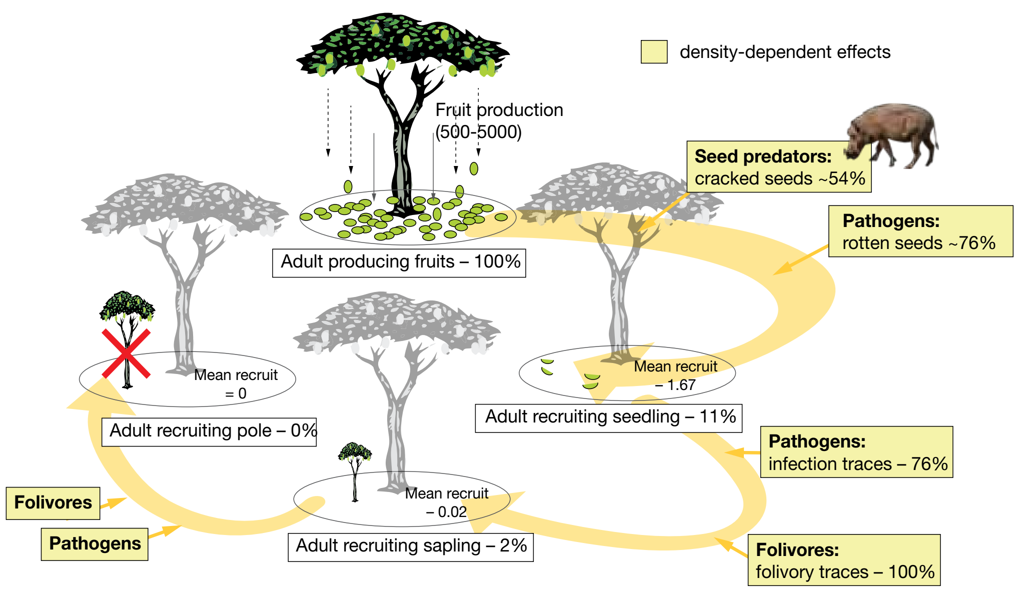

Figure 2. The density-dependent effect of *Irvingia gabonensis*. There was no recruitment under the parental trees (n = 54).

Figure 3. Seedling and adult tree of *Irvingia gabonensis.*

Seedlings

Only 6 (11%) of the 54 trees showed seedling recruitment. All 90 of these seedlings were infested by pathogens or showed traces of folivory whereas some of the other surrounding seedling species and the *Irvingia* of the nursery did not (unpublished data). Although these adult trees reproduced, no established offspring (i.e. those producing fruit) was found beneath the adults' crowns. A total of 48% ($n = 26$) of the fruit-fall zones clearly showed tracks of animals leading to the feeding place.

Saplings

A single sapling recruit (< 2 m high) was found below an adult crown.

Poles

No pole was found below an adult crown.

Conclusion

Our results showed a high mortality for *Irvingia* seeds and recruits on all levels, with a seed loss of 54% to predation and 76% to pathogens and seedling loss of 100% due to predation and pathogens. These results can be explained by the density-dependent effect, also named the Janzen-Connell effect (Janzen 1970; Connell 1971; Burkey 1994), where the mortality of seeds, eggs or other immobile organisms is correlated with their density, which attracts predators and pathogens. In the absence of an endozoochoric partner such as the elephant, this putting-all-your-eggs-in-one-basket adaptation is likely to turn out as a maladaptation, unless a tree species has alternative dispersal partners or mechanisms.

In the southern area of the Congo River, bonobos, the second biggest frugivores, are unable to replace elephants as seed dispersers, as the seeds are too large for them to swallow. They may contribute in some cases to dispersal outside the fruit-fall zone by short distance ectozoochoric transport, similar to what rodents can disperse (Forget & Wall 2001). For *I. gabonensis*, bonobos can be considered as a poor disperser, dispersing over much shorter distances than elephants and omitting passage through their digestive tract.

The survival of *I. gabonensis* is compromised without a seed-dispersal vector such as forest elephants.

References

Alers, M.P.T., Blom, A., Kiyengo, C.S., Masunda, T. and Barnes, R.F.W. 1992. Preliminary assessment of the status of the forest elephant in Zaire. *African Journal of Ecology* 30:279–291.

Atangana, A.R., Tchoundjeu, Z., Fondoun, J.M., Asaah, E., Ndoumbe, M. and Leakey, R.R.B. 2001. Domestication of *Irvingia gabonensis*: 1. Phenotypic variation in fruits and kernels in two populations from Cameroon. *Agroforestry Systems* 53:55–64.

Beaune, D., Bollache, L., Fruth, B. and Bretagnolle, F. 2012. Bush pig (*Potamochoerus porcus*) seed predation of bush mango (*Irvingia gabonensis*) and other plant species in Democratic Republic of Congo. *African Journal of Ecology* 50(4):509–512.

Blake, S., Strindberg, S., Boudjan, P., Makombo, C., Bila-Isia, I., Ilambu, O., Grossmann, F., Bene-Bene, L., de Semboli, B., Mbenzo, V., S'Hwa, D., Bayogo, R., Williamson, L., Fay, M., Hart, J. and Maisels, F. 2007. Forest elephant crisis in the Congo Basin. *PloS Biology* 5:945–953.

Burkey, T.V. 1994. Tropical tree species diversity: a test of the Janzen-Connell model. *Oecologia* 97:533–540.

Connell, J.H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine mammals and in rain forest trees. In: Boer, P.J.

and Gradwell, G. (eds.), *Dynamics of populations*, PUDOC. pp. 298–310.

Forget, P.M. and Wall, S.B.V. 2001. Scatter-hoarding rodents and marsupials: convergent evolution on diverging continents. *Trends in Ecology and Evolution* 16:65–67.

Grossmann, F., Hart, J.A., Vosper, A. and Ilambu, O. 2008. Range occupation and population estimates of bonobos in Salonga National Park: Application to large-scale surveys of bonobos in the Democratic Republic of Congo. In: Furuichi, T. and Thompson, J. (eds.), *Bonobos: behavior, ecology and conservation.* New York: Springer Science+Business Media, pp. 189–216.

Hohmann, G. and Fruth, B. 2003. LuiKotal—A new site for field research on bonobos in the Salonga National Park. *Pan Africa News* 10:25–27.

Janzen, D.H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* 104:501.

Leakey, R.R.B., Greenwell, P., Hall, M.N., Atangana, A.R., Usoro, C., Anegbeh, P.O., Fondoun, J.M. and Tchoundjeu, Z. 2005. Domestication of *Irvingia gabonensis*: 4. Tree-to-tree variation in food-thickening properties and in fat and protein contents of dika nut. *Food Chemistry* 90:365–378.

Mohneke, M. and Fruth, B. 2008. Bonobo (*Pan paniscus*) density estimation in the SW Salonga National Park/Democratic Republic of Congo: Common methodology revisited. In: Furuichi, T. and Thompson, J. (eds.), *Bonobos: Behavior, ecology, and conservation.* pp. 151–166.

Morgan, B.J. and Lee, P.C. 2007. Forest elephant group composition, frugivory and coastal use in the Reserve de Faune du Petit Loango, Gabon. *African Journal of Ecology* 45:519–526.

Nchanji, A.C. and Plumptre, A.J. 2003. Seed germination and early seedling establishment of some elephant-dispersed species in Banyang-Mbo Wildlife Sanctuary, south-western Cameroon. *Journal of Tropical Ecology* 19:229–237.

Paine, C.E.T., Norden, N., Chave, J., Forget, P-M., Fortunel, C., Dexter, K.G. and Baraloto, C. 2012. Phylogenetic density dependence and environmental filtering predict seedling mortality in a tropical forest. *Ecology Letters* 15:34–41.

Theuerkauf, J., Waitkuwait, W.E., Guiro, Y., Ellenberg, H. and Porembski, S. 2000. Diet of forest elephants and their role in seed dispersal in the Bossematie Forest Reserve, Ivory Coast. *Mammalia* 64:447–459.

Van Krunkelsven, E., Bila-Isia, I. and Draulans, D. 2000. A survey of bonobos and other large mammals in the Salonga National Park, Democratic Republic of Congo. *Oryx* 34:180–187.

White, L. and Abernethy, K. 1997. *A guide to the vegetation of the Lope Reserve, Gabon.* New York: Wildlife Conservation Society.