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Preface

Frugivores and seed dispersal (1985–2010); the 'seeds' dispersed, established and matured

1. Definition and history of FSD

'Dispersal' refers to the movement of individual organisms away from their natal origin (Clobert et al., 2001). Although established plants are sessile, their progeny are often dispersed by external vectors that transport them, sometimes very long distances (van der Pijl, 1982). 'Frugivores' are animals that eat fruits, and play the role of dispersal agents when they move viable propagules or seeds away from the parent plants (Howe, 1986), a key life-history stage during plant life cycle (Howe and Smallwood, 1982). Seed dispersal by frugivores therefore contributes to the spatial dynamics of plant populations (Cousens et al., 2008). It is now recognized as an important ecosystem service (MEA, 2005) that is threatened in the Anthropocene, especially in the tropical regions (Primack and Corlett, 2005). With this common interest, 220 participants gathered together to discuss Frugivores and Seed Dispersal (FSD) in June 2010 at Montpellier, France. Although much frugivory and seed dispersal work has been conducted in the tropics, this meeting was intentionally held in the temperate zone where animals also actively disperse seeds, such as jays and squirrels dispersing acorns, in order to highlight the geographical extent of these critical ecological interactions.

Biologists (Howe and Vande Kerckhove, 1980; Janzen, 1969, 1970; McKey, 1975; Snow, 1965, 1981) acknowledged early on that frugivores were critical to the dynamics of plant populations and thus for the selection and evolution of life-history traits. From its inception, the research field of frugivory and seed dispersal has been tightly linked and conceptually framed on the idea of coevolution (Ehrlich and Raven, 1964; Futuyma and Slatkin, 1983; see also Herrera, 2002). This field of research catalyzed a diversity of ideas on how plant–animal interactions have shaped natural ecosystems. Central to this framework was the pioneering Janzen–Connell Connell (Connell, 1971; Janzen, 1969, 1970) and the "escape hypothesis" (Howe and Smallwood, 1982), used for decades in studies of seed dispersal. Hence, the field of Frugivores and Seed Dispersal was born, with many ideas ready to "*disperse, take root and grow*" (Levey et al., 2002/page xvi). Between 1985 and 2005, the students and colleagues of Daniel Janzen, Henry Howe, and the late David Snow successfully organized four FSD symposia-workshops in Mexico (1985, 1991), Brazil (2000) and Australia (2005) to exchange new and emerging ideas within and across continents. The plenary presentations given at these conferences yielded important edited volumes that brought together key issues and identified central themes in the study of frugivory and seed dispersal (Dennis et al., 2007; Estrada and Fleming, 1986; Fleming and Estrada, 1993; Levey et al., 2002). The first two of these edited volumes stemmed from FSD conferences held in Mexico, and had a geographical focus on the Neotropics, primarily Central America (Estrada and Fleming, 1986; Fleming and Estrada, 1993). The two next symposia were held in Brazil (2000) and Australia (2005), and produced edited volumes (Dennis et al., 2007; Levey et al., 2002) and sought to balance the early geographical bias.

2. Growth of the field

Today, the topic of frugivory and seed dispersal has garnered further attention in biology more generally, as evidenced by the growing number of edited books, volumes and special issues that focus on seed dispersal by either animals or abiotic agents (Bullock and Nathan, 2008; Cain et al., 2003; Campos-Arceiz et al., 2011; Carlo et al., 2011; Dew and Boubli, 2005; Forget et al., 2005; Nathan, 2005, 2008). Journal editors also published special virtual issues on the theme by compiling articles published on seed dispersal, mostly by tropical frugivores (Ghazoul, 2008). To quantify the development of the field during the last 25 years, we searched the literature using ISI Web of Knowledge (®Thomson Reuters) using the two key terms 'frugivor* AND seed_dispersal' in Topic for the time span between 1969 and 2010. All Citation Databases listed by ISI were used. We compiled the number of articles using the graph provided between 1986 and 2010, and the number of citations for all published items in each year between 1969 and 2010. The results, presented in Fig. 1, show that there was no record of published items before 1986, and that the number of published items steadily increased after the release of the first FSD volume (Estrada and Fleming, 1986), with an important increase in the literature for the next decades, reaching ca. 2000 citations per year in the last couple of years (Fig. 1). These numbers demonstrate that research on frugivory and seed dispersal continues to flourish a quarter of a century after the first symposium. It is certain that the development of new technology and easy access to published material on line (this volume) contributed to spreading the information, especially in the last decade when the number of citations quadrupled (Fig. 1). However, similar searches for other fields, such as "general_ecology" have not shown such an increase, suggesting this surge in publications and citations is real and that the field of frugivory and seed dispersal is very relevant in 2011. A similar search in Acta Oecologica gives a total of 38 papers most of them since 2000.

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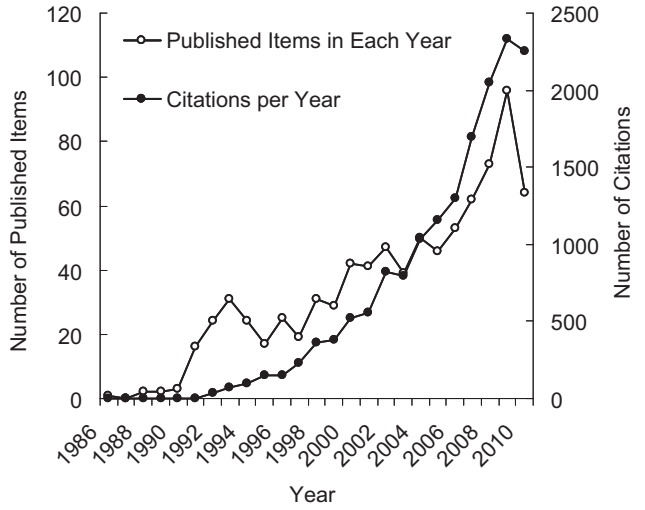

Fig. 1. Number of published items published in each year on Frugivores or Frugivory and Seed Dispersal ('frugivor* AND seed_dispersal') and number of citations per year referenced by ISI Web of Knowledge ®THOMSON REUTERS) between 1986 and 2010 (no indexed reference before 1986: updated 31 August 2011).

3. FSD2010

This volume presents papers based on the plenary addresses and one oral presentation from the *Fifth International Symposium on Frugivores and Seed Dispersal* (Jordano et al., 2011), with additional talks having been published in other journals (Bullock et al., 2011; Hansen and Traveset, in press). Like earlier volumes stemming from previous FSD symposia, this issue is, composed of four parts: 1) animal strategies and natural history oriented research, 2) plant strategies, life-history and physiological traits, 3) movement ecology, dispersal kernels, and genetic effects and, finally, 4) consequences of anthropogenic disturbance and climate change on seed dispersal systems. By publishing this 5th volume in a peer-reviewed journal, our hope is that the ideas that were presented and debated during this event will continue to disperse, establish and mature even more so than in the past.

Throughout this volume, authors emphasize the importance, as consumers of fruit and dispersers of seeds, of frugivores as well as seed-dispersing granivores, including animals as diverse as hornbills, toucans, elephant, squirrels and other rodents, fishes, primates, and earthworms (Campos-Arceiz and Blake, 2011; Chen and Chen, 2011; Forey et al., 2011; Gross-Camp and Kaplin, 2011; Horn et al., 2011; Kitamura, 2011; Steele et al., 2011). Other contributions discuss the evolution of life-history traits and adaptations ensuring both short- and long-term benefits of plant and animal partners in mutualisms (Borges et al., 2011; Chen and Chen, 2011; Fleming and Kress, 2011; García and Grivet, 2011; Hamrick and Trapnell, 2011; Schaefer, 2011; Tomás, 2011). In some instances, frugivores may benefit from and interact with introduced plants despite the obvious lack of coevolution (Hardesty et al., 2011; Westcott and Fletcher, 2011), the reciprocal being possible when introduced animals disperse native, as well as non-native plants (Shiels, 2011; Shiels and Drake, 2011).

In June 2010, one focal point during plenaries and symposia was on the interaction and mutualism between oaks and their seed dispersers (Steele et al., 2011), and the consequences of frugivore-mediated seed dispersal for the genetic diversity and spatial pattern of tree recruitment (García and Grivet, 2011). In the temperate regions of the world the maintenance of many oak forests critically depends on natural regeneration mediated by jays (*Garrulus glandarius*) and other animal dispersers (Bossema, 1979; Moore et al., 2007; Pons and Pausas, 2008). Hougner et al. (2006) have argued that although oaks (*Quercus robur* and *Quercus petrea*) were originally planted in a national park in Sweden, 85% of trees can be considered to have resulted from seed dispersal by jays. Hougner et al. (2006) have estimated the economic value of the service of oak seed dispersal performed by jays concluding that "*The continuous temporal and spatial oak dispersal service provided by jays holds several benefits compared to a man-made replacement of this service*." Likewise, in North America, Moore et al. (2007) demonstrate the keystone influence of tree squirrels (Sciuridae) on the dispersal of establishment of oaks.

Despite being a key stage in the plant life cycle and complementing pollination, dispersal of seeds remains barely mentioned in frameworks of ecosystem services (Costanza et al., 1997; Norberg, 1999). The Millenium Ecosystem Assessment report (MEA, 2005) mentions the example of the introduction of carnivorous mammals into the Balearic Islands, Spain, and the subsequent extinction of a frugivorous lizard (*Podarcis lilfordi*), a major seed disperser. The importance of pollination for agriculture, horticulture and the seed industry has repeatedly been acknowledged, and the negative effects of pollinator decline on seedset have been emphasized. In contrast, there has been scant interest in how human activities in natural and disturbed habitats have degraded an equally important ecosystem service, seed dispersal. The same statement likely holds for most frugivores that have a key role during the life cycle of plants, especially in the tropics where most plant species will not be able to move from one habitat patch to the next in the face of climate change (Corlett, 2011b; Hampe, 2011) and habitat alteration (Corlett, 2011a).

In the last decades, however, there has been much evidence of the importance of frugivorous animals as seed dispersers, and of the importance of seed dispersal as an ecosystem service. For instance, Fujita and Tuttle (1991) listed 289 plant species producing nearly 450 economically valuable products that rely to varying degrees upon flying foxes for propagation. Twenty years later, Kunz et al. (2011) reviewed the ecosystem services provided by bats, such as arthropod suppression, pollination, and seed dispersal, and concluded that services provided to humans offer important indirect benefits for well-being-the economic value of which have hardly been analyzed. In contrast, the ecosystem services provided by birds have been reviewed thoroughly, and seed dispersal by birds in tropical ecosystems is argued to be among the most important (Sekercioglu, 2006). Many of the frugivores and seed dispersers reviewed in this volume are equally important and play roles in plant community dynamics in ecosystems around the globe - at no cost to humans. In addition, frugivores indirectly contribute to many other ecosystem services offered by forests to people, including fruit, wood and non-timber forest products, carbon sequestration and forest cover. All of this comes at a modest cost — that of conserving frugivores and their staple resources (Corlett, 2011a; Fleming and Kress, 2011; Lambert, 2011).

4. Looking forward on frugivores and seed dispersal

The world changed rapidly between 1985 and 2010, and it is still uncertain how many of these changes will impact biodiversity. Seed dispersal by animals provides a fundamental service for ecosystems, ranging from the preservation of some important types of agroecosystems (e.g., the *Quercus* landscapes in Mediterranean habitats, Joffre et al., 1999; Pulido and Díaz, 2005) to the regeneration of Non-Timber Forest Products harvested in natural forests (e.g., the Brazil Nut and Carapa oil, Forget and Jansen, 2007; Peres et al., 2003; Weber et al., 2010; Zuidema and Boot, 2002). The key relevance of seed dispersal processes should not be overlooked. Indeed, seed dispersal plays a crucial ecological role for the

maintenance of biodiversity and the natural regeneration of habitats worldwide, thus contributing to the resilience of ecosystem services. As vividly stated by John L. Harper, plants are the stage where seeds start to make more seeds (Harper, 1977), emphasizing the central importance of the dispersal stage for maintaining the natural regeneration cycle of plants. We know that the disappearance of large frugivores will impact forest recruitment and tree diversity (Vanthomme et al., 2010; Wright et al., 2007a, 2007b). If the process of seed dispersal collapses, as illustrated in many examples of the extinction of the major animal dispersers, the entire regeneration cycle will also be affected. Certainly, habitat loss and defaunation are major drivers of plant demographic collapse in many habitat types (e.g., Wright, 2005).

The contributions in this special issue of AO illustrate the fascinating natural history details of the mutualisms between animal seed dispersers and their food plants, and they also provide a rich and diversified conceptual background for their study demonstrating their importance in providing ecosystem services. We are confident that the 2010 symposium in Montpellier and this special issue will continue to further stimulate attention and study in this important field. Let's meet again during the 6th International Symposium-Worskshop on Frugivores and Seed Dispersal (1985–2015) in KwaZulu-Natal, South Africa (http://www.fsd2015.org).

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