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Review

Synecological farming: Theoretical foundation on biodiversity responses of plant communities

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Abstract A novel farming method, namely synecological farming (synecoculture in short), based on theory and observation of synecology has been proposed as total optimization of productivity, product quality, environmental load and adaptation capacity to climate change. Synecoculture is designed on a variety of environmental responses within ecological optimum in high-density mixed polyculture where various edible species were intentionally introduced. The whole methodology can be considered as anthropogenic augmentation of ecosystem functioning that promotes dynamic biodiversity–productivity relationship prevalent in natural ecosystems.

In this review we summarize the theoretical foundation to provide a systematic definition of synecoculture and clarify the relationship with existing farming methods. We also collate previously reported analyses of organic and mineral components in farm products, and outline their physiological characteristics and functions in response to culture environments.

Key words: community ecology, ecological optimum, physiological optimum, secondary metabolites, sustainable agriculture.

Agriculture is an important field of application for basic plant science, in view of achieving sustainability of social-ecological systems. Although genetic improvement of crops has been largely contributed to augment the productivity (e.g. Pingali 2012), the expansion of agricultural practice exacerbated environmental degradation both in large-scale monoculture and smallholding countries, causing desertification (UNEP 1991), which may lead to global collapse of biodiversity (Barnosky et al. 2012).

Conventional agriculture is facing serious need of the reformation, for its production and distribution system is considered not being sustainable for the next generation (IAASTD 2009). It is now an urgent task to seek for alternatives with broader perspective incorporating both social and ecological effect of food production (SCBD 2014).

Plants grow in ecological conditions with complex intra-community interactions and responses to their abiotic environments. Physiological characteristics are expressed under ecological contexts, which constantly provides diversity and plasticity both in individual and community organization as a coevolution process (Schemske 2002). Heterogeneous diversity of interactions presumably contributes to stability of complex ecosystems (e.g. Mougi and Kondoh 2012). To make use of such self-organizing property of natural ecosystems to tackle agriculture and associated environmental problems, we need to connect the gap between laboratory-based basic plant science and field-based ecosystems behavior. For that purpose, it is necessary to reconsider a global perspective of growing condition ranging from isolated physiology of individual plants to elaborated dynamical responses in community ecology.

This perspective corresponds to concepts of physiological and ecological optima established in ecology (Putman and Wratter 1984). Plants growth can be characterized between 2 extreme conceptions with respect to the environment: Individual growth within least ecological situation with isolated physiological trait, and overall growth of community responsive to natural complex interactions. On this typology, it becomes possible to align existing farming methods including synecoculture with an integrated perspective accessible both to agronomy and ecology. The same coordinate can be applied to classify distribution of bioactive compounds in various food products, with respect to the growing condition as a distinctive parameter related to both environmental and human health (Funabashi 2015a).

This review summarizes the facts and concepts of plants environmental responses in an integrated entity of physiology and ecology, in which various farming methods, natural ecosystems, synecoculture can be situated distinctively along with characterization of their products.

Models Integration

Physiological Optimum

Physiological optimum is defined as “the range of condition under which a species can exist best in isolation” (Putman and Wratter 1984). The major environmental conditions that restrict physiological growth of plants are typically temperature, humidity (precipitation), and sunlight. Taking the average of enough diverse fluctuating environmental condition, the distribution of the mean yield of a crop converges to unimodal distribution, the top of which corresponds to a physiological optimum in open culture (Figure 1 top). In vivo laboratory experiments in plant science are generally performed with isolated condition taking reference to their physiological optima (Larcher 2003). The maximum growth rate on a physiological optimum varies between species, from which selection effect arises (See section “Biodiversity and Ecosystem Functions in Ecological Optimum”).

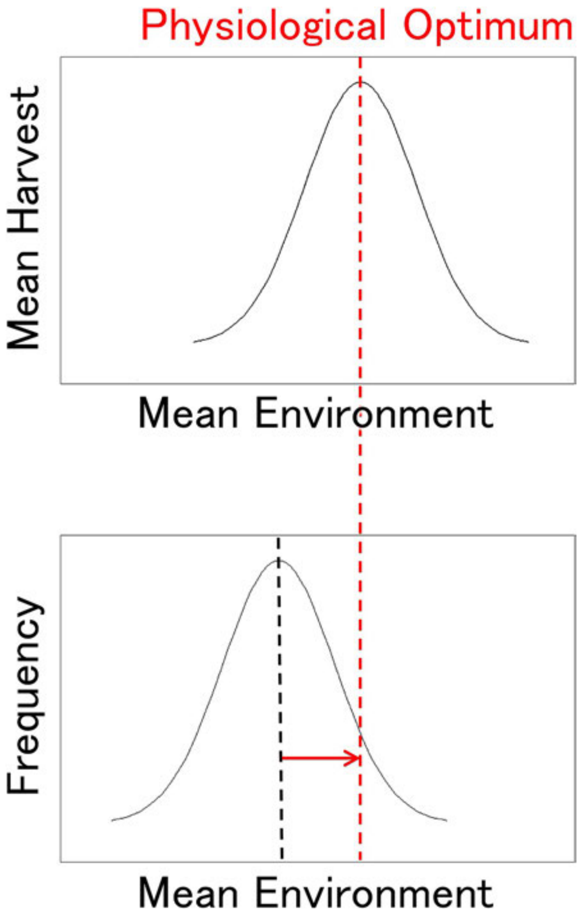

Figure 1. Physiological optimization in open monoculture. Top: Mean environmental condition vs mean harvest. Bottom: Mean environmental condition vs frequency distribution of culture. Physiological optimization can be achieved by matching the frequency distribution to the harvest distribution (red arrow), in order to obtain maximum yield at physiological optimum (red dashed line).

Monoculture Optimization with Physiological Optimum

Conventional monoculture systems aim to optimize the yield by approximating environmental conditions to the physiological optima of crops (Figure 1 bottom), typically with the use of tillage, fertilizer, and chemicals such as pesticide and herbicide (Curran and Lingenfelter 2015; Martin et al. 2005). These artificial interventions can also be represented as a part of environmental parameters, as well as environmental stress and intensity of management such as grazing and mowing (Grime 1973). Such concise triad of methodologies for plant individual-wise physiological optimization is prevalent from small to large scale, from ancient to modern time through the history of agriculture.

Ecological Optimum

Ecological optimum is defined as “(the) actual observed range (of conditions) in nature where it (a species) grows in association with others” (Putman and Wratter 1984). High-density mixed polyculture is a dominant condition in natural environment. When physiological optima of 2 different species are closely situated, mixing them generates competition. According to the physicochemical characteristics of each species such as allelopathy, plant growth may be inhibited, viable range of environmental parameters may be limited, displaced, and divided as the interactive results of coexistence (Putman and Wratter 1984; Reigosa et al. 2006). It may also contain delayed feedbacks of multiple temporal scales (Verbitskii and Verbitskaya 2007). This results in a formation of ecological niche structure, in which each species attains its possible maximum growth as a result of the ecological optimum (Figure 2). Environmental conditions may also include geographical gradients of other environmental factors in explaining spatial localization of vegetation.

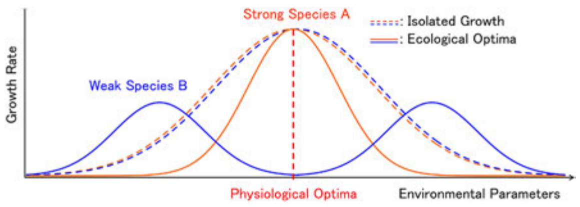

Figure 2. Pattern diagram of niche formation in ecological optimum. Example of the competition between vegetation A (orange) and B (blue) with closely situated physiological optima (red dashed line). A and B grow with similar physiological condition in monoculture (orange and blue dashed line, respectively). A is supposed to be stronger than B for resource competition at physiological optimum range, though compete poorly at marginal tolerance conditions. As the result of competitive interaction, ecological optimum of A is confined in narrower range (orange solid line), while that of B is displaced and divided into 2 separate ranges (blue solid lines). Other typologies of ecological niches exist in between, including asymmetric deformation. Each niche distribution is not necessary normal distribution but generally unimodal.

Growth in ecological optimum can be both inferior and superior to the isolated physiological growth rate (Putman and Wratter 1984), and in general terms the former can be conceptualized as competitive loss and the later symbiotic gain (See next section).

Ecological optimum presupposes natural environment that cannot be totally simulated in confined laboratory conditions. This complexity is a premise of real-world practice with open environment, in some cases coined as in natura that entails environmental contexts beyond in vivo response (e.g. Quintana-Murci et al. 2007). Traditionally, it was treated with synecology, which has been renamed to community ecology with extensive supports of modeling (Strong et al. 1984; Webb and Williams 1973). Mathematical modeling and computation have drastically augmented the simulation and on-site interactive management capacity, allowing *trans*-disciplinary integration to tackle open complex systems (Tokoro 2010).

Biodiversity and Ecosystem Functions in Ecological Optimum

The complexity of ecological optimum arises from the relationship between biodiversity and ecosystem functions. Biological diversity, generally classified into genetic, species and ecosystem diversities (UN 1992), has been studied on relationship with ecosystem functioning. Based on empirical field experiments, variation in genes, species, and functional traits were revealed to positively correlate with major ecosystem functions such as drought resistance, resource capture, biomass production, decomposition, and nutrient recycling in wide situations (Cardinale et al. 2012; Tilman et al. 2014). Diversity–productivity and diversity–stability are considered to be a generic linkage in sufficiently diverse ecosystems. These measured functions usually saturate as the species richness augments, which can be numerically fitted with logarithmic function of species diversity.

With a more precise multivariate analysis that incorporates causal effect of latent environmental variables, the net logarithmic saturation of ecosystem productivity could be decomposed and isolated as the positive linear increase over the whole range of observed species diversity, without a scale limit (Grace et al. 2016). This implies that species richness by itself expresses consistent enhancement of ecosystem functioning, while other latent variables such as soil fertility and climate factors saturate productivity in communities with greater richness.

Reciprocally, productivity also influences biodiversity. Resource competition in species-rich communities enhances exclusion of species in highly productive domain, which results in the maximum species coexistence at intermediate productivity level of the environment (Grime 1973). Optimization of coexistent species diversity in intermediate productivity environment is explored theoretically with multi-resource competition (Huston and DeAngelis 1994) and bi-directionally coupled productivity–diversity model (Gross and Cardinale 2007), which also support the observed unimodal response.

Several other models have been proposed to explain underlying mechanism of the biodiversity–productivity relationship, such as overyielding by selection effect and niche differentiation, increase of resource use, productivity and its variation by resource competition (Tilman et al. 1997). These theoretical models reproduce well the logarithmic saturation of biomass production and other ecosystem functions observed in the field experiments. It also lead to an integrative view on the contribution degree of different competition effects to niche formation, such as the transition from the selection effect (of sampling effect) to the complementary effect as the grassland ecosystem evolves (Fargione et al. 2007). Such spatial diversification process is not only promoting ecosystem functioning but is also a self-organizing driver of biodiversity maintenance mechanisms.

Biodiversity Maintenance Mechanisms in Ecological Optimum

As biodiversity enhances ecosystem functioning, it also maintains and reproduces the diversity by itself. The self-organizing property of biological diversity is called the biodiversity maintenance mechanism, and has been studied in theory (e.g. Chesson 2000) and field observation (e.g. Wilsey et al. 2009).

Historically, the mechanism that supports the coexistence of many species was first considered with the theory of limiting similarity based on the inter-species competition for resource, which lead to the conception of ecological niche (MacArthur and Levins 1967). In contrast to the niche theory based on the deterministic interaction property between species, the unified neutral theory of biodiversity provided simplified stochastic modeling based on random demography of individuals, and derived explanation on community distribution with neither specificity of each species nor heterogeneity of environment (Hubbell 2001). The deterministic niche theory and stochastic neutral theory recently find its place of convergence in the metacommunity theory, which treats the linkage between different spatial scales (Leibold et al. 2004). The metacommunity approach can integrate several models according to their effective scales, and clarify the complementarity. By taking reference between opposing models, it can detect the limitation that a single model can fall, and expand the understanding of process where different scales are mutually engaged. Examples are such as the evaluation of over-fitting of neutral theory out of realistic premise (Takeuchi and Innan 2015), and resolution of the bidirectional relationship in coupled productivity–diversity model within resource supply from the environment (Gross and Cardinale 2007).

On the way to metacommunity integration, biodiversity maintenance mechanisms have been explored in debate between deterministic interaction and stochastic process, in conjunction with niche formation vs neutral theory. Extensive studies on geographical and environmental distributions of species have formalized ecological niche formation as the synergy of 3 categorical factors, biotic, abiotic, and mobility (Soberón and Peterson 2005; Peterson and Soberón 2012).

Biotic factors refer to deterministic interactions between species such as negative density effect and competition that contribute to achievement of higher species diversity (e.g. Grace et al. 2016; Harms et al. 2000). It also includes hysteresis of life histories ranging from individual to community scales such as vegetation succession (Huston and Smith 1987).

Abiotic factors correspond to environmental constraints by which species survival and growth are determined, locally such as temperature, water, light, soil property, and globally such as climate that produce macroscopic gradient of vegetation. Projection of the effect of climate change on future biodiversity is highly variable according to the model, but forecasts predict overall decline of biodiversity by the modification of abiotic factors, such as material and energy cycle, and consequent reduction of acceptable niche diversity (Bellard et al. 2012; IPCC 2002; Thomas et al. 2004).

Mobility is expressed as relatively stochastic factors such as migration, ecological drift, and disturbance. Migration of plants is based on the balance between exclusive suppression from the community and seed dispersal by mainly wind and animals (Sauer 1988). Ecological drift is a stochastic fluctuation of individuals in local communities, modeled in the assumption of neutral theory (Hubbell 2001). It does not assume any prior distinction between species nor individuals, and simply describes the community demography with stochastic parameters such as birth, death, and migration rate.

Disturbance includes both natural and human-driven disruption of ecosystems. Although the origin of disruption may be classified as abiotic factor, the consequence of disturbance influences the mobility such as creation of the spatial gap and introduction of outside species. Analogous to productivity–diversity hypothesis, the intermediate range of natural disturbance is considered to produce the maximum species diversity through ecological response by preventing ecological succession from converging to a low-diverse climax phase (Connell 1978; Huston 1994). Reported effect of herbivory on ground vegetation also draws the intermediate response on species diversity (Suzuki et al. 2013). The intermediate disturbance hypothesis is further studied in interaction with other factors, such as exotic species invasion under human disturbance (Catford et al. 2012). Disturbance in agriculture is also consistent with the hypothesis, where low intensity initially provokes biodiversity beyond the natural state in surrounding environment, allowing the low to intermediate practice to perform as the high nature value farmland (EEA 2004). A theoretical model is developed to further encompass controversial examples into interactive effect of environmental productivity and disturbance on species diversity (Kondoh 2001).

As overviewed, ecological optima foster spatial and temporal rich dynamics in both biodiversity and ecosystem functioning. Although the combinatory complexity of species and interactions account for the observed divergence in niche theory, reducing the system always finds its limit at the physiological property. The integration of physiological and ecological optima therefore represents scale transformation between isolated elements to a whole system with interactions, ranging in all hierarchies of individual, population, community, and meta-community, providing an integrative platform between plant science and ecology.

Integrated Model of Physiological and Ecological Optima (IMPEO)

Based on the reviewed knowledge, we consider the integrated model of physiological and ecological optima (IMPEO) to obtain a coordinate system for the characterization of farming methods. We consider a parameter m ($0 \leq m \leq 1$) to represent the degree of mixture of 2 vegetations A and B, whose physiological optima coincide. Relative ratio of A and B will be given as $m : 1-m$. We then consider mean values of environmental parameters including spatial distribution in open environment, in order from which to extract an average behavior of productivity: The diversity of niche structure will be represented as longer tail of averaged unimodal distribution.

Suppose the vegetation A is more competitive than B. When ecological niche diversifies as in Figure 2, growth rate distribution of mixed polyculture ($0<m<1$) in ecological optimum converges to normal distribution with longer tail than isolated state ($m=0,1$) with respect to the mean environmental condition (Figure 3). Parameters out of consideration need to be randomized or fixed as a stable value in this representation.

This situation integrally generates competition and symbiosis between A and B. Here, we distinguish between the competitive loss and the symbiotic gain by the difference of growth rate at the same environmental condition between isolated ($m=0,1$) and associated states ($0<m<1$). Competitive loss means the decrease of mean growth rate by resource conflict when plants

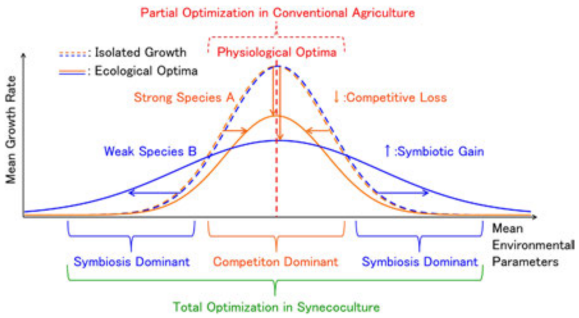

Figure 3. Integrated model of physiological and ecological optima (IMPEO). Both optima are expressed with unimodal distributions based on numerical simulation taking mean environment parameters from randomized situations. X-axis: mean environmental parameters. Y-axis: Mean growth rate renormalized by the maximum value of physiological optima. orange dashed line: Isolated growth of vegetation A ($m=1$). blue dashed line: Isolated growth of vegetation B ($m=0$). orange solid line: Mixed polyculture growth of vegetation A ($0<m<1$). blue solid line: Mixed polyculture growth of vegetation B ($0<m<1$). A is supposed to win competition against B in high productivity range, as represented in Figure 2. Weak species B can prevail in symbiosis-dominant ranges under favoring environmental variation. Other types of niche differentiation with competing physiological optima can be represented as intermediate distributions between those of A and B with solid lines. Orange arrows: Attenuation of physiological growth by ecological competition effect. Blue arrows: Enhancement of physiological growth by ecological symbiotic effect. Red dashed range: Physiological optimization range of isolated growth in conventional agriculture. Orange range: Competition-dominant range in ecological optimum. Blue ranges: Symbiosis-dominant ranges in ecological optimum. Green range: Total optimization range in synecoculture including both competition and symbiosis dominant conditions.

grow with others (Figure 3 orange arrows). Symbiotic gain represents the increase of growth rate in association than in isolated state (Figure 3 blue arrows). It is also mentioned as facilitation, mutualism and beneficial interactions (Hooper et al. 2005; Paquette and Messier 2011). The symbiotic gain mainly generates from the complementarity of various foliage layers and regulatory effects of environment that contribute to the total photosynthetic yield (Larcher 2003). Current arguments of overyielding only address net community productivity, without referring to species-wise responses that create a shift. They aggregate competitive loss and symbiotic gain over a community, and provide a coarse phenomenological description of total yield variation (Fargione et al. 2007; Hector et al. 1999, 2010; Paquette and Messier 2011). Most of the modeling is preferential to the explanation limited in competitive and complementary effects (Chesson 2000; Gross and Cardinale 2007; Tilman et al. 1997).

Although overyielding is commonly observed phenomenon in ecology, little has been investigated on the generating structure in multi-scale perspective in relation to both physiological and ecological optima. The differentiation between competitive loss and symbiotic gain on IMPEO provides finer theoretical conjecture on the efficiency of open field cultivation: Growth of crops at their physiological optimal range requires constant elimination of competing species, except strong plants that remain stable in competition-dominant range. While weak species, as are most of the vegetables, could be more cost-effective at resulting niche condition in ecological optimum within symbiosis-dominant relationship.

Classification of Existing Farming Methods between Physiological-Ecological Optima

With the use of the integrated model of physiological and ecological optima (IMPEO), we evaluate the optimization scale of existing farming methods and situate the relationship with each other.

Conventional Agriculture

Conventional agriculture is based on the triad that controls the monoculture condition closer to physiological optimum: Tillage, fertilizer, and chemicals (Curran and Lingenfelter 2015; Martin et al. 2005). The methodology is consistent in a wide range of crops and scale, including centralized large-scale production to smallholding farms. This paradigm is based on control of culture environment into a physiological optimum range, using principally fossil fuel and mineral resources such as phosphorus and potassium.

Recent challenge for the high throughput optimization of conventional system is called precision agriculture (Gebbers and Adamchuk 2010; Stafford and Werner 2003). Facing population growth, resource depletion and environmental problems, widely prevalent conventional systems are in serious need for elevating efficiency, resource management and environmental conservation (Tilman et al. 2002).

The extreme implementation of physiological optimum is pursued in the plant factory, where major productivity factors such as temperature, water, light and trophic condition are artificially controlled in an isolated culture bed (Kozai et al. 2015). Factory culture can selectively maximize production of specific nutrients and phytochemicals, though the expression is limited to physiological control and not associated with ecological interaction.

Genetic engineering is another yet developing technology in monoculture system. Genetically modified organisms (GMO) introduced preferential genes such as for the stress–tolerance, efficient resource acquisition and enhanced nutrition, based on the artificial genetic transformation (e.g. Gilbert 2010; Gutiérrez 2012). Commercial varieties also incorporate herbicide tolerance and pesticide-production trait (e.g. Hellmich and Hellmich 2012; James 2011). These features strengthen the capacity of growth and competition in a broader range around physiological optimum, converting the control cost of environment to the genetic function. Despite some prevalent use in cash crop, GMO production and trade are in serious dispute for the threat to surrounding ecosystem diversity (e.g. Gilbert 2013). The impacts of transgenic plants to genetic diversity are currently less understood. Genetic pollution cannot be prevented without screening the whole possible crossing interaction of plants, microbial gene transfer, and other indirect effects on genetic diversity of community in ever-changing ecological optimum in open environment. Most of these factors are usually outside of concern in genetic engineering.

These conventional technologies can be situated in the far physiological side in IMPEO (Figure 4). Culture condition has been largely modified from natural ecosystem to support physiological optimum range of crops, which requires non-renewable resources and produce massively environmental load, most devastatingly causing the loss of biodiversity. The extinction rate of vascular plants by the expansion of farmland overwhelms that by climate change (Pereira et al. 2010). Criticism arises that these business-as-usual scenarios are considered not sufficient for global food security and sustainability of sane social-ecological system, calling for the need of small-scale diversified form of agriculture favoring ecosystem functioning (IAASTD 2009; WRI 2005).

Organic Farming

Organic farming is the most popular alternative to conventional agriculture, internationally regulated and reinforced in many nations. The standards were set to cope with the demand of sustainable food production mainly with the initiative of developed countries (CFR 2016; EUR-Lex 2007; IFOAM 2008; MAFF 2012). As a farming method, it is based on the monoculture system with tillage, the use of organic fertilizer, restriction of synthetic chemicals under the regulation with environmental and health concerns. Efforts include soil conservation such as minimum tillage, rotation and cover crops, biodiversity promotion around the plot, efficient resource management such as judicious use of water and local recycling of organic materials, other health-related quality measures, etc (e.g. Hole et al. 2005). These principles are promoted in multiple aspects of production, processing and distribution, which presumably contribute to increase health beneficial phytochemicals and decrease risk components in organic foods (Baranski et al. 2014).

Although biodiversity is partially promoted compared to conventional practice (e.g. Bengtsson et al. 2005; Holzschuh et al. 2007; Pfiffner and Balmer 2011; Tuck et al. 2014), it does not fully recover the impact of land conversion by tillage. The productivity and conservational effort are in trade-off in a wide range of certified organic practice (Seufert et al. 2012). The yield reduction becomes even proportional to biodiversity promotion (Gabriel et al. 2013). Environmental impact in total is generally reduced per unit surface of production but not per product unit (Tuomisto et al. 2012). Nitrate leaching rate to ground water per unit output could be even higher in organic practice (Stolze et al. 2000). Integrated lifecycle assessment also failed to differentiate between organic and conventional systems, only settled for partial characterization (Meier et al. 2015).

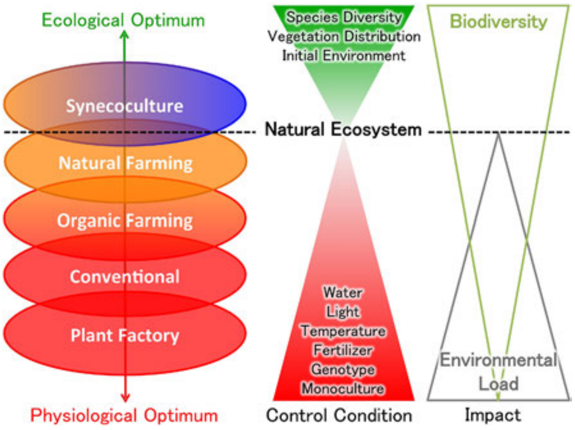

Figure 4. Relational classification of farming methods based on IMPEO. Existing farming methods, conventional, organic, and natural farming try to control the growth condition of crop to achieve closer condition to physiological optimum in trade-off with environmental conservation effort. Plant factory represents the extreme control in confined environment. Production at physiological optimum range turns out to cope with competition-dominant interaction when associated with other vegetation of concurrent physiological property. Synecoculture targets the mixed cultivation of both competition-dominant and symbiosis-dominant niches under fluctuating environment, by controlling plant species diversity and its distribution. Colors in accordance with Figures 1–3.

In total, organic farming is situated slightly closer to natural ecosystem than conventional, but still based on a monoculture situation that relies on the physiological optimum as the foundation of productivity, therefore producing similar or effort-wise reduced impact on environment per production (Figure 4).

Natural Farming

More conservational efforts are introduced in so-called natural farming, usually in small scale (e.g. Fujita 2001; Fukuoka 2010; Xu 2001). Only producer-wise definition is available for each school of practice categorized as natural farming. Although concern on environmental impact with respect to tillage, fertilizer and chemical is generally more strict than organic standards, it is largely based on practitioner-wise local experience and varies accordingly. In most cases they adopt reduced tillage including manual ploughing, and/or organic manure and compost. Culture may incorporate rotation, intercropping, companion planting, cover crops, living mulch and other organic mulch. It ranges between monoculture to polyculture with no more than a few crops at the same location, which forms a mosaic landscape of small culture patches with different crop composition. Although it is still controlled from natural variability, crops grow in a wider range of environmental and ecological condition than in organic farming.

This category also qualitatively includes small-scale practice of traditional sustainable agricultural communities such as in Satoyama farming landscape, where strong interactions with the local ecosystems create overall profit to ecosystem services and human well-being (JSSA 2010). Appropriate management of the landscape promotes biodiversity across the heterogeneous variety of ecosystems with diverse degrees of human disturbance (Berglund 2008; Uchida et al. 2016). Such species diversity specifically coupled with social-ecological interactions can only be sustained with human intervention (Liu et al. 2007; Normile 2016). The ecological and cultural values of these traditional ways of living are under international conservation effort such as the globally important agricultural heritage systems (GIAHS; FAO 2002).

Natural farming and the equivalent categories are situated somewhere between organic practice and natural ecosystem with partial overlaps (Figure 4). In some situations, human activity can even enhance unique biodiversity beyond natural state. Although it can minimize environmental impact, the productivity is low and not scalable, and generally remains at the level of self-sufficiency.

Large-scale conception of natural farming, namely natural systems agriculture, is pursued by mimicking natural prairie with polyculture of perennial grains, in an effort to substitute the conventional production and eventually escape from environmental load and dependence on fossil fuel (Jackson 2002). Perennial varieties of grain crops produced by crossing with wild relatives generally outperform annuals in maintaining ecosystem functions in variable conditions, especially in marginal land and with limited resources (Glover et al. 2010).

These conceptions of natural farming define the natural state as an ideal norm, in contrast to human civilization that degrades its organization. They learn from nature to better assimilate natural state and returning agricultural practice to its original ecological cycle. Proceeding to further organized stage of ecosystem that exceeds the natural state, however, is not explicitly implemented nor oriented in developmental strategy.

Integrated view

The IMPEO provided the view that existing methods are the exploitation of ecosystem by means of conversion to physiological optimum (Figure 4). This means that the intensity of agricultural practice and biodiversity are in fundamental trade-off in existing farming methods, which is summarized in Figure 5 (EEA 2004; Hooper et al. 2005; Vandermeer et al. 1998). Although natural ecosystems have evolved with the self-organized diversity–productivity relationship, agricultural application did not incorporate the self-sustaining nature of ecological optimum. Adaptive responses through biodiversity maintenance mechanisms of plants contradict with monoculture optimization: Monoculture management requires synchronization of growth and harvest in a uniformly controlled condition without competing species. While growth of natural vegetation desynchronizes through competition and disturbance, creating various species composition spread in heterogeneous fractal patterns with power-law size distribution (Farrior et al. 2016). Ecological succession is based on asynchronous renewal that provides robustness to ecosystem functioning as insurance effect (Hector et al. 2010). Flowering and fruiting in densely mixed vegetation are intermittent with large temporal fluctuation varying over taxonomies (Sakai et al. 1999). In such ecological optimum with high biodiversity, symbiotic interactions exert positive feedback to productivity (Scanlon et al. 2007).

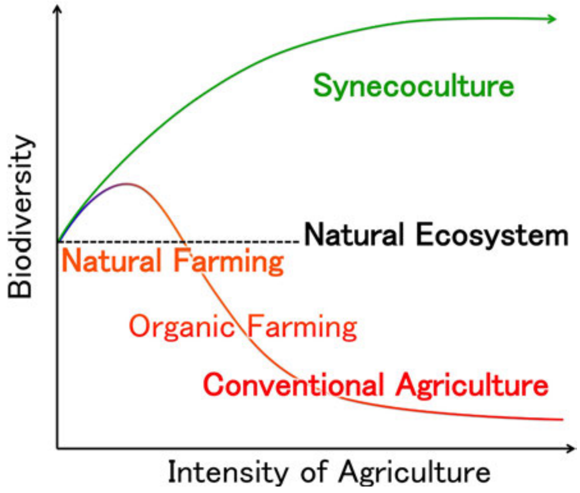

Figure 5. Intensity–biodiversity relationship of open-field culture. As the intensity of farming increases, biodiversity is lost along with negative impacts to environment in existing methods, except slight disturbance that promotes unique biodiversity. Synecoculture aims to fundamentally shift this trade-off to the culture diversity positively enhanced by the intensification of ecosystem functioning through biodiversity operation.

When crops are cultivated at the physiological optimum range, the competitive loss becomes dominant in ecological response within crops and with other intervening species (Figure 3). High-yield environment condition triggers excess competition that eventually decreases biodiversity (Gross and Cardinale 2007), which leads to instability of monoculture system against weed invasion. Resources in conventional systems are invested to maintain high-productivity low-diversity condition in order to protect highly competitive niche of weaker crops at primary succession stage. Such control is supported by the entire disturbance of soil by tillage and eutrophication by fertilizer, unavoidably associated with erosion and leaching. The recovery reactions of farmland ecosystem are considered as the weeds and pests, which are constantly wiped out with chemicals. Interactions with local flora and fauna are minimized. The vicious cycle dismantles the mutually enhancing ecological relationships in nature between productivity, biodiversity, and ecological succession.

Competition of fertilizer in primary succession favors locally dominant species, considered as weeds. In Figure 3, invasive species typically corresponds to the strong vegetation A. On the other hand, crops do not easily disseminate in the surrounding wild environment, which can be represented as weak species B. The dominance also depends on the order of introduction. For example, grown seedlings could suppress germination of other species and maintain stronger position.

If we consider maximization of the weak crop B in monoculture, the best productive condition lies at the physiological optimum (Figure 3 dashed red line), at a primary stage after tillage. Yield improvement is the synonym of environmental control to this unstable narrow range in conventional systems, with the use of irrigation, tillage, fertilizer and chemicals.

In terms of ecological optimum, on the other hand, this range is competition-dominant and requires intensive intervention to protect targeted crop against other species, costly as it counteracts against succession dynamics. Abandoned farmland easily allows invasion of various plant species, shifting to ecologically sustainable trophic condition through diverse niches formations (Osawa et al. 2013).

If we include the spontaneous niche diversification process in the basis of production, symbiosis-dominant ecological niche can be found in a wider range of ecological optimum (Figure 3 solid lines). When growth in such condition happens, it requires less control as it is already supported by the biotic and abiotic environment. Theoretical prediction indicates that high-diversity condition is situated at the intermediate productivity (Gross and Cardinale 2007; Huston and DeAngelis 1994), which may be widely distributed in natural environment (Grime 1973).

There exist empirical evidences that overyielding by symbiosis-dominant ecological niche is prevalent in grassland ecosystems (Hector et al. 1999). In European countries where the conventional systems were developed, plants are inherently thriving with mutually beneficial interactions in an incremental way with respect to biodiversity, not by monocultural dominance. In high-diverse community, most plants are displaced from their physiological optima by niche differentiation, where community growth profits more from symbiotic interactions (Figure 3 blue ranges). This can be interpreted as the buffering function of natural ecosystem as a complex adaptive system: Niche diversification creates a longer tail of survival and expresses a higher growth rate in a wider range of environment, which could mitigate reduction of total biomass and loss of habitats in response to environmental fluctuation. In a long term, this dynamics is consistent with the coevolution of plants and land environment, through which essential ecosystem engineering was performed to cover wider surface with self-promotive complexity and autotrophic productivity of terrestrial ecosystems (Graham 1993). Evolutionary stable strategies are shaped on the long-term adaptability to environmental fluctuation exposed to contingent events, which contradicts with short-term fitness on limited variability (Yoshimura and Clark 1969).

It should be noted that competition-dominant range in Figure 3 does not necessarily reduce productivity at community level in polyculture, depending on the vegetation profile. Negative effect on the individual growth rate and resulting community biomass is not necessary proportional to the number of competing species, as they may live on the complementarity of resources with higher density (Li et al. 2014). In classic consumer-resource competition models, in contrast, relative contribution of species diversity to primary production was suggested to generally decrease in high productivity environment (Gross and Cardinale 2007). This relationship was simulated by interactively linking environmental productivity to diversity responses, which consequently derived combined effect on primary production. The results may not hold for the set of species that is designed from the resource mobilization mechanisms beyond the randomized and simple trade-off assumptions in these models.

These facts are important when we consider a novel farming system with extended insights on ecosystem dynamics with a more comprehensive evaluation of existing methods. In considering sustainable farming over the long term with benefit of ecological optimum, the adaptive reactions of plant community to environment, including biotic, abiotic, and mobility elements, become key factors of productivity and sustainability. Yet these have never been put on the foundational basis of agricultural production. Only rudimentary effects were used occasionally as the fallow process, as a spontaneous recovery of degraded fertility in a black box. Conventional systems are biased in a short-term, physiology-oriented approach compared to the whole potential that IMPEO can outreach. They blindly pay the cost for a strongly isolated homogenization, without considering the self-multiplying fluctuation that the ecosystem functionally possesses in multiple scales. Novel technologies such as genetic modification and plant factory are also developed along the same line, pursuing further promotion of monoculture paradigm: How to stabilize the targeted optimum by cutting complex interactions and removing inhibitory factors with limited rationality.

The conventional methodology approaches its global exploitation limit and one third of the global production of rice, wheat, and maiz are already facing yield plateaus (Grassini et al. 2013; Ort and Long 2014). Since the control cost is required separately for each crop and does not cancel out with synergistic building effect of ecosystems, the cost-effectiveness only decreases as it approaches to biophysical limit.

Other alternative methods are in compromise between ecology and productivity, the majority of which still reduces biodiversity and ecosystem functioning far below natural ecosystems. Substantial benefit of biodiversity-driven ecosystem dynamics is neither integrated in culture systems nor defined as an intensively operational target. The merit of alternative systems is evaluated within the framework of economical cost-effectiveness and environmental mitigation efforts without deviating from intensity–biodiversity trade-off (Figure 5 orange-red line) (e.g. McBride and Greene 2015). Future projections of agricultural impact on biodiversity including current conservation and mitigation efforts draw devastating loss in both small and large-scale practices around the globe (Alkemade et al. 2009). Soil degradation is also concentrated by 1.6 times in cropland at the global scale (Bai et al. 2008).

Environmental problems and production barrier in monoculture paradigm is based on the twisted application of physiological optimization to inherently ecological situation. In some cases, important progress on sustainability and development was made by dissenting agronomists by thorough engagement to surrounding social-ecological contexts and working across disciplinary boundaries (Prasad et al. 2012). The important task then is the concrete design of alternatives that would convert the conception of food production to a total optimization.

Synecological Farming (Synecoculture)

In view of incorporating ecological optimum into food production, synecological farming, in short synecoculture, has been proposed and tested with field experiments (Funabashi 2011, 2013a; Funabashi et al. 2015). It is based on the no-tillage, no-fertilizer, no-chemical practice with strategic introduction of edible species and management of vegetation distribution at community scale. Beneficial functions for agricultural production are obtained by replacing tillage, fertilizer, chemicals, and other element-wise control of physiological condition totally with ecosystem functions by strategic augmentation of biodiversity. The framework of productivity is also shifted from crop-wise biomass to community-wise product portfolio, with concern to food quality and diversity. It intends to attain maximally incremental solution of biodiversity and productivity with the intensification of ecological optimum.

Here we review the relevance of synecoculture methodologies to ecological responses of plant community on which these principles were founded.

Ecological Premise: High-diversity, high-density mixed polyculture

Diversity entails productivity and stability in various ecosystems (Cardinale et al. 2012). Making use of this natural mechanism to farming can expect total optimization of sustainable productivity in a long run (Li et al. 2014). Enriching the ecological functioning for agricultural production, especially overyielding in multiple combinations of edible species in symbiosis-dominant niches formation, should rely on the enhancement of biodiversity, which leads to upgrading of the productive and regulating relationships in ecological optimum.

In conventional systems and basic plant science, the possibility of the physiological optimum is investigated in artificially isolated conditions that can never exist in open field. In contrast, the concept of ecological optimum remains only descriptive, as a mere interpretation of natural vegetation. It can be further pursued beyond the natural state with artificially enhanced biodiversity.

Ecological optimum that exceeds the natural state can be considered as the productive range of ecosystem with higher expression of coexistent species diversity, along with the number of associated ecological interactions of direct and indirect effects. Therefore, the intensification of ecological optimum can be defined as the augmentation of species diversity and interactions that are engaged to the maintenance of ecosystem, in a way higher than the corresponding successional stage of natural ecosystem. This can be interpreted in farming strategy as the promotion of edible species diversity, elaborated management of vegetation distribution during growth, and configuration of initial abiotic condition such as amelioration of soil texture and topographic effect of the field, in an integrated way for higher diversity–productivity response. Ecologically viable range of crops need to be extended through plants interactions, which means the direct operation of environmental productivity is not the control variable for ecological optimum. These strategies for ecological diversification correspond to the complementary set of conventional physiological control, and can be distinguished with opposing directions on IMPEO (Figure 4).

From this perspective, monoculture optimization is determined to fight against totally negative effect of competition with respect to other species (Figure 3 red range). Besides the cost of environmental control to maintain physiological optimum, it requires thorough elimination of other species, typically by cultivation and chemicals. Weak species need to be protected in isolated growth, otherwise vulnerable to interactions at competition-dominant range. In terms of ecological adaptation, however, chemical resistance of weeds and pests is steadily increasing and limiting the application range (e.g. Curran and Lingenfelter 2015; Gut et al. 2002).

On the other hand, widely fluctuating natural environment could harbor a variety of ecological niche situated in symbiosis-dominant ranges of given ecological optimum (Figure 3 blue ranges). The niche condition is sustained and the productivity promoted by interactions and responses of multi-species community. Yield maximization becomes the matter of search for vegetation portfolio that could maximize the symbiotic gains without controlling environmental parameters.

As a result, high-diversity introduction of edible plants in high-density mixed polyculture becomes the most basic design of community structure for the maximization of ecosystem functionality including yield, which synecoculture adopts. This principle breaks the conventional intensity–biodiversity trade-off and shifts to substantially positive increase of biodiversity driven by intensification (Figure 5 green line). The total optimization of yield can be obtained as the integral of multiple niches responses over the varying range of natural environment (Figure 3 green range). To maximally profit from environment diversity, crops include all kinds of vegetables, herbs, wild edible plants, fruit trees, and other commodity species (Funabashi 2011; Funabashi et al. 2015). With sufficiently diverse portfolio of vegetation, productivity could be maintained in wide environmental variation.

This design renounces the crop-wise strong control of culture not only by the complexity of internal dynamics but to positively accept dynamical fluctuation range of environment. Response diversity plays particularly important roles for ecosystem renewal and reorganization following change (Elmqvist et al. 2003). Instead of focusing on the simple input–output relationship subject to reproducible control in conventional systems, synecoculture relies on autonomous adaptive process of diversity responses with effective management scheme in open systems (Funabashi 2015b; Tokoro 2015a, 2015b). Ecological niche is difficult to reproduce as it involves a variety of biotic–abiotic-mobility factors, therefore top-down control is oblivious to latent variables, which account for endemic characteristic of actual spatial distribution of plants (Soberón and Peterson 2005).

Artificial establishment of high-density mixed polyculture creates unique ecosystem that incorporates both propagation of crops and invasion of local species (Funabashi 2013a; Funabashi et al. 2015). Such change could be commonly found in the developmental phase of agriculture, as the generation of human-related boundaries of different ecological communities (Kark 2013; Stohlgren 2006). These interfacing zones between different types of biomes, such as the edge of grassland and forest, are termed as ecotone, which cultivates unique biogeographic diversity compared to adjacent ecosystems (Décamps and Naiman 1990; Terrell-Nield 1986). Species specifically localized around ecotone are reported as the result of the juxtaposition of contrastive environments, known as edge effect (Kark 2013). Patterns of increased species richness dynamically surge and shift through multiple vegetation responses to environmental variation (Risser 1995). Inherent ecotone dynamics intensifies material cycle, facilitates exchange of species and can be managed to produce natural products, the comprehensive intensification of which converges to synecoculture principles.

No Tillage, No Fertilizer, No Chemicals—Positive Disturbance, Niche Formation, and Food Chain Construction

High-density mixed polyculture of species with various physiological functional traits naturally provokes competition effect that works positively to diversity (Harms et al. 2000). In the early stage of succession, selection effect could be expected from the overyielding, which would subsequently be replaced to complementary effect as niche differentiation proceeds (Fargione et al. 2007; Tilman et al. 1997). This can be achieved with edible plants by portfolio-based management with sufficiently diverse variety of crops in densely mixed culture. As a consequence of competition, crop-wise productivity would vary according to species, though the productivity at the community level is expected to stabilize with proportional increase with species diversity (Tilman et al. 2014). Once complementary niches occupied a wide range of environment, strong inhibition is expected against the weed invasion of competing physiological properties (Fargione et al. 2003). Established edible community will profit from the increased productivity, stability, and decreased invasibility that arise from diversity-based ecological coherence. Complete occupation of land surface with crops and other useful vegetation such as living mulch become a default premise of production. This tendency is also observed in less biodiverse conservation agriculture, such as with cover crops (Kaneda et al. 2012) and intercropping (Li et al. 2014; Vandermeer 1989).

In maintaining diverse niches distributions, conservation of soil environment becomes crucial. Soil ecosystem contributes to both plant vigor and soil quality, and needs to be preserved for multiple improvements of ecosystem functions (Siddiqui et al. 2008). Root interactions with soil biota play a central role in community responses to biodiversity (de Kroon et al. 2012). Conventional tillage essentially destroys the soil faunal abundance and microbial activity, which degrades the productivity (Yagioka et al. 2014). In some cases, even reduced tillage could bring devastating impact on soil aggregate formation, depending on the texture (Kaneda et al. 2014). It is also the structural source of soil erosion and ground water pollution. Uniform tillage application must be strictly eliminated from the standard management process of synecoculture.

On the other hand, partial and intermediate disturbances generally trigger positive responses to biodiversity, which consequently increase the yield in ecological optimum (Cardinale et al. 2012; Connell 1978; Gross and Cardinale 2007; Tilman et al. 2014). Soil disturbance should be evaluated not by the form of practice but the consequent effects on biodiversity. An integrative modeling revealed that selective disturbance on the biomass and not on the species richness would promote the overall plot richness (Grace et al. 2016). This indicates that thinning harvest of crops from densely mixed community would maximize the turnover and total yield in synecoculture field (Funabashi 2011). Seed and seedling introduction to the gaps after harvest corresponds to the control of mobility factors in niche formation (Peterson and Soberón 2012). This asynchronous strategy of unified harvest and sowing is similar to forest renewal (Farrior et al. 2016), which augments and stabilizes the community yield in response to environmental variability (Hector et al. 2010).

The positive disturbance effect on the primary productivity of community is estimated to maximize at the intermediate productivity level of environment, by combining productivity–diversity (Huston and DeAngelis 1994), disturbance-diversity (Connell 1978) and diversity-biomass responses (Tilman et al. 2014) in consideration with unified frameworks (Gross and Cardinale 2007; Kondoh 2001). Excess fertilization could result in the reduced diversity by the dominance of competition, which decreases the relative contribution to primary production. This explains the burden of physiological optimization in which existing farming methods confront ecological circumstances: Fertilization based on the crops physiological standards increases production costs including the control of competitive weed, as well as the risk of pest and leaching. As a transitory measure, conventional systems compromise productivity and environmental load with partial incorporation of ecological factors in isolated populations, such as rotation.

On the other hand, total optimization requires involvement of the whole integrated process of ecosystem, which expresses as history-dependent irreversible dynamics of community emerging from heterogeneity of individuals (e.g. Huston and Smith 1987). If we take the path toward ecological optimum, amelioration of productivity should be conducted with development of ecological succession stages, in order to assure sufficient complexity of ecosystem that maintains appropriate flux of nutrient without external resource input (Figure 4). With this respect, weed species can also be utilized for efficient improvement of soil environment in synecoculture, along with strategic introduction of tree species (Funabashi 2011). The associated faunal abundance of insects also play essential role in enriching soil environment by accelerating decomposition and affecting belowground microbial process (Lovett and Ruesink 1995; Madritch et al. 2007).

In total, ecologically constructed intermediate fertility of soil is situated at mutual optimization of biodiversity promotion, cost-effective productivity, stability of weed and pest control, which can be achieved as an interactively enhancing feedback between biodiversity and productivity (Figure 3 blue ranges). The intermediate environment needs to be realized by ecological succession, without the application of fertilizer and other material inputs that cause environmental load. This process is consistent with formation of soil in terrestrial ecosystems through ecosystem engineering capacity of plants in the course of evolution. Topsoil formation by photosynthesis and associated faunal interactions could be expected to maximize in the intermediate transition process from low to high productivity of soil environment, at symbiosis-dominant ranges.

No-fertilizer practice also conforms to the future need of resource management, as important soil nutrients such as phosphorus need to be preserved in natural grassland without mobilizing it to cropland through livestock manure (Sattari et al. 2016). Essential limiting materials for photosynthesis, such as phosphorus, nitrogen, and trace elements lost by harvesting need to be eventually supplied from a more macroscopic geophysical cycle through ecological pathways. By artificial means, recycling efforts particularly need to focus on eutrophic costal seawater and lake sediment, where overall agricultural runoff accumulates (Diaz and Rosenberg 2008; Holtgrieve et al. 2011; Jackson 2008). Conventional human mobilization of manure is coupled with leaching that heavily impacts watersheds. In contrast, ecological diffusion through development of complex vegetation establishes buffering cycles of materials that make ends meet between inputs and outputs without polluting groundwater. It rather ameliorates water quality with soil functions such as filtering and purification (WRI

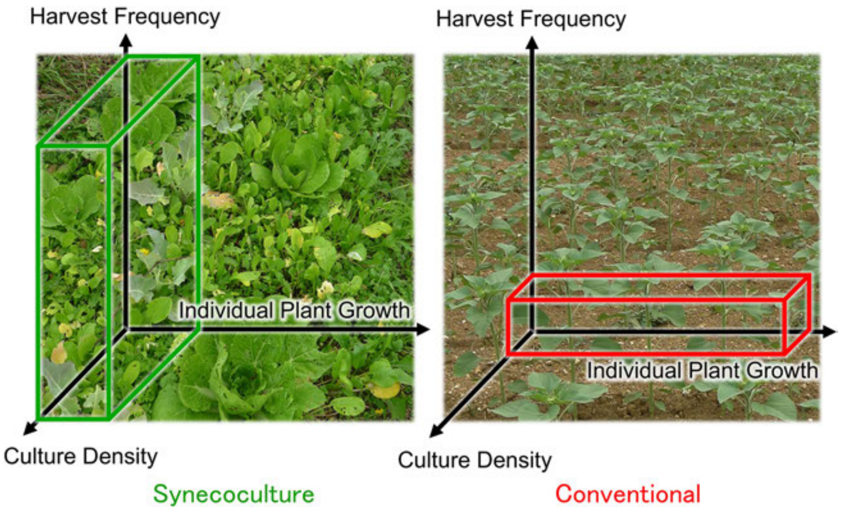

Figure 6. Modality of harvest in synecoculture vs conventional agriculture. Conventional systems optimize individual plant growth with constrains on harvest frequency for the synchronization of growth and culture density to avoid competition of resources. Synecoculture is based on ecological optimum that cannot maximize individual plant growth, instead it can augment thinning harvest frequency and mixed polyculture density that promote overall yield in community level. Other conservational farming methods exist in between.

2005). Synecoculture aims to positively contribute to environmental functionalities even in sensitive ecological zones such as upstream of water reserves. Keeping the balance of intermediate fertility of soil through construction of ecosystems is beneficial for promoting both terrestrial and aquatic biodiversity.

Rich vegetation nurtures elaborate food chain. Mixed polyculture of diverse crops mitigates the pest impact by diversity (Andow 1991), and provides essential ecosystem functions such as pollination and micronutrient concentration (Smith et al. 2015). Intensification of ecological optimum would resolve the pest management in wider contexts through diversity-induced stability effect such as natural predators, and by adapting the crop portfolio to make use of positive effects of insects. Diverse responses to herbivory in metabolism, growth pattern, morphology, and phenology are observed over wide taxonomies of plants (Karban and Baldwin 1997), through which insects also play the role of ecosystem engineers (Marquis and Lill, 2007). The complex insect–plant interactions alter the community dynamics by the web of indirect effects, which is an important aspect of resilience in ecological optimum. Nutrients removed by crop harvesting, such as phosphorus, nitrogen and minerals, could be refilled by diffusion from surrounding ecosystems through concentrated food chain in the plot. In this prospect, introduction of tree species is essential to secure phytophagous insects abundance (Lawton 1983) and their predators such as avian species as the bearer of material cycle. Other pests and pathogens should also be interpreted in the diversity maintenance mechanism of whole ecosystem. Therefore, the use of chemicals must be avoided in the context to eliminate pest species, as for weeds and diseases, to protect the self-organizing complexity of the food chain. Chemicals should be replaced with a novel strategy of vegetation portfolio that would yield richer regulation dynamics with extensive interaction between flora and fauna. Making positive use of faunal interaction including even large apex consumers is an urgent task to halt trophic downgrading of global ecosystem (Estes et al. 2011). Such mutualistic relationships are also important evolutionary drivers of taxonomical diversification (Dodd et al. 1999; Hodges 1997).

Based on IMPEO, conditions for the extreme conception of production in ecological optimum are derived: The conventional triad methodologies, i.e. tillage, fertilizer, and chemicals, need to be totally replaced with positive disturbance, niche formation, and food chain construction by augmenting biodiversity with edible species beyond natural state. The resulting ecological optima could be highly transient, though reproducibility could be attained in various species compositions, as multiple stabilities are inherent in ecosystems with complex interactions (Lewontin 1969).

Modality of harvest and maintenance

In order to profit from response diversity, harvest and maintenance modalities need to structurally adapt to the production with ecological optimum. Conventional systems synchronize and maximize individual growth of crop (Figure 6 right). Oh the other hand, culture density is limited to avoid competition of resources that is situated at competition-dominant range in ecological situation (Figure 3 orange range). Harvest occasion is also limited in a few times per year, leaving the rest of time as the preparing period without any yield. The conventional methodology is efficient for collective harvest at the expense of maintenance cost, but increases the risk of vulnerability to environmental change.

Harvesting operation in synecoculture is based on thinning harvest from mixed vegetation (Funabashi 2011). Since it is based on ecological optimum, growth of individual crop cannot be maximized (Figure 6 left). Instead, it is possible to increase culture density along with frequency of harvest, in order to amplify yield through disturbance-induced renewal of community. To maximize the turnover, it is necessary to consider various efficient association and succession strategies with ecological property of crops. Although the facility of harvesting work should be prioritized in commercial practice, synecoculture fields need to utilize multi-faceted spatio-temporal structure of vegetation. This includes combination of plants with different and complementary height, depth, morphology, resource requirement, life cycle, succession order and stage, together with various topographic effects of field such as ridge, fence and other regulatory structures of environment. Highly diverse options of seeds and seedlings are necessary at the initial stage, which could be gradually replaced with self-seeded varieties on site.

Biodiversity is generally a trade-off with harvest efficiency in conventional systems. If we pursue the scalability of synecoculture, it becomes necessary to call for an automation with technologies compatible to the complex vegetation. Possibilities may lie in robotic arms, for example, which would enable the management of higher and more complex vegetation without disturbing the diversity of environment (e.g. Jenkins 2013).

Experimental Reports on Productivity and Profitability

Since natural niches distributions are based on power-law distributions, the productivity of synecoculture does not conform to the reproducibility argument based on the mean value of yield (Farrior et al. 2016; Scanlon et al. 2007). It should be rather managed with the risk hedging principle on vegetation portfolio, in order to ensure the minimum productivity level with all possible environmental changes being taken into account. This approach can be extended from plot to regional level as a bottom-up framework of food security with the use of information technology (e.g. Bagla and Stone 2013; IBRD/WB 2011).

The overall yield of synecoculture is still tested in experimental phases, including small-patch experiments on citizen science basis and commercial production (Funabashi 2011; Funabashi et al. 2015). Profitability of farming methods generally depends on the amount of biomass, price of products, and cost-benefit ratio. In 3-year continuous production with synecoculture at a commercial farm of 1000 m^2, despite species-wise high variability of biomass, net profit and cost-benefit ratio were reported to be higher than conventional truck farming, with the price rate equivalent to organic products (Otsuka 2015). Related experiments showed that introduced crop diversity in a few small-scale synecoculture fields exceeded that of biodiversity-valued traditional farming in regional scale (Funabashi et al. 2015). Synecoculture excels in the diversity of products, which is an essential factor of local production for self-sufficient sustainability (Hashiguchi 2005).

Food Components Analysis

Food quality is another important issue for food and environmental security. Diets are key factors to resolve linked burdens between environment and health (Tilman and Clark 2014). Sustainable diet requires substantial health benefits with ecologically sound production, on which synecoculture is designed (Funabashi 2015a). Enhanced ecological interactions in synecoculture may enrich consequent physiological responses of crops. Diversity of phytochemicals is the major source of pharmaceutical substances (Johns 1996), the majority of which relies on the production in natural environment as medicinal plants are typically found in ecological niche conditions (FAO 2005). Plant diversity responses may also affect our metabolic diversity as an important ecological foundation of human health.

Studies on wild products in comparison with cultivated ones have reported general differences in their metabolic profiles. Wild edible plants tended to contain more health-protective bioactive compounds in comparative analyses between dietary patterns (Leonti et al. 2006; Simopoulos 2003; Trichopoulou 2000). Such as omega-3 fatty acids and minerals in primary metabolites, as well as flavonoids and alkaloids in secondary metabolites were observed to be highly expressed in wild plant species grown in ecological optimum. These wild products can be commonly found in traditional and indigenous food systems (Colfer 2012; FAO 1995; Kuhnlein et al. 2013; Smil and Kobayashi 2012) and expected for global adaptation (Tilman and Clark 2014). They are considered to complement important micronutrient requirement for agriculturalists' dietary patterns with less-diverse staples than hunter-gatherers (Brown et al. 1985). A food system analysis indicates that locally available wild products in traditional diet can also satisfy macronutrient requirement and nutritionally substitute conventional products (Roger et al. 2012).

Synecoculture products were partially studied with metabolomics in comparison to cultivated products. Case studies indicated that secondary metabolites such as terpenoids, flavonoids, possibly alkaloids for bitterness, and primary metabolites especially carbohydrates and lipids such as omega-3 fatty acids were highly expressed in cultivars raised with synecoculture (Yoshida 2015; Yoshida and Funabashi 2014; Yoshida et al. 2014; Ohta et al. 2016). Mineral concentrations were compatible to conventional products despite lower contents in soil (Funabashi 2013b). These results were in accordance with the property of wild edible species and could be commonly distinguished with statistical measures (Funabashi 2015a). This suggests that ecological interactions are more dominant than genotypic background in determining the richness of phytochemicals and other health-beneficial compounds.

Secondary metabolites of plants are originally expressed for chemical communication of plants and other interactions mutually maintaining diversity of ecosystems (Larcher 2003; Reigosa et al. 2006; Weng et al. 2012). Although these compounds do not account for immediate survival, these are required for the adaptive responses of community to environment, and are also important mediators of plants–animals interactions (Dearing et al. 2005; Hay and Steinberg 1992).

In terms of diets, important benefits on micronutrient are supported by open ecological interactions such as pollination by insects (Smith et al. 2015). Plant–soil interactions also nurture soil microorganisms (Lange et al. 2015), important suppliers of diversity in human gut microbiota (THMPC 2012; Wall et al. 2015). These health benefits can be widely expected in wild edible species and synecoculture products as well, as the fruit of ecological optimum.

The long-tail of micronutrient in naturally grown plants can be considered as a prominent resource for drug discovery with systems biology perspective (De Luca et al. 2012; Kitano 2007). Recent increases of chronic diseases that cannot be totally explained with genetic profiles are expected to stem from environmental factors (Furukawa and Izumida 2004; Kung et al. 2008), with important relation to dietary patterns (Hu 2002; Kant 2004, 2010). The ecological responses of dietary plants and their physiological effects on human metabolisms could account for the missing heritability of globally burdening non-communicable diseases (Slatkin 2009). The complex relation between dietary patterns and health benefits or risks is recently being clarified with massive data analysis (e.g. Zeevi et al. 2015). Further incorporation of ecological variables in relation to health effects would contribute to assessing the overall benefit of wild and synecoculture products, which could expand accessibility to the growing market of alternative diets.

Other Implication in Relation to Meta-Community

Ecological optimum is inherently connected to the surrounding environment, which can be described as an open complex system (Funabashi et al. 2015). Optimization of synecoculture is open to ecological drift, through which interactions with meta-community can be influential with each other (Leibold et al. 2004). In explaining the complexity of the food chain, for example, the global size effect of ecosystem is hypothesized to be superior to the local effects such as primary production and disturbance (e.g. Cohen and Newman 1992). As synecoculture aims to optimize ecosystem functioning in multiple scales, the synergetic effects between different fields and meta-community should be further investigated, with respect to hierarchical measures of biodiversity (Whittaker 1972). For example, alpha-diversity is central to the field-wise effect, while beta-diversity may refer more to the support of cross-field species such as pollinators and natural predators. Gamma diversity would represent overall operational diversity including meta-community.

Hierarchical management allows more dynamical strategies beyond artificial introduction of species. Besides the coexistence of multiple stable states with different species composition (Lewontin 1969), permanent endcycle with cyclic migration of edible species from meta-community can be considered (Morton and Law 1997; van Nes et al. 2007). These open dynamics and transient processes are also important consideration to cope with environmental change.

Relation to exotic invasive species is another global issue. About 13 thousands species, 4% of global flora are exchanged and causing impact on biodiversity throughout farmland expansion (van Kleunen et al. 2015). The introduction of exotic species is reported to positively correlate with invasion status in surrounding matrix vegetation, jointly leading to homogenization of local flora (Wiser and Buxton 2008). The intermediate disturbance hypothesis is studied in mixed communities of native flora and alien species under human disruption mainly with conventional agricultural practice (Catford et al. 2012). Although synergistic biodiversity promotion could be expected in certain range of invasion, best-effect scenario depicted decline in total biodiversity. In synecoculture case, however, the disturbance may further shift biodiversity upward, since the introduction is limited to less-invasive crops, invasive plants can be selectively controlled, and actual diversification including native flora and fauna is observed (Funabashi 2013a). This interpretation coincides with the biodiversity maintenance mechanisms in grassland dynamics that differ between native and exotic-dominated communities (Wilsey et al. 2009): Exotic communities correspond to competition-dominant range (Figure 3 orange range) then express overyielding by selection effect, while native communities represent symbiosis-dominant ranges (Figure 3 blue ranges), which is mainly targeted in synecoculture. Recently increasing abandoned farmland could serve as good matrix vegetation for synecoculture, as it already harbors the revival of threatened plant species, indicating the symbiosis-dominant environment

(Osawa et al. 2013).

Conclusion and future perspective

Economy-driven physiological intensification of agriculture has pushed our civilization out of sustainable planetary boundaries (Hall and Day 2009; Turner 2008). Especially biodiversity loss and distortion of nitrogen cycle are ranked on top of climate change (Rockström et al. 2009; Steffen et al. 2015). These environmental loads cannot be resolved without fundamentally restructuring agriculture over the globe (Foley et al. 2011).

Synecoculture incorporates crucial countermeasures to this global agenda. It structurally removes the origin of environmental load unavoidably associated with monoculture practice throughout the history of civilization (Carter and Dale 1975; Jackson 2002), and replaces with diverse combinations of ecological processes that have transformed the planetary biosphere during the evolution of life. Most of edible species could express their inherent traits in synecoculture, as they have originally co-evolved in ecological niches amid exuberant complexity.

Current impacts of human activity, especially agricultural land conversion, relegates the vascular plants to 500–1,000 times elevated rate of extinction compared to natural background (Pereira et al. 2010; Proença and Pereira 2013). As a possible source of ecological redemption, historically known edible plants count more than 30,000–50,000 species, which corresponds to 1,000–3,300 times more diversity of 30–15 major cultivated crops that account for estimated 90% of global food calories, respectively (FAO 1995; Yong et al. 2006). Incorporation of underutilized and neglected edible species into local production has multi-faceted benefits on biodiversity, social autonomy, and health (Burlingame and Dernini 2010; Jaenicke et al. 2009; Padulosi et al. 2012). Enriching forest genetic resources including edible species also augments food security, total livelihood, restoration status, and adaptation to climate change (Alfaro et al. 2014; Bozzano et al. 2014; Dawson et al. 2014). Diversifying food through diversity of agriculture is a subsistent path toward solving the production-environment-health trilemma with sustainable diet (Fanzo et al. 2013; Tilman and Clark 2014).

The world regions most susceptible to profit by synecoculture are distributed in smallholder countries where conventional systems fail to manage environment. Countries most vulnerable to climate change with high risk of corruption are situated in developing countries in tropical regions (Petherick 2012), which also harbor important values of global ecosystem services (Costanza et al. 1997). Vulnerability index is particularly high among countries whose survival depends on smallholders. Actually, small-scale, family-owned farms with less than 2 hectares are estimated to produce 70% of the world food, cultivate 80% of arable land, and count 1/3 to 1/2 of the world population (FAO 2014; FIR 2013). They are important majority of agriculture and yet at the same time substantial cause of land degradation all over the world (UNEP 1991), typically including China (Zhang et al. 2013), India, other South-East Asia, sub-Saharan Africa and Latin America (FAO 2014; Gaiser et al. 2011; IFAD 2013). These regions require organized effort of investments on human, social and natural capital to support smallholder agriculture, in order to establish food security and fight against poverty (HLPE 2013). Situations surrounding smallholders widely vary in both socio-economical and ecological contexts, and therefore require diverse adaptations with tailor-made small agriculture, especially for resource-poor farmers estimated about 1.4 billion people (Altieri 2002). Site-specific development of synecoculture with the support of seed bank and management information technologies could be an important contribution (Funabashi 2013a, 2015b; Funabashi et al. 2015).

Each agriculture system has its own advantage and disadvantage as summarized in Figure 4. Conventional systems are able to support massive production of cereals but cannot avoid environmental load. While synecoculture pursues diversity at the other extreme, it is associated with high volatility and not suitable for the mass production of single crop with conventional market standard. Compromises can also be found with organic and natural farming practices in between. The optimum solution for future agriculture could be obtained by finding optimal distribution of different farming systems according to the social-ecological contexts in each region. With this respect, integrated assessments of agriculture system should be extended in reference to IMPEO for comprehensive evaluation and adaptation of farming methods (Binder and Feola 2012).

Application of relevant biotechnology can be further introduced in synecoculture. Although genetically modified organisms are refrained by principle, development of breeds and natural variants could spread more choices in vegetation portfolio. Important adaptation mechanism to seasonal changes such as photoperiodic responses are intensively studied in Arabidopsis (Nefissi et al. 2011), which also relates to productivity response such as flowering (Fujiwara et al. 2008). Variation of crops in photoperiodic control could introduce *trans*-seasonal portfolio in synecoculture (Hayama et al. 2003). Important features such as drought resistance and low nitrogen tolerance could also be developed faster in traditional breeding than genetic engineering (Gilbert 2014). Perennial varieties of crops could improve robustness in limited resources environment and become important substitute of staples (Glover et al. 2010). Hybridization is also expected to bring advantage to cope with rapid environmental change in forest restoration, with possible application to agroforestry (Aitken et al. 2008; Bozzano et al. 2014). Genetic diversity of crops with extensive ecological traits could be enhanced without the use of transgenic technologies.

The reviewed principles of synecoculture were founded on the reported ecological responses of plant community. These studies generally only focused on a single trophic level such as primary production, neither discussed how the observed species diversity came into realization. Especially, diversity–stability relationships qualitatively alter and thicken in multi-trophic ecosystems (Jiang and Pu 2009; Naeem et al. 1994). Therefore the interpretation is still limited compared to the whole complexity of ecosystem processes that synecoculture can exploit. Another blind spot exists in the role of symbiosis to niche formation. Although theories of niche differentiation have been much developed from the perspective of competition effects (Chesson 2000), little has been investigated from the symbiotic interactions. These missing aspects of biodiversity responses can be scientifically investigated with the use of synecoculture fields, with operational development of community structure and food chain under dominance of symbiotic effects.

Agricultural development has been historically based on the fundamental trade-off with biodiversity conservation. In compensating for the amplitude of current biodiversity loss, protected area should be expanded to sustain globally important species habitats (Visconti et al. 2015) and cover intact primary vegetation that holds ideal conservational value in rapidly converging tropical forests (Gibson et al. 2011). Nevertheless, we are facing a tipping point on the verge of 6th massive extinction as a consequence of anthropocene (Barnosky et al. 2011; Steffen et al. 2011). Demographic pressure continues to increase (Rosa et al. 2004), which forces us to act beyond local development-conservation conflict and globally resolve fundamental limits of conventional scenario (Barnosky et al. 2012; Chapin et al. 2009; Godfray et al. 2010; Nelson et al. 2006). Human activities need to qualitatively transform into ways that could bring positive impact on biodiversity. Agriculture that could support population growth of next generation needs to promote biodiversity and leverage ecosystem functioning in proportion to its intensification of productivity (Figure 5 green line) (Funabashi et al. 2015).

Synecoculture is not only a method of sustainable farming, but most importantly an interface for cooperation between humans and nature to build synergistically augmented social-ecological systems. Ecosystem services that support human welfare could further extend their current boundaries with wider incorporation of ecological optima into agricultural production (Costanza et al. 1997). The transformation should also respond to ecosystem-based multiple needs of social adaptation, in order to maximize the stakeholders' contribution to distributed management for securing natural capital (Bodin and Prell 2011; Boyd and Folke 2011; Crona and Hubacek 2010; Liu et al. 2007; van Beukering et al. 2013). Synecoculture is oriented towards leveraging natural capital through enrichment of human and social capital with joint and several liability of primary industries.

The elaborated phase of synecoculture can be represented as lightly to intensively used secondary vegetation, which is among other categories of land use such as primary vegetation, globally reported to excel in both species richness and abundance (Newbold et al. 2015). The gamma diversity of planetary ecosystem could be maximized with intelligent human interventions sensible to ecological responses. The most intensive biodiversity hotspots in life history, as well as the earth's life-support of growing population, could be realized as augmented ecosystems with anthropogenic drivers.

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