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Seed exchange networks for agrobiodiversity conservation. A review

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Abstract The circulation of seed among farmers is central to agrobiodiversity conservation and dynamics. Agrobiodiversity, the diversity of agricultural systems from genes to varieties and

crop species, from farming methods to landscape composition, is part of humanity's cultural heritage. Whereas agrobiodiversity conservation has received much attention from researchers

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and policy makers over the last decades, the methods available to study the role of seed exchange networks in preserving crop biodiversity have only recently begun to be considered. In this overview, we present key concepts, methods, and challenges to better understand seed exchange networks so as to improve the chances that traditional crop varieties (landraces) will be preserved and used sustainably around the world. The available literature suggests that there is insufficient knowledge about the social, cultural, and methodological dimensions of environmental change, including how seed exchange networks will cope with changes in climates, socio-economic factors, and family structures that have supported seed exchange systems to date. Methods available to study the role of seed exchange networks in the preservation and adaptation of crop specific and genetic diversity range from meta-analysis to modelling, from participatory approaches to the development of bio-indicators, from genetic to biogeographical studies, from anthropological and ethnographic research to the use of network theory. We advocate a diversity of approaches, so as to foster the creation of robust and policy-relevant knowledge. Open challenges in the study of the role of seed exchange networks in biodiversity conservation include the development of methods to (i) enhance farmers' participation to decision-making in agroecosystems, (ii) integrate ex situ and in situ approaches, (iii)

achieve interdisciplinary research collaboration between social and natural scientists, and (iv) use network analysis as a conceptual framework to bridge boundaries among researchers, farmers and policy makers, as well as other stakeholders.

Keywords Biodiversity · Complex networks · Global change · Landscape genetics · Methods in ecology and evolution · Participatory approaches · Review · Scenarios · Seeds · Simulation models

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1 Introduction: seed exchange networks and agrobiodiversity conservation

Agricultural biodiversity (in short, agrobiodiversity) is the diversity of agricultural systems from genes to varieties and species, from farming practices to landscape composition. The conservation and management of agrobiodiversity is a key issue in the struggle to achieve food security for a growing world population in the face of global change (Thrupp 2000; Cavatassi et al. 2011; Chappell and LaValle 2011). In spite of ongoing conservation efforts, in many regions, agrobiodiversity is under severe threat (Lotti 2010; Shen et al. 2010; Engels et al. 2011). One example is the widespread disappearance of landraces, i.e., traditional, locally adapted crop varieties with historical origins and cultural significance, as well as high genetic diversity (Lehmann 1981; Camacho-Villa et al. 2005; Negri 2007; Angioi et al. 2011). Threats to landrace conservation include land use intensification, structural changes in the agricultural sector (including seed regulation), invasive species, climate change, and urbanization. In addition to reducing diversity at the genetic and varietal level, these processes and their interactions also reduce diversity at the species and landscape level, affecting crop communities and associated ecosystem services (Biesmeijer et al. 2006; Chambers et al. 2007; Flynn et al. 2009; Fig. 1).

Threats to agrobiodiversity are numerous, but there are also many reasons to preserve it (see Jarvis et al. 2011). More diverse (agro-)ecosystems tend to show higher socio-ecological resilience to disturbances and unforeseen events (Folke 2006; Dulloo et al. 2010; Narloch et al. 2011). Multi-species cropping systems can enhance soil fertility, diminish



Fig. 1 Planting an annual and vegetatively propagated plant, the taro (*Colocasia esculenta*), in an irrigated water garden (Vanua Lava, Vanuatu). Each year, farmers have to find new planting stock from their old gardens, the edge of other gardens, in irrigation canals or through their social exchange network (when they do not have enough material or when they want to experiment a new cultivar). Picture taken in November 2007 by Sophie Caillon

losses due to pathogens and pests, and help farmers adapt to changing environmental, socio-cultural, and market conditions (Bellon 1996; Malezieux et al. 2009; Mercer and Perales 2010; Bellon et al. 2011; Ratnadass et al. 2012). Together with better nutrition made possible by a diversity of crops and varieties, these factors contribute to food security, human well-being, and sustainability (Flora 2010; Nesbitt et al. 2010; Frison et al. 2011; Fig. 2). Biodiversity has also been shown to have psychological/health benefits (Ulrich 1984; Fuller et al. 2007; van den Berg et al. 2010; Dean et al. 2011; Bratman et al. 2012; Dallimer et al. 2012) and may well increase tolerance to cultural differences.

Several reviews related to agrobiodiversity conservation have recently appeared (Table 1). They include:

- an analysis of the economic consequences of losing wild nature (including wild crop relatives; there comes a point in biodiversity decline when the marginal benefits of conservation exceed its marginal costs; Balmford et al. 2011),
- overviews of the conservation of crop wild relatives both ex and in situ (both are woefully neglected; Heywood et al. 2007; Guarino and Lobell 2011),
- contributions to the debate on land sparing vs. biodiversity-friendly farming (should we separate nature conservation and agricultural production or integrate them on the same land? Green et al. 2005; Fischer et al. 2008; Perfecto and Vandermeer 2008; Lambin and Meyfroidt 2011; Phalan et al. 2011a, b; Tilman et al. 2011),
- and a discussion of the effectiveness of organic farming in preserving and enhancing biodiversity in today's human-modified landscapes (Mäder et al. 2002; Bengtsson et al. 2005; Crowder et al. 2010; Winqvist et al. 2011).

Only rarely, however, has the issue of agrobiodiversity conservation been considered from the perspective of seed



Fig. 2 Sustainable transport of seed (sorghum?) in Kathwana market, Kenya. Picture taken in 2008 by Christian Leclerc

Table 1 A selection of recent reviews related to agrobiodiversity conservation and (in some cases) seed exchange networks

| Topic | Reference |
|--|---|
| Assessing the economic consequences of losing wild nature | Balmford et al. 2011 |
| Olive and grapevine biodiversity in Greece and Cyprus | Banilas et al. 2009 |
| Spatial networks | Barthélemy 2011 |
| Landraces (reappraisal of terminology) | Berg 2009 |
| The relationships between food insecurity and rapid biodiversity loss | Chappell and LaValle 2011 |
| Conserving biodiversity in human-modified tropical landscapes | Chazdon et al. 2009 |
| Local seed systems in traditional Amazonian societies | Coomes 2010 |
| Network analysis in conservation biogeography | Cumming et al. 2010 |
| Genetic resource conservation to increase the robustness of seed systems | de Boef et al. 2010 |
| Ex and in situ conservation of agrobiodiversity | Dulloo et al. 2010 |
| Ethics of agro-biodiversity research, collecting and use | Engels et al. 2011 |
| Dynamic on-farm management of crop biodiversity | Enjalbert et al. 2011 |
| Agricultural biodiversity and food/nutrition security | Frison et al. 2011 |
| Conservation and sustainable use of crop wild relatives | Heywood et al. 2007 |
| Parasites and ecosystem health | Hudson et al. 2006 |
| Conservation and use of agro-biodiversity | Jackson et al. 2007 |
| Richness and evenness of the diversity of traditional crop varieties | Jarvis et al. 2008 |
| Supporting the conservation and use of traditional crop varieties | Jarvis et al. 2011 |
| Genetic, environmental and social interactions in crop systems | Leclerc and Coppens d'Eeckenbrugge 2012 |
| A typology of community seed banks | Lewis and Mulvany 1997 |
| Integrated seed sector development in Africa | Louwaars and De Boef 2012 |
| Designing ecologically intensive agroecosystems | Malézieux 2012 |
| Social network analysis applied to veterinary medicine | Martínez-López et al. 2009 |
| Interrelations between seed provision and food security | McGuire and Sperling 2011 |
| Chemical ecology in coupled human and natural systems | McKey et al. 2010a |
| Evolutionary ecology of clonally propagated domestic plants | McKey et al. 2010b |
| Evolutionary response of landraces to climate change | Mercer and Perales 2010 |
| Functional diversity in agroecosystems | Moonen and Barberi 2008 |
| Networks in plant epidemiology | Moslonka-Lefebvre et al. 2011 |
| Biodiversity conservation in tropical agroecosystems | Perfecto and Vandermeer 2008 |
| Weeds in agricultural landscapes | Petit et al. 2011 |
| Seed exchange and on-farm crop diversity conservation | Thomas et al. 2011 |
| Anthropological contributions to agrobiodiversity studies | Veteto and Skarbø 2009 |
| Biodiversity, evolution and adaptation of cultivated crops | Vigouroux et al. 2011 |
| Seed replacement and exchange | Zeven 1999 |

circulation (a more general term than “seed exchange”, but we follow the literature in using the latter term) (Thomas et al. 2011; Leclerc and Coppens d'Eeckenbrugge 2012; Fig. 3). Many of the issues revolving around agrobiodiversity conservation would benefit from the integration of concepts from network theory, given the importance of seed exchange networks for conservation of agricultural/cultural diversity and identity (Heckler and Zent 2008; Bezañon et al. 2009), for coping with environmental and economic shocks (Sperling and McGuire 2010a; Cavatassi et al. 2011), and for achieving an

understanding of the effects on biodiversity of the adoption of GM crops (Stone 2010). While complex networks are being used in a variety of ecological, epidemiological, and social applications (Jeger et al. 2007; Borgatti et al. 2009; Apicella et al. 2012), there has been little use of network analysis in relation to the in situ conservation of crop varieties so far (Subedi et al. 2003; Aw-hassan et al. 2008; Demeulenaere et al. 2008; Emperaire et al. 2008; Abay et al. 2011), so that there is little knowledge about which network structure(s) would be best under which conditions to preserve which level of agrobiodiversity.



Fig. 3 Threshing area of dry season sorghum. Tupuri farmers (North Cameroon) gather their harvest sorghum and beat it with a stick. When the threshing is over each farmer takes a share of leaves with seed. Picture taken in January 2011 by Clélia Soler

Networks, however, are only one of the methodological approaches to the study of seed exchange. Other methods include ethnographic fieldwork, participatory approaches, seed release and public good experiments, spatial analysis from landscape to geographic levels, simulation models and scenarios, impact evaluations, life cycle assessments, statistical and meta-analysis. A diversity of approaches is needed because of the interdisciplinary nature of the subject, the difficulties in distinguishing the biological and cultural factors shaping agrobiodiversity through seed exchange, the interactions between such factors and their potential scale dependence. For example, the introduction of new varieties in a seed system may or may not result in agrobiodiversity loss depending on these biological and social interactions. In addition to introducing network analysis to scientists studying seed exchange, our literature survey suggests that there is a need for an overview of the various methods available to study seed exchange networks in the context of agrobiodiversity conservation.

The aims of the present contribution are to:

- (i) present a review of recently published studies on seed circulation and agrobiodiversity conservation,
- (ii) describe key concepts and working hypotheses in relation to seed exchange networks,
- (iii) review several methods now available to investigate the links between social and seed exchange networks in shaping the dynamics, adaptation and conservation of crop genetic diversity,
- (iv) and outline the major challenges ahead.

We believe that a synthesis of the status and direction of this key topic in agronomy, applied ecology, biogeography, evolution, food security, and sustainable development is essential to make progress in the field, to recognize interdisciplinary research opportunities, and to

find common ground among farmers, scientists, and policy makers (Barlow et al. 2011).

2 Concepts

Based on a review of the literature, in this section, we introduce key concepts that are relevant to agrobiodiversity conservation and seed exchange networks. A basic awareness of these concepts is necessary to move forward in the area. For example, studying how seed exchange networks enable the maintenance of local crop varieties only makes sense if the conservation of agrobiodiversity is recognized as a fundamental goal by scientists (farmers may preserve agrobiodiversity with their practices and exchanges but without conservation as their intended goal; Fig. 4). There are of course other objectives in the study of seed exchange networks, e.g., the recognition of indigenous rights, the study of local identities and traditions, the development of alternative systems of production, and the understanding of cultural norms governing seed exchange in various societies. In introducing these concepts, we present a series of working hypotheses and assumptions, to be further tested and refined as new data become available.

2.1 Agrobiodiversity depends on farmers

Crop varieties, species, and communities are often the result of the work of generations of farmers and farming communities. It can be hypothesized that without their cultivation and exchange by farmers, most of the still existing crop varieties and assemblages would disappear (Emperaire et al. 1998; Jarvis et al. 2008; Engels et al. 2011). In fact, many crop varieties have already disappeared over the last decades, in parallel with a reduction



Fig. 4 Sorghum seeds preserved for the next cropping season in Kenya. Picture taken in 2011 by Adeline Barnaud

in the number of farmers of developed countries. It is important to recognize that in many developing countries, but not exclusively there, farmers are still using, exchanging, and creating their own varieties, largely using local germplasm and drawing on traditional practices (Emperaire and Peroni 2007; Jackson et al. 2007; Ellen and Platten 2011; Leclerc and Coppens d'Eeckenbrugge 2012). Cultivated varieties originate from the domestication of wild crop relatives, a process continuing to this day and involving both farmers and professional breeders (Döring et al. 2011; Fig. 5). Just as there is a continuum between traditional and improved varieties, it is possible to identify a continuum between purely wild plants and completely domesticated crops (Larson 2011).

2.2 Farmers are connected in complex seed exchange networks

Even if some farmers mostly save their seeds and only rarely acquire them from elsewhere, they are still part of a web of exchanges (Almekinders et al. 1994; Badstue et al. 2006; Dyer et al. 2011). A useful assumption is that farmers are members of a society with rights, expectations, contacts, and traditions. Farmers are typically actively exchanging seed material with neighbours, relatives, and even distant strangers, thereby moving crop genetic diversity across farming units (Emperaire et al. 1998; Chambers and Brush 2010; Coomes 2010). Even when it occurs in markets, seed circulation is typically a social process: it is based on trust, may or may not be reciprocal, and is influenced by socio-cultural norms and practices, e.g., seed inheritance via gifts at weddings in developing countries (Sirabanchongkran et al. 2004;



Fig. 5 Head woman of the village in Shangrila, China, identifying non-diseased plants of a mixed seed population of three traditional barley varieties for seed. Picture taken by Devra Jarvis

Delêtre et al. 2011; Vigouroux et al. 2011; Leclerc and Coppens d'Eeckenbrugge 2012). How socio-cultural factors shape seed exchange networks also changes in relation to socio-economic pressures on farmers and their communities (Richards et al. 1997; McGuire 2008; Leclerc and Coppens d'Eeckenbrugge 2012). Both in developing and developed countries (although to varying degrees), these pressures include increasing use of hybrid varieties (but also the revival of heirloom varieties), the development of intellectual property legislation and seed marketing regulation (adoption of the UPOV convention), and issues related to land and market access (Tripp et al. 2007; Ranjan 2009; Aistara 2011; Brahmi and Chaudharya 2011).

2.3 Seed exchange networks are keys to agrobiodiversity conservation

Seed transactions, even when operating outside a specialized social organization to mediate seed flows, tend to follow unwritten rules. It is likely that the underlying networks are keys to understanding and managing agrobiodiversity in a time of globalization and the struggle to save local varieties from disappearance (Serpoly et al. 2011). For example, a classic study of maize seed flow in a traditional village of Jalisco State, Mexico, showed maize diversity to be the result not of geographical isolation, but of the introduction of both improved cultivars and of landraces from neighboring communities (Louette et al. 1997). Even if the primary aim of seed exchange in many agrarian communities is use rather than conservation, there is a growing consensus that use and conservation are interdependent. Increasingly, NGOs and grass-root associations of farmers (in Europe, e.g., Arche Noah, Kokopelli, Pro Specie Rara, Red de Semillas, Réseau Semences Paysannes, Rete Semi Rurali) organize seed exchanges as planned activities with the explicit aim of preserving agrobiodiversity (Hammer et al. 2003; Bardsley and Thomas 2004; Amdorfer et al. 2009; Thomas et al. 2012).

2.4 Seed exchange is relevant to many issues other than agrobiodiversity conservation

Seed exchange is fundamental to agrobiodiversity conservation, but it can be reasonably assumed to be also relevant to a broad range of other phenomena, from plant diseases transmitted by seed to the cultural significance of seeds, from social organization to the transmission of knowledge, from geographical and landscape genetics to the sustainability of rural economies (Stukenbrock and McDonald 2008; Carvalho 2011; Guei et al. 2011; Wu et al. 2011). These other dimensions are in turn important for a more holistic understanding and management of agrobiodiversity (Richards et al. 2009; de Boef et al. 2010; Brooks and Loevinsohn 2011; Mendenhall et

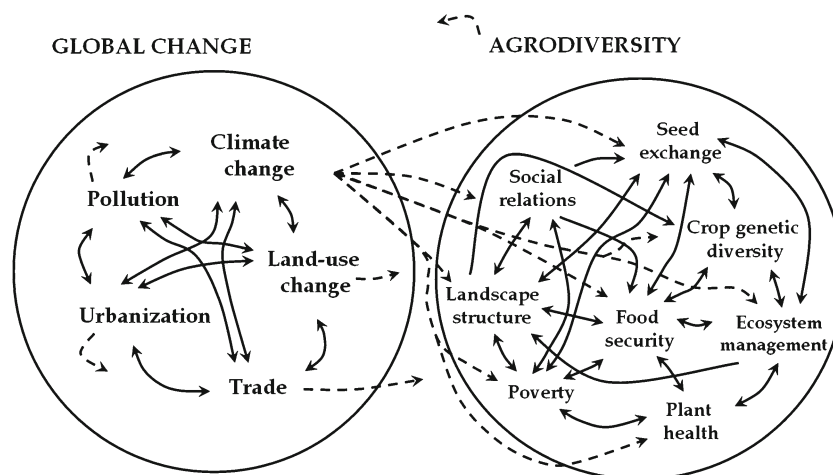


Fig. 6 A heuristic model of global change impacts on agrodiversity (the diversity of agricultural systems, which includes but is not limited to agrobiodiversity; Brookfield and Padoch 1994). Global change is composed of the interactions of various drivers (climate change, increased trade, land-use change, pollution, urbanization). All these factors will have an impact on agricultural diversity, through direct effects on crop genetic and specific diversity, but also via influences on cultural factors, plant health, social relations, poverty, food security,

ecosystem management and seed exchange systems. The *arrow* from agricultural systems back to global change reminds us that changes in, e.g., plant health will have repercussions on the capacity of ecosystems to sequester carbon. To be successful in the face of global change, management of crop diversity will have to take into account this complexity of interactions. The figure is modified from Pautasso et al. (2012)

al. 2011; Fig. 6). As with seed exchange itself, it is difficult to separate purely biological from social factors when considering these wider issues; rather, these factors interact to a considerable degree, both in cause and effect. Such a cross-disciplinary perspective is becoming more prevalent in related fields of conservation (e.g., Ohl et al. 2010; Young 2010; von Glasenapp and Thornton 2011).

2.5 There is a continuum between formal and informal seed exchange networks

Although often referred to as “informal”, local seed networks follow social norms and rules, and can thus be considered as being entirely “formal” in their local contexts. Similarly, conventionally “formal” seed systems are guided by a variety of informal rules and understandings. As such, the opposition between “formal” vs. “informal” can be misleading, also given the drive towards integrated systems that merge formal and informal approaches (Hirpa et al. 2010; Louwaars and De Boef 2012). Nonetheless, it is possible to distinguish formal vs. informal seed systems, as was recently done by a study of rice seed supply in the Mekong Delta of Vietnam. Here, informal seed systems were shown to outperform formal ones not just in the quantity of delivered seed, but also in the diversity of cultivated rice landraces (Tin et al. 2011). Recent decades have seen progressive loss of local varieties and widespread adoption of the mono-cultural production of a few crops with low intra-specific diversity in most developed countries (Dawson et al. 2011). There is a hypothesis that these processes were enabled and enhanced by modern seed supply systems, i.e.,

the commercial seed trade, patents and regulation of intellectual property, although some researchers also recognize the role of market failures in agrobiodiversity loss (Kloppenburg and Kleinman 1987; Brush 1993). Although this shift towards a handful of productive crops made it possible to partly meet growing food needs, it is now recognized by many that sustainable agriculture cannot be achieved without the conservation of agrobiodiversity (Mercer and Perales 2010; Carvalheiro et al. 2011; Ebert 2011; Vigouroux et al. 2011). Local seed exchange networks are essential to agrobiodiversity conservation, because they permit access to seed and the maintenance of landraces in agro-ecosystems throughout the world, despite the trend towards more uniform seed material flowing through formal, commercial seed systems. An example of the importance of local seed networks (despite decades of focus on the national extension system) is provided by a recent analysis of institutions and stakeholders involved in the rice seed system in Guinea (Okry et al. 2011).

3 Methods

Methods for studying seed exchange networks in relation to agrobiodiversity conservation range from experimental studies to ethnographic fieldwork, from modelling to meta-analysis. In this section, we briefly present some of the available methods, comparing their strengths and weaknesses and pointing out their complementarities. Our main aim is not just to show the methodological diversity available, but to advocate the use of a variety of research approaches (Fig. 7).

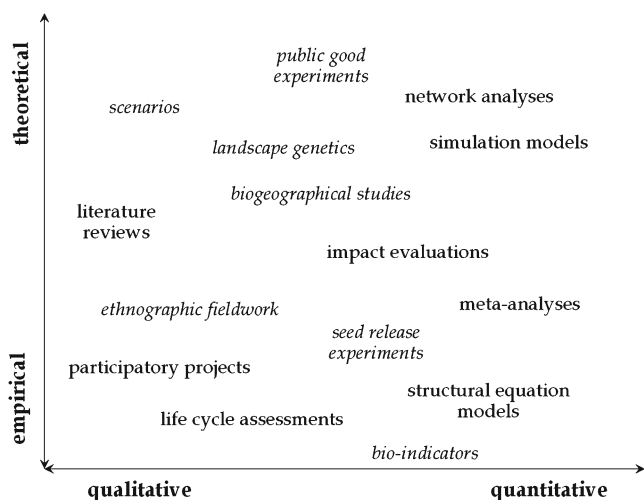


Fig. 7 A selection of methods available to study seed exchange networks in the context of agrobiodiversity conservation. The figure shows that there is a continuum between qualitative and quantitative approaches, as well as between empirical and theoretical perspectives. In some cases, the position of the method in the graph may vary depending on how the method is used (e.g., interviews in ethnographic fieldwork may also result in quantitative data) or which sub-methodology is adopted (e.g., statistical vs. theoretical models). Methods in *italics* focus on data generation, whereas the other ones tend to deal with data analysis and evaluation (although this distinction may be fuzzy)

The methods presented can be roughly divided in two subsets. One subset of methods focuses on the generation of data (ethnographic fieldwork, seed release and public good experiments, biogeographical, and landscape genetic studies). The other subset deals with data analysis and evaluation (statistical models, network analysis, meta-analysis, impact evaluation, and life cycle assessments). There is of course a continuum between data generation and analysis, with some methods not falling neatly in one or the other subset (e.g., participatory projects, bio-indicators, simulation models, scenarios).

The choice of methods used to study seed exchange networks should be guided by a thorough review of the available options and will depend on the questions to be addressed, the underlying hypotheses, the background of the scientists involved, their propensity towards interdisciplinary collaboration, the availability of data and previous studies, the level of agrobiodiversity studied (genetic diversity, diversity of landraces, crop richness and evenness), the importance given to quantification, the necessity to predict or to plan the future, the focus on system outputs or inputs, and the spatial and temporal scale of the study.

3.1 Ethnographic fieldwork

Observation of practices and interviews with farmers featuring both open-ended and closed questions can yield important knowledge on seed circulation and network structure.

For example, information can be obtained on whether there is a continuous or sporadic process of adoption of new crop varieties (McKey et al. 2010b; Temudo 2011). Ethnographic fieldwork (including participant observation) can also shed light on a variety of important issues, e.g., the ethnobotanical knowledge of communities and the social and cultural significance of their exchange practices. The motivation behind such studies may simply be obtaining knowledge on communities for its own sake, but also for enhancing seed systems through collaborative research and participatory projects (Drury et al. 2011). Findings from interviews and participant observation may complement data gathered through field experiments (Fritch et al. 2011; Mortensen and Jensen 2012), thus allowing a more profound understanding of local strategies (Chambers and Brush 2010; Leclerc and Coppens d'Eeckenbrugge 2012). Interviews can produce data to be further analyzed using some of the other approaches described below. They can reveal what works or does not work in the field as perceived by farmers, who often have a long-term experience of a given agro-ecosystem and seed exchange network (Bishaw et al. 2011).

3.2 Participatory approaches

Participatory approaches recognize that research on agro-ecosystems has little hope of delivering useful knowledge to farmers if it does not directly involve them (Martin and Sherington 1997; Dawson et al. 2008). The separation of research on crop improvement from farming communities and environments has led to the selection and release of inappropriate or homogeneous varieties and the loss of landraces adapted to marginal and low-input environments (Ceccarelli and Grando 2009; Gyawali et al. 2010). Participatory projects try to overcome the lack of connection between plant breeding, seed provision, and cultivation that has developed over the last decades (Bishaw and Turner 2008; Mendum and Glenna 2010). Participatory and decentralized plant breeding and seed supply systems deserve to be treated as a methodology to study seed exchange networks in its own right, because many agrobiodiversity conservation projects involving seed systems are more likely to succeed with an involvement of a broad basis of stakeholders from the very beginning (Almekinders et al. 2007; Lauber et al. 2011). Participatory approaches may require more time and effort than top-down interventions, but the expectation is that there will often be conservation rewards in the long term (Cundill et al. 2012; Susskind et al. 2012). This is just as true for the release of new seed varieties (which are likely to be better suited to a certain agro-ecosystem and farmers' needs if they have been directly selected by farmers in a variety of locations; Dawson and Goldringer 2012) as for the development of agronomic models, geographic information systems, and

experiments (Whitbread et al. 2010; Bernard et al. 2011; Prost et al. 2011).

3.3 Seed release and public good experiments

An experiment is a manipulation of nature under controlled conditions to establish, other things being equal, which factors are likely to cause a given phenomenon (Fara 2009). Although experimental approaches are difficult in the context of seed exchange networks, not just because of the logistical constraints, but also due to ethical considerations, they have been attempted. For example, 3 years after the distribution of high-yielding Carioca bean seeds to 400 farmers in Zambia in 1986, 3.7 times as many farmers were estimated to be growing the new variety, although only about half of the farmers who originally received the seed were still sowing it (Grisley and Shamambo 1993). Fifteen years after the introduction of 0.5 kg of seed of a new rice variety to a single farmer in Ghana in 1987, about 73 % of farmers in the Western part of Ghana were believed to have grown the new variety (Marfo et al. 2008). Such introductions of new varieties have occurred innumerable times over the last decades, but there has been little recording of if, how, and why they spread among farmers under various conditions (Witcombe et al. 1999). In some cases, farmers may grow a landrace whose name does not change but whose genetic make-up is evolving due to the introduction of new alleles from elsewhere (Deu et al. 2008). In others, the same crop variety may be called with different names by different groups of farmers.

Another type of experiment, public good experiments under controlled conditions (Fehr and Gächter 2000), may be adapted to seed exchange to deliver useful knowledge. Public good experiments make use of human subjects (typically university students) to test under which conditions people tend to behave altruistically or egoistically in experiments informed by game theory. The often invoked absence of representativeness of this subset of the population may be obviated by devising seed exchange experiments, in which farmers or other sectors of societies may be invited to participate. Such seed exchange experiments could help explain how socio-cultural diversity of farming communities may promote cooperativeness in seed exchange practices (Santos et al. 2012). Even if such experiments and simulations are likely to oversimplify the complexity of seed exchange networks and agrobiodiversity conservation, they could provide insights on the conditions which tend to favor long-term collaboration and biodiversity maintenance in a seed exchange network (Tavoni et al. 2011; Bonsall and Wright 2012). Interestingly, social network structure has been shown to have an important influence on the outcome of these experimental games (Fehl et al. 2011; Rand et al. 2011).

3.4 Biogeography and landscape genetics

Biogeographical research and landscape genetics are two examples of approaches which can yield useful data on agrobiodiversity patterns in relation to seed exchange networks (Zimmerer 1991; Pusadee et al. 2009; Lewis 2010; Gravel et al. 2011; Burnside et al. 2012; Sardos et al. 2012). While biogeography tends to deal with broad regions, landscape genetics is typically more focused on studying patterns and processes over areas intermediate between local and regional. Some studies are bridging the gap between biogeography and landscape genetics by investigating geographical patterns in the genetic diversity of various cultivated species and varieties (Hunt et al. 2011; Sreejayan et al. 2011). There are great opportunities to merge such genetic studies with the study of seed exchange networks, e.g., by using genetic markers to reconstruct the spread of new varieties and the structure of exchange networks (Dyer and Taylor 2008; de Boef et al. 2010; Rabbi et al. 2010; van Heerwaarden et al. 2010). Recently, a biogeographical approach was applied to the study of the distribution of human pathogens, which were shown to follow a latitudinal gradient in species richness (Guernier et al. 2004; Dunn et al. 2010), a pattern commonly observed in nature for many taxa, including the crop richness of subsistence-oriented farming communities (Freeman 2012). Seed agrobiodiversity is influenced by the form and operation of the underlying social networks of exchange (Eloy and Emperaire 2011) but also by interrelated biogeographical variables such as energy availability, latitude and length of the growing season (Freeman 2012), and aspects related to plant biology (annual versus perennial; vegetative versus sexual reproduction; allogamous versus autogamous). A working hypothesis suggests that the type of factors that influence agrobiodiversity may be scale dependent. Preliminary evidence from local seed markets supports this notion of scale-dependent networks, as the geographic scale of seed provision to these markets differs by crop, reflecting agroecology, among other factors (Sperling and McGuire 2010a, b). Over global to continental scales, biogeographic factors may be essential in explaining observed patterns in agrobiodiversity variation (Amano et al. 2011). At local to regional scales, social issues such as how networks operate (whether or not they are hierarchical, polycentric, reciprocal; Emperaire et al. 2010) and farming practices may predominantly shape crop gene flow and thus agrobiodiversity (Jarvis and Hodgkin 1999; Pujol et al. 2005; Dyer and Taylor 2008; Barnaud et al. 2009). Climate change may well act at both levels, disrupting local communities and traditions, but also changing patterns of precipitation and temperature across regions and continents. Both processes may encumber the movement of environmentally matched propagating material over appropriate distances and networks (Bellon et al. 2011).

3.5 Simulation models

Modeling is a further tool to investigate the role of seed exchange networks in the conservation of agrobiodiversity. In this section, we describe simulation models, whereas statistical modeling and network models are treated below. Simulation models attempt to predict the future development of a system based on assumptions about how the system works (which translate into a set of mathematical equations) and data on the likely initial conditions. For example, genetic metapopulation models simulate in a quantitative way the genetic make-up of dynamic crop metapopulations (Neuenschwander et al. 2008; Ray et al. 2010; Chan et al. 2011), whereas bio-economic models try to merge ecological and economic perspectives (Holden and Shiferaw 2004; Lowe et al. 2009; Louhichi et al. 2010). Such models at the interface between natural and social sciences are essential to capture the reality of today's agriculture (Carpenter and Folke 2006; Cooke et al. 2009; Mills et al. 2011). Integrated models can be very helpful because they enable to study potential reactions of stakeholders, the relative importance of various model assessment criteria, as well as dynamic and spatial perspectives (Phillipson et al. 2009; Jacquet et al. 2011; Mouysset et al. 2011). Also, when modeling seed exchange networks, there is a trade-off between the coverage of features deemed to influence a certain system and the ease with which a model can be run and understood (Levins 1966; Matthewson 2011; Orzack 2012). Models are particularly useful when baseline data are lacking, when rare events play an important role or where the available data span a period which is too short to allow the perception of a temporal trend (Schönhart et al. 2011; Jensen et al. 2012; Savary et al. 2012). These situations are common for seed exchange networks. Results from models are always fraught with uncertainty; they need thus to be interpreted with caution, due to the many simplifications inherent in modeling and the dependence of model outcomes on initial conditions and unforeseen developments (Pilkey-Jarvis and Pilkey 2008; Spiegelhalter and Riesch 2011; Hanski 2012). For example, a model may predict that the amount of exchanged material has more influence on the persistence of landraces in a region rather than differences in network properties such as the number of farmers' contacts, but this finding may or may not apply in reality depending on other factors such as reciprocity, memory, and trust (Yeaman et al. 2012).

3.6 Scenarios

Scenarios are conceptually similar to models but are largely based on qualitative rather than quantitative input and help planning rather than predicting the future. Scenarios explore the potential trajectories of a system depending on a set of possible choices; they thus recognize the need for multiple

points of view and the pervasiveness of uncertainty (Biggs et al. 2010; Coreau et al. 2010). The main aim of scenarios is to anticipate changes to the status quo and to identify the strengths and weaknesses of ways to deal with such changes (Polasky et al. 2011). Scenario planners recognize more than modelers the unpredictability of complex systems and focus on what if, how and why questions, rather than where, when, and how much (Pilkey and Pilkey-Jarvis 2007). In natural resource management, scenarios have been frequently used as an aid to decision-making, whereas scenarios are still rarely used in local biodiversity conservation (Kass et al. 2011). For seed exchange networks, scenarios could be developed to prepare for diverging developments such as (i) the end of cheap oil and transportation, (ii) a marked increase in global trade, (iii) the widespread adoption of GM crops throughout the world, (iv) the banning of a majority of the currently used pesticides/herbicides, or (iv) a major shift in societal priorities towards achieving sustainability and biodiversity conservation. There is a recognition that models and scenarios need to be complemented by long-term monitoring, so as to be able to better validate these theoretical tools. Long-term monitoring, in turn, requires reliable agrobiodiversity indicators (Goffaux et al. 2011). Local experts and stakeholders can also be involved, adding their knowledge to researchers' for developing scenarios (Brook and McLachlan 2008; Haines-Young 2011; Swetnam et al. 2011; Montesano et al. 2012). Moreover, long-term research is advocated not just from an ecological point of view, but also at the interface between social and ecological sciences. Long-term socio-ecological research sites would enable a more realistic ecological-economic modeling and an improved understanding of perceptions and benefits of biodiversity (Haberl et al. 2009; Ohl et al. 2010; Rounsevell et al. 2012). The long-term research site approach is gaining importance in socio-ecological research, but is still underused in the study of seed exchange networks.

3.7 Statistical analysis (e.g., structural equation models)

Statistical analysis has long been used in the study of agroecosystems. It involves the examination of data so as, e.g., to detect the presence of differences among subsets of data which differ in some other interesting way (in seed exchange networks, e.g., age of farmers, inheritance patterns, longest distance of exchange). Statistical tests typically result in likely and not certain knowledge (Johnson and Bhattacharyya 2009). For seed exchange networks, an example is the finding by Tin et al. (2011) of a significantly higher diversity of rice landraces in informal seed systems compared to formal ones in the Mekong Delta, Vietnam. Structural equation modeling is a statistical approach to analyze data so as to test between alternative hypotheses linking the putative causal factors (Nettle et al. 2007; Nettle 2009; Budtz-Jorgensen et al.

2010). Given that seed exchange networks are not easily amenable to controlled experiments, it is often difficult to infer causation from correlation. Structural equation modeling can help disentangle the potential pathways of causality among the measured variables (Grace 2006; Golding et al. 2010; Rosa et al. 2011). This approach has the potential to deliver information on the factors driving the loss (or maintenance) of biodiversity in agro-ecosystems, particularly if coupled with the knowledge obtained from participatory approaches and reliable bio-indicators (Neef and Neubert 2011).

3.8 Indicators

For seed exchange networks, indicators are needed to enable the assessment of the agrobiodiversity hosted by these systems, but also to gauge their value from a socio-cultural perspective (Rana et al. 2007). In both cases, however, the development of quantitative indicators might lead to an oversimplification of the complex reality of socio-ecosystems because these systems are not controlled experiments. Bio-indicators are groups of organisms whose ease of sample and sensitivity to environmental conditions make them well suited as surrogates for monitoring the status of biodiversity and the health of ecosystems (Duelli and Obrist 2003; Rodrigues and Brooks 2007; Barbosa et al. 2010; Rüdiger et al. 2012). For example, birds, mammals, invertebrates, and the arable flora have been used to show that organic farming generally benefits biodiversity (Hole et al. 2005). The underlying assumption is that if the presence and abundance of bio-indicators declines (e.g., due to human activities such as habitat degradation, enlargement of fields, air pollution), then also many other groups of organisms are likely to have declined at the same time (Büchs 2003). Bio-indicators are one of the basis for the current attempts to slow down the loss of biodiversity, e.g., with the (largely missed) 2010 targets (Butchart et al. 2010; Perrings et al. 2011; Sparks et al. 2011). There have been recent attempts to link bio-indicators with environmental risk assessment approaches, i.e., the evaluation of how a given human activity is likely to perturb a whole ecosystem (Galic et al. 2012; Safont et al. 2012). Just as with long-term monitoring, there is a need to merge genetic, ecological, and socio-cultural perspectives in the development of (bio)-indicators of socio-ecological resilience (Cumming 2011; Goffaux et al. 2011; van Oudenhoven et al. 2011).

3.9 Life cycle assessments and impact evaluations

Like experiments, life cycle assessments have so far been neglected in seed exchange research. They comprehensively assess the relevant environmental impacts in the life cycle of a product, from the extraction of the resources to the

production, transport, storage, use, and waste disposal (Heinonen and Junnila 2011; Nemecek et al. 2011; Wiedmann and Barrett 2011). Although they have been used also in agricultural settings (Heller et al. 2003; Capper 2011; Espinoza-Orias et al. 2011), life cycle assessments are typical of industrial products (- but they have now dealt with, e.g., knowledge systems, museum loans, urban green space (Chowdhury 2010; Lambert and Henderson 2011; Strohbach et al. 2012). With some adaptation, such an approach may deliver new insights into how seed exchange networks promote biodiversity and sustainability (Cambria and Pierangeli 2011). For example, an assessment of the life cycle of seeds produced in developed countries and air-shipped to developing countries would show a much higher environmental impact compared to local seed production and exchange. Impact evaluations are conceptually similar to life cycle assessments but focus on desired outcomes rather than unwanted side-products (Jalan and Ravallion 2003). Impact evaluations have assessed, e.g., whether health sector reforms have achieved their intended aims (Wagstaff and Yu 2007). For seed exchange, impact evaluation can be envisaged for top-down vs. bottom-up attempts to introduce new varieties both in developed and developing countries (Cromwell et al. 1992; Goffaux et al. 2011). One example is a study showing increased household income and decreased poverty due to the adoption of improved maize varieties by farmers in Oaxaca and Chiapas, Mexico (Becerril and Abdulai 2010). There is the need to link such studies with indicators of agrobiodiversity.

3.10 Meta-analyses

Meta-analysis is the statistical analysis of the results of studies that investigate a set of related research hypotheses (Batáry et al. 2011; Lehmann et al. 2012; Vranckx et al. 2012). Meta-analysis does not preclude a narrative review of a series of studies but provides a synthesis of quantitative data in a way that is less prone to subjective bias (Gurevitch et al. 2001; Ahtiainen and Pouta 2011; Doré et al. 2011). One problem with meta-analysis derives from the necessity to obtain comparable data (McLaren et al. 2005; Harrison 2011; Philibert et al. 2012), although it is possible to control for potentially confounding factors (in seed exchange networks, e.g., farmers' age, gender, genealogy, wealth). Just as with modeling, meta-analysis is particularly useful when it results in counterintuitive findings, so as to challenge conventional wisdom. For example, there is increasing evidence that higher parasite species diversity is not just associated with, but is also a likely cause of a better ecosystem functioning, given that parasites diminish the likelihood that some species will become dominant (Ameloot et al. 2005; Hudson et al. 2006). This result may now be well established in ecology (together with the reverse link from higher

biodiversity to lower incidence of diseases; Keesing et al. 2010; Vourc'h et al. 2012), but it is still normal in agriculture to regard parasites and diseases as problematic (Döring et al. 2012a; Keesing et al. 2012; van den Berg 2012). Similarly, meta-analysis of seed networks may uncover hitherto disregarded factors affecting diversity, for instance revealing how particular nodes shape diversity patterns across local vs. broad scales, the role of the economic and cultural context (e.g., developing countries vs. industrial ones) in influencing the form of seed exchange networks, as well as the importance of seed characteristics in how exchange networks evolve.

3.11 Network analyses

Last but not least, network analysis is a new, promising tool to study seed exchange networks. In this context, networks are sets of nodes (e.g., farmers, households, communities, villages, towns, countries) connected by links (e.g., seed exchange, borrowing, trade, aid). We believe that networks are essential for an understanding of how to preserve agrobiodiversity, both at the intra- and inter-specific levels. Network analysis offers a conceptual framework to investigate contact patterns, hierarchical structures, connectivity, asymmetry, and degree distributions (Martínez-López et al. 2009; Kiss et al. 2010; Pautasso et al. 2010b; Ames et al. 2011; see e.g., Moslonka-Lefebvre et al. 2011 for network terminology). All these factors have been shown in social and epidemiological studies to be essential for a predictive understanding of the spread of ideas/pathogens in networks (Bettencourt et al. 2006; Carrington and Scott 2010; Danon et al. 2011). They are thus likely to be just as important for the circulation of seeds among farmers in a particular region. Network theory offers considerable potential to bridge the divide between natural and social sciences, given that both increasingly use this approach (Hirsch Hadorn et al. 2006; Borgatti et al. 2009; Mills et al. 2011; Alam and Geller 2012). This is especially relevant for seed exchange networks, as these encompass the flow of both genes and knowledge. For example, seed aid may weaken locally adapted systems by helping introduce inappropriate plant material or it may increase biodiversity and social capital in these systems, thereby increasing their resilience in the face of global change. Network analysis may help us understand how to shape networks to reduce their vulnerability, but few results from network analyses of seed exchange networks are available (Thomas et al. 2011).

4 Challenges

4.1 How to slow down the loss of agrobiodiversity?

There are many outstanding challenges related to seed exchange in agrobiodiversity conservation. One major issue

for humanity as a whole as well as for individual countries is to slow the loss of genetic resources, local varieties, and seed exchange networks. Some of this loss may happen suddenly during times of drought, war, and social upheaval (though evidence suggests that seed networks play a crucial role in restoring diversity after disasters; Sperling et al. 2008). However, much agrobiodiversity is being lost progressively due to more insidious factors such as climate change, market integration, misguided agricultural policies, long-distance trade, land use intensification, and cultural changes (e.g., in dietary habits). The introduction of new varieties may be one of the causes of the disappearance of local varieties (e.g., due to deskilling processes; Stone 2010), but this does not need to be the case. When included in the available mix of folk varieties rather than used as a wholesale replacement for them, additional varieties may and do enrich the biodiversity in a particular region (Berg 2009; Chambers and Brush 2010), although they might result in homogenization of agrobiodiversity at the global level. The same point can apply to urbanization, which does not necessarily result in the loss of agrobiodiversity (Emperaire and Eloy 2008). One of the challenges is to understand how to enable the coexistence of new and old varieties in such dynamic systems (not forgetting that landraces are not fixed objects but evolve as well).

4.2 How to integrate ex and in situ conservation approaches?

Country-wide seed bank collections are important, but it is now clear that they are not the only solution to slowing agrobiodiversity loss, particularly in the long term (Maxted et al. 2002, 2010; Hagenblad et al. 2012). Genetic resources of traditional crops are best preserved in situ to maintain the potential for adaptation of farm varieties (Chable et al. 2008; Haouane et al. 2011). An improved integration of ex and in situ approaches is certainly worth pursuing. One way this can be achieved is by integrating community-level seed collections with existing local seed exchange networks (Almekinders and Louwaars 1999; Smith et al. 2011). This could add value to efforts undertaken to build extensive seed collections, as these would not be preserved in a vacuum, but in a network of transactions and cultivation decisions (Tapia 2000; Guarino and Lobell 2011). A commendable example is the recent release of a sweet potato cultivar bred by participatory plant breeding in Uganda, with involvement both in the conservation and distribution of the variety of the Ugandan National Sweetpotato Program (Gibson et al. 2011). Also, a simplistic opposition between traditional and modern agro-ecosystems may be a barrier to more effective agrobiodiversity conservation regimes (Pascual and Perrings 2007). Although there is growing recognition that multi-centric, in situ conservation approaches have

more long-term potential than top-down, hierarchical, ex situ programs, the two strategies need to be reconciled both in developing and industrialized countries (Oldfield and Alcorn 1987; Thomas et al. 2011).

4.3 How to promote interdisciplinary collaboration in the study of seed exchange?

The same point can be made in research policy settings about creating the conditions for the coexistence of various ways of thinking about and approaching the study of agrobiodiversity and seed exchange networks (Rafols and Meyer 2010; Baumgart-Getz et al. 2012; Wagner et al. 2012). There is a need to transcend boundaries between disciplines, perspectives, and kinds of expertise (holistic and multidisciplinary approaches; Malézieux 2012) as well as stakeholders. Collaboration is required among the diverse research communities involved in the study and management of biodiversity, seed exchange, and ecosystem services (Jarvis and Hodgkin 1999; Barnaud et al. 2009; Hicks et al. 2010; Pautasso et al. 2010a; Brummer et al. 2011; Díaz et al. 2011; Fischer et al. 2011; Thomas et al. 2011; Hoban et al. 2012; Leclerc and Coppens d'Eeckenbrugge 2012; Fig. 8). Similar collaborations can be envisaged in animal husbandry and in forestry (Berthouly et al. 2009; Nyoka et al. 2011; He et al. 2012). Perspectives vary, sometimes markedly, among stakeholders (e.g., botanic gardens, farmers, government agencies, indigenous peoples, land managers, NGOs, rural movements, and seed companies) (Aplin and Heywood 2008; Chazdon et al. 2009; Dawson et al. 2011; Fischer et al. 2012; Kennedy 2012; Rounsevell et al. 2012).

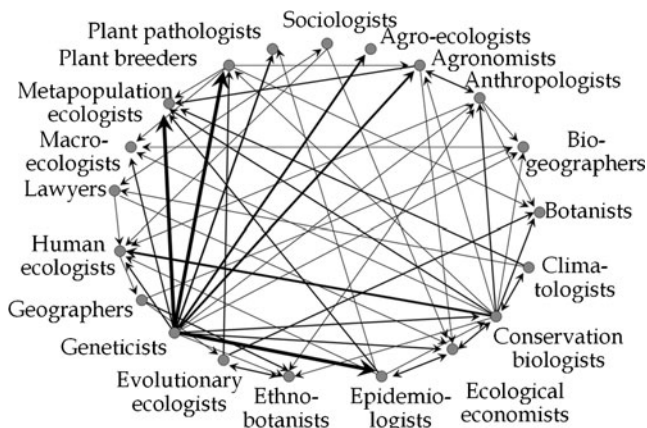


Fig. 8 Hypothetical network of interdisciplinary collaborations among scientists interested in seed exchange networks. The network is neither exhaustive (there may be many other scientists involved, e.g., dispersal and disturbance ecologists, landscape ecologists, modellers, molecular ecologists, plant ecophysiologicals, protection scientists, restoration, and seed ecologists) nor fixed (the presence, strength and direction of the interactions among two groups of scientists are likely to vary in space and time)

For agrobiodiversity conservation to be possible, efforts are needed to help these diverse groups find a common language and ways of working together. Complex networks can be a tool to make this possible: they can provide a flexible framework within which to analyze seed exchange from different perspectives (conservation, genetic, social) but using a common set of concepts (Garroway et al. 2008; Dale and Fortin 2010; Fontaine et al. 2011; Rooney and McCann 2012).

4.4 How to use network analysis to model seed exchange?

Network analysis needs to be adapted to the particular conditions of seed exchange systems. In seed systems, obtaining seeds from near-by farmers is likely to be the most common pattern, not only because of physical proximity, social relationships and availability of information about the seeds, but also because seeds from distant places are less likely to be adapted to the environment where they are to be planted (Hodgkin et al. 2007; Stromberg et al. 2010). However, although there is considerable evidence that farmers exchange seed preferentially with neighbors and relatives, occasionally transactions occur with distant villages and markets (Delaunay et al. 2009; Enete 2009; Chambers and Brush 2010; Ellen and Platten 2011). This property—mostly local connectivity and some long-distance connections—suggests that seed exchange networks may be small-world networks (Watts and Strogatz 1998; Barthélemy and Amaral 1999; Jeger et al. 2007). Such a structure may be the consequence of specific features of agricultural systems such as complementarities among cultivated crops. If seed exchange were to take place within small-world networks (rather than purely local ones), it would be easier for new varieties to spread throughout a region, thus making seed systems potentially more resilient to environmental and social change. This conclusion is based on the assumption that the introduction of new varieties may be needed for farmers to cope with such changes. Most research on small-world networks has been carried out with undirected links, i.e., in the presence of symmetric connectivity (Meyers et al. 2006; Pautasso and Jeger 2008; Foster et al. 2010). In the case of seed exchange, however, the connection of farmer x to farmer y does not necessarily imply the reverse connection (although it might in some cases). Similarly, most network models have treated individuals as either having a certain property or not, whereas there are many situations (including seed exchange) where a continuum between two states would be more realistic (Moslonka-Lefebvre et al. 2009; Pautasso et al. 2010c). For example, seed exchange does not just result in the presence or absence of a certain landrace, but in a proportion of farmers' seed belonging to that landrace. For a number of reasons, farmers may adopt a variety one season, drop it or reduce its extent the next, and obtain the same variety from a different source, at a later date. It can be hypothesized that it

would be more appropriate to model seed exchange in directed networks along a continuum, but such a network type has received little attention by researchers interested in networks (Moslonka-Lefebvre et al. 2012).

4.5 Can the study of seed exchange networks benefit from insights from network epidemiology?

In epidemiology, much more research using network theory has been performed than is the case for seed exchange (Jeger et al. 2007; Chadès et al. 2011; Danon et al. 2011; Brauer and Castillo-Chavez 2012; House 2012). In both cases, there are elements (seeds/pathogens) moving thanks to a network of contacts (farmers/human beings). Whereas pathogen diffusion occurs mostly inadvertently, seed transactions are carried out by agents aware of what they are doing (although in some cases they might exchange seed lots containing seeds of landraces other than what they thought they were). However, disease prevention, avoidance and cure are conscious acts by human agents, who actively exchange information on disease management practices (Rebaudo and Dangles 2011; Stevenson et al. 2011). Conversely, there may be little awareness among farmers of the role of seed exchange in preserving agrobiodiversity. While in epidemiology the aim is to minimize the risk of disease spread under a budget constraint, in the case of seed exchange networks (again under resource limitations), farmers wish to obtain enough seed of the landraces they plan to sow, and conservation activities aim to ensure that traditional varieties persist in the meta-population of crops grown by farmers in a given region. Despite the differences between epidemics and seed exchange, there are many similarities. In epidemiology as well as in seed exchange, involving stakeholders in field projects makes it more likely that these will be successful, because of the stronger local support and the incorporation of local knowledge (Steingröver et al. 2010). Moreover, seed exchange networks that are efficient in maintaining biodiversity may also be efficient in spreading seed-borne plant diseases (e.g. *Fusarium circinatum*) (Muskett 1948; Burgess and Wingfield 2002; Leal et al. 2010), if not carefully managed (Gildemacher et al. 2009; Chadès et al. 2011; Corbineau 2012). It has been shown that networks of infinite size with a scale-free degree distribution (i.e., the presence of heterogeneity in the contact structure, with most nodes having a few connections and only a fraction of nodes having many connections) are particularly efficient at spreading diseases, since they have no epidemic threshold (the boundary between no epidemic and an epidemic). This implies that pathogens with very low transmission potential will persist in such networks (Pastor-Satorras and Vespignani 2001; Jeger et al. 2007; Chakrabarty et al. 2008). This has the potential to be a key result for agrobiodiversity conservation because it suggests that even non-mainstream crop varieties have a

chance to be preserved if they are exchanged in a very large seed exchange network (e.g., national or continental networks, even if mainly composed of local transactions) with scale-free connectivity (the presence of hubs), but very few scientists active in agrobiodiversity conservation may have heard of this result.

4.6 Which seed exchange network structure(s) would be best to maintain agrobiodiversity?

Farmers have to be well connected in groups and networks for conservation activities to succeed, particularly if their knowledge is used in conservation and development activities (Pretty and Smith 2004; Bajracharya et al. 2012). However, we have still an imperfect understanding of what this “well connected” means and how it may vary for different crop types. For example, if crops are reproduced sexually rather than vegetatively, a rather small part of the harvest is needed for farmers to have enough seed for the following season (McKey et al. 2010b; McGuire and Sperling 2011), which could have an influence on which seed network structure is more appropriate to preserve such crops. In many developing countries, national seed systems are little used, due to their inherent economic limitations (Tripp 2001), the inadequacy of the registered varieties for farmers in low-input areas (Ceccarelli and Grandi 2009), and the strength of traditional solidarity networks, which are less hierarchical and more pervasive across countries (Bazile 2006; Delaunay et al. 2009). Similar issues are arising for the diffusion of organic varieties. Nonetheless, markets and community seed banks make it possible for farmers to obtain seed material which would not normally be present in their fields or village (Lewis and Mulvany 1997). Access to a diversity of seed sources can be a good strategy to cope with bad harvest, drought, or other unforeseen events. This is particularly the case when it is a challenge to obtain the right amount, type, and quality of seed at the right time (Sperling et al. 2008). However, there is still limited understanding of which seed exchange network/social structure(s) and properties would be the most appropriate to preserve agrobiodiversity. The same point applies to the resilience of seed systems to disturbances. We also lack knowledge about how to maintain or enhance the socio-ecological resilience of local seed exchange networks (apart from an intuitive sense that not intervening may be preferable to many of the well-intended seed improvement programs of the past).

5 Conclusions and research needs

Despite the still limited attention given to agrobiodiversity in modern agricultural landscapes, local crop varieties are fundamental for the food security of much of the world's population. In developing countries, the importance of

agrobiodiversity and local seed systems is likely to further grow, given the forecasted increase in human population, shifts towards urbanized areas and changed environmental conditions (Cleveland et al. 1994; Bretting and Duvick 1997; Banilas et al. 2009; Abay et al. 2011; Jalloh et al. 2012). In developed countries, the awareness of the importance of agrobiodiversity is growing, both from a conservation biology point of view and in anticipation of fossil fuel shortages (Fess et al. 2011; Rudd 2011b; Tilman et al. 2011; Pautasso 2012; Portis et al. 2012). Seed exchange is an important, yet poorly understood, factor shaping agrobiodiversity and helping its dynamic conservation. Since seed exchange networks are likely to become even more essential for the conservation of agrobiodiversity in the coming decades, we need to make use of the diversity of methods available to study them. There is not only a need to describe and preserve cultivated and wild germplasm but to conserve these resources through use and circulation in a sustainable way. Understanding how to maintain, monitor, and propagate seed exchange structures will help to preserve agrobiodiversity and use it sustainably (as well as reintroduce it where it has been lost).

One of the key problems is our limited knowledge about how seed exchange networks and the social dimensions of agriculture will react to bio-physical hazards (McGuire and Sperling 2008; Darnhofer et al. 2010; Namanda et al. 2011). Targeted agro-environmental programs could help avoid the widespread implementation of inappropriate interventions, such as the one-size-fits-all adoption of varieties that have performed well for a short while in agro-industrial landscapes (Batáry et al. 2011; Altieri et al. 2012; Oliver et al. 2012). Similarly, knowledge about the role of seed exchange networks in maintaining and adapting agrobiodiversity could be instrumental in mitigating the risks arising from the introduction of GM crops (Kwit et al. 2011) and in improving the prospects for organic farming, which is currently often limited by the absence of well-developed organic seed supply systems (Dawson and Goldringer 2012; Döring et al. 2012b).

Seed exchange networks have a social reality and significance (Heckler and Zent 2008; McGuire 2008) but also a spatial dimension: most seed transactions in rural areas appear to take place within a 10-km radius (Chambers and Brush 2010; Bellon et al. 2011), thus possibly mimicking the dispersal kernel of many plant species (Nathan et al. 2008; McConkey et al. 2012). An important research question concerning spatial networks is the investigation of how topological quantities (e.g., degree distribution, clustering, connectance) are related to social factors (e.g., local norms, kinship ties, folk knowledge) (Barthélemy 2011). This issue is likely to be important also in the case of seed exchange and agrobiodiversity conservation.

Integrating the analysis of social and ecological networks is one of the outstanding challenges in network

biogeography (Cumming et al. 2010). Adding a scale-dependent perspective to integrative analyses may help us to avoid overlooking the potential role of biogeographical factors in shaping regional patterns in seed exchange. Interdisciplinarity is here thus not just across two fields, but among many (e.g., agronomy, anthropology, biogeography, genetics, and network theory). The need for such collaboration is clear, but limited attention has been paid to how best to integrate empirical experience accumulated by rural societies within such academic endeavors (Deconchat et al. 2007; Brookfield and Gyasi 2009; Leclerc and Coppens d'Eeckenbrugge 2012). One potential way to improve the dialogue between farmers, policy makers, scientists, and other stakeholders in agrobiodiversity conservation may be a participatory exercise to identify research priorities about seed exchange networks (Vanderhoeven et al. 2010; Rudd 2011a; Sutherland et al. 2011).

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