

Integrating methods that investigate how complementarity influences ecosystem functioning

Owen L. Petchey

Petchey, O. L. 2003. Integrating methods that investigate how complementarity influences ecosystem functioning. – *Oikos* 101: 323–330.

Separating the mechanisms that influence ecosystem functioning has been a goal of recent high profile experiments. Integrating the various experimental and analytical methods that attempt this goal across terrestrial and aquatic ecosystems, as well as careful definition of 'complementarity', produces novel insights and valuable lessons about new directions for research. (1) Experimental designs differ in temporal scale and whether standing stock or another ecosystem process was the response variable. (2) Mathematically identical variables in different designs have contrasting ecological interpretations. For example, different sets of ecological processes can contribute to different variables in different experimental designs. (3) The frequency of transgressive overyielding of standing stock (e.g. total above ground biomass) in polycultures implies little about the prevalence of transgressive overyielding in other ecosystem processes. (4) Measuring the contribution to ecosystem functioning of individual species, rather than just total ecosystem functioning of a polyculture, is not essential for estimating effects of complementarity. (5) Further research will profit from distinguishing standing stock from all other ecosystem functions. (6) None of the analytic methods can distinguish the effects of individual processes or mechanisms such as resource use differentiation, facilitation, or allelopathy, for which additional experimental treatments are required.

O. L. Petchey, Dept of Animal and Plant Sciences, Alfred Denny Building, Western Bank, Sheffield, U.K. S10 2TN (o.petchey@sheffield.ac.uk).

Species richness can influence ecosystem functioning (EF) by a variety of mechanisms (Huston 1979, Aarssen 1997, Wardle 1999, Chapin et al. 2000, Loreau 2000, Tilman 2000, Fridley 2001). Detecting and measuring the effects of these mechanisms is necessary for interpreting experiments (Aarssen 1997, Garnier et al. 1997, Huston 1997, Loreau 1998, Wardle 1999, Hector et al. 2000, Huston et al. 2000, Deutschman 2001, Loreau and Hector 2001), knowing why effects of species richness vary among experiments (Schläpfer and Schmid 1999, Schwartz et al. 2000, Loreau et al. 2001), and for predicting EF when species disappear from communities (Petchey 2000).

Recently developed methods for measuring the effects of complementarity use data from biodiversity-ecosystem functioning (BD-EF) experiments, where biodiversity (usually number of species) was manipu-

lated directly and ecosystem properties were measured (Tilman 1997). Most methods use monoculture performance to predict polyculture performance (Lepš et al. 2001, though some use covariates to determine this, e.g. McGrady-Steed et al. 1997). Several papers have discussed methods that were developed for detecting complementarity in terrestrial plant communities (Trenbath 1974, Harper 1977, Garnier et al. 1997, Hector 1998, Hooper 1998, Loreau 1998, Jolliffe 2000, Fridley 2001, Williams and McCarthy 2001). Currently, however, no general methodological framework examines the implications of subtle differences in experimental design or cuts across terrestrial and aquatic experiments.

This article integrates the methods that can detect and measure the effects of complementarity on the EF of an individual polyculture in a BD-EF experiment. Integrating previous methods reveals the relationships

Accepted 7 October 2002

Copyright © OIKOS 2003
ISSN 0030-1299

between different experimental designs and analytical methods, the relative advantages of different methods, and that seemingly similar diagnostic statistics have different ecological interpretations in different methods. In addition, this article develops a clear and efficient research program for further BD-EF experiments.

What is complementarity?

Because the word complementarity has taken on a range of meanings in biodiversity-ecosystem functioning literature it is worth proposing a clear definition here. Hence, "Complementarity is a property of sets of objects that exists when at least some of the objects in one set differ from the objects in another set" (Williams 2001). The critical aspect of this definition is that complementarity is a property of a set of objects (species here) and not a mechanism (such as resource use differentiation, facilitation, or allelopathy) or an effect of mechanisms. This makes discussions about whether complementarity should describe a single mechanism (Fridley 2001) or a class of mechanisms (Loreau and Hector 2001) unnecessary: it is neither. Rather, mechanisms can result from complementarity, and these mechanisms can have effects on ecosystem level processes, such as primary productivity.

The second aspect of this general definition is that it equates any differences between objects as being complementary. This is a slight deviation from common use of the word, where it seems to refer to differences that have some positive connotation.

In ecology, it is most often used with respect to a specified type of difference between objects. For example, early use in ecology,

"... in the case of the Meso-pteridatum (*Scilla*, *Holcus*, and *Pteris*) dealt with we have a *complementary association*, the subaerial parts being in, or tending to occupy, definite and different layers, i.e. edaphically complementary, and the aerial parts are seasonally complementary."

(page 396, Woodhead 1906), focuses on spatial and temporal complementarity. Hence, a set of species that have different resource use requirements (i.e. they partition resources) are complementary in that respect. The same set of species may overlap completely in phenology and not complement each other in that respect. Measures of functional diversity such as functional group diversity (Tilman and Lehman 2002) and FD (Petchey and Gaston 2002) attempt to quantify the extent of complementarity in the functional characters of a group of species. Hopefully the definition of complementarity given above will at least prompt clear and critical use of the word in the future.

This article considers recent work that attempts to measure the net effect of complementarity; that is, the consequences of the functional differences among species. These consequences could include changes in rela-

tive abundance (or biomass, vegetation cover, density, etc.) that might result from lack of resource use differentiation and changes in how the biomass of organisms present determines ecosystem functioning, for example by modification of the local environment (Emmerson et al. 2001). Previous definitions of complementarity may have sought to exclude changes in relative abundance; the general definition of complementarity used here does, however, include them. This article does not address the potential ecological importance of selection-probability (Huston 1997) or sampling effects (Tilman et al. 1997).

A common framework

Two different BD-EF experimental designs have been used to measure the effect of complementarity on polyculture performance by comparison to monoculture performance (Fig. 1). These designs differ from analyses that use multiple regression to attribute explanatory power to covariates, such as the species richness, functional richness, and/or biomass across a set of polycultures (Tilman 1996, McGrady-Steed et al. 1997, Hector et al. 2001).

The first experimental design (design 1) is when the initial abundance of each species is controlled and an unspecified (for generality) EF is measured after sufficient time has passed for significant changes in abundance and/or standing stock (a long-term experiment). Loreau and Hector's (2001) theoretical analysis and previous texts on this subject (Garnier et al. 1997, Hector 1998, Loreau 1998) assume this general design. A special case of this first design (design 1a) occurs when a measure of the total standing stock (for generality; e.g. total biomass, total vegetation cover) of organisms is the EF and corresponds accurately to many BD-EF experiments in terrestrial plant communities (Tilman 1997, Hooper 1998, Hector et al. 1999, Lepš et al. 2001). Total standing stock at the end of a growing season is often used as the EF in terrestrial plant communities as a measure of annual net primary productivity.

The second experimental design (design 2) is when the initial standing stock is controlled and any EF except standing stock is measured after so little time has passed that no significant changes in the standing stock of each species occur (a short-term experiment). If, for example, mortality causes changes in standing stock, these are compensated for by addition of individuals (Cardinale et al. 2002). Design 2 corresponds accurately to Emmerson et al. (2001), Wardle et al. (1997), and Cardinale et al. (2002), for example. Design 2 could include experiments that control other initial conditions, such as total metabolic rate (Ruesink and Srivastava 2001). Here, two general experimental designs (1

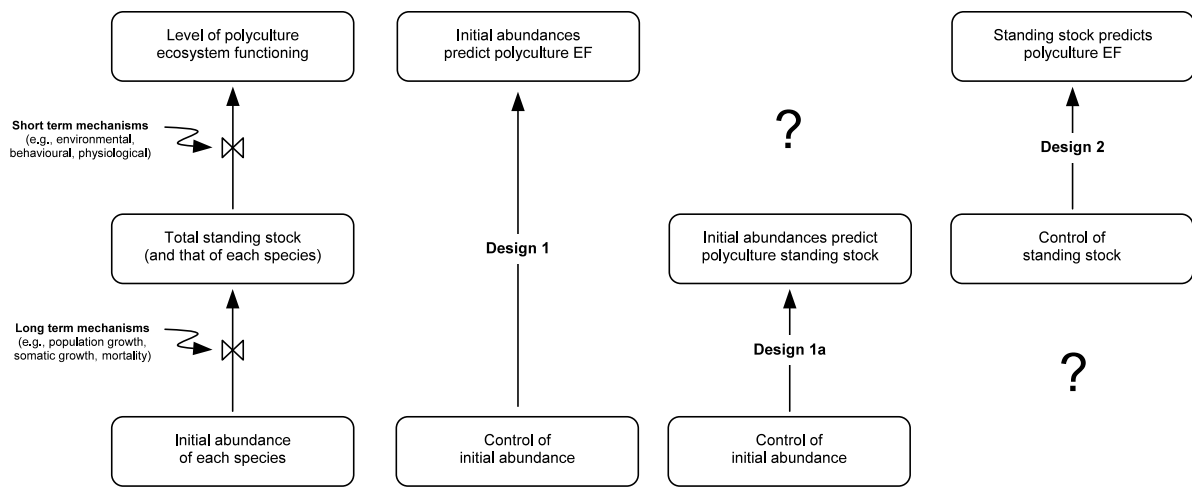


Fig. 1. The conceptual view of the determinants of ecosystem functioning (EF) assumed by biodiversity-ecosystem functioning experiments is that initial abundances determine standing stock (over longer temporal scales) and that standing stock determines EF (over shorter temporal scales) (left-most column). The experimental designs used to investigate complementarity in BD-EF experiments are also shown. Question marks indicate conceptual areas that designs 1a and 2 do not address.

and 2) and one special case design (1a) cover previous BD-EF experiments.

Analyses of each experimental design results in diagnostic variables that have important ecological interpretations (Hector 1998, Loreau 1998, Emmerson and Raffaelli 2000, Jolliffe 2000, Lepš et al. 2001, Loreau and Hector 2001). Here, all the diagnostic variables used in previous experiments are expressed in the same notation but labeled with the number of the design they result from (Table 1). For example, $D_{max}1$ is the value of D_{max} in design 1. The diagnostic variables previously identified as having particular ecological importance are: D_{max} (the extent of transgressive overyielding, Trenbath 1974), ΔEF (the net effect of diversity or the extent of non-transgressive overyielding, Diemer et al. 1997, Fridley 2001, Loreau and Hector 2001), RYT (the total change in relative yields of component species), and ΔEF_{comp} (the fraction of EF attributable to the 'complementarity effect', Loreau and Hector 2001). Other diagnostic variables are closely linked to these four (Loreau 1998, Loreau and Hector 2001), for example $RYT = 1 + \sum p_i D_i$, and are therefore not discussed further.

The diagnostic variables divide into three categories within which all of the statistics can be calculated without reference to variables in any of the other two categories (Table 1). These three categories also correspond to (i) statistics that can only detect the presence of strong effects of complementarity (if $D_{max} > 0$) (ii) statistics that can detect the presence of effects of complementarity (all $D_i > 0$) and measure the net effect of diversity (ΔEF); and (iii) statistics that can detect an effect of complementarity (RYT) (though see Loreau 1998) and measure the magnitude of the 'complementarity effect' (ΔEF_{comp}).

The choice of an additive or substitutive design (Harper 1977) influences D_{max} because D_{max} compares observed performances, which may depend on initial densities (e.g. sown or planted). In this paper, calculation of D_{max} implicitly assumes a substitutive design because it compares polyculture performance to a monoculture with equal initial density or biomass. There are, however, reasons for using additive designs beyond the scope of this article (Harper 1977). The explicit definition of the expected performance of species in a polyculture ($\epsilon l(EF_{i,poly}) = p_{i,N} EF_{i,mono,N_{poly}}$) makes no assumptions about whether the design is substitutive or additive, however, and therefore applies equally to substitutive and additive designs.

The 'complementarity effect'

Loreau and Hector's (2001) additive partition between the 'complementarity effect' and 'selection effect' has been widely misinterpreted as separating the effects of mechanisms from the effects of potentially less relevant probabilistic mechanisms (Sala 2001, Špačková and Lepš 2001, Cardinale et al. 2002). Loreau and Hector (2001) define the 'complementarity effect' mathematically as the net effect of diversity (ΔEF) minus the 'selection effect' (ΔEF_{selec} ; Table 1). The covariance measured in the 'selection effect' is positive and indicates a positive 'selection effect' when, for example, a species with high monoculture yield dominates mixtures. Generally, however, any relationship between complementarity based mechanisms, such as resource use partitioning, and monoculture traits will cause the effects of complementarity to enter the 'selection effect'. For example, if resource use differentiation occurs dis-

Table 1. The predictor and diagnostic variables that are used in different types of biodiversity-ecosystem functioning experiments. The different designs are described in detail in the text. The variables separate into three groups (separated by horizontal lines in the table) where variables within a group can be calculated in the absence of variables from the other two groups. Bold type indicates variables that require measurement of the contribution to EF of each species in a polyculture ($EF_{i,poly}$). For clarity only, biomass is used to illustrate a standing stock measure of EF in design 1a. Every effort has been made to use intuitive notation: EF = ecosystem functioning; B = biomass; N = abundance or density; $poly$ = polyculture; $mono$ = monoculture; i = species i ; $\varepsilon 1(x)$ = expected value of x in design 1; $p_{i,N}$ ($p_{i,B}$) = initial proportion by abundance (biomass) of species i ; This notation combines to produce for example N_{poly} (initial total polyculture abundance), $EF_{i,mono,N_{poly}}$ (ecosystem functioning of species i in monoculture at initial abundance N_{poly}), $B_{i,poly}$ (biomass of species i in polyculture). All other symbols are derived within the table.

Predictors and diagnostic variables	Design 1 Long-term experiment; any EF	Design 1a Long-term experiment; EF is standing stock	Design 2 Short-term experiment; any EF
Proportional difference between EF of polyculture and the maximum EF produced in any monoculture	$D_{max1} = \frac{(EF_{poly} - \max(EF_{i,mono,N_{poly}}))}{\max(EF_{i,mono,N_{poly}})}$	$D_{max1a} = \frac{(B_{poly} - \max(B_{i,mono,N_{poly}}))}{\max(B_{i,mono,N_{poly}})}$	$D_{max2} = \frac{(EF_{poly} - \max(EF_{i,mono,N_{poly}}))}{\max(EF_{i,mono,N_{poly}})}$
Expected level of EF contributed by species i in polyculture	$\varepsilon 1(EF_{i,poly}) = EF_{i,mono,N_{i,poly}} = p_{i,N} EF_{i,mono,N_{poly}}$	$\varepsilon 1a(B_{i,poly}) = B_{i,mono,N_{i,poly}} = p_{i,N} B_{i,mono,N_{poly}}$	$\varepsilon 2(EF_{i,poly}) = EF_{i,mono,B_{i,poly}} = p_{i,B} EF_{i,mono,B_{poly}}$
Proportional deviation of EF of species i in polyculture from expected EF of species i in polyculture	$D_{i1} = \frac{(EF_{i,poly} - \varepsilon 1(EF_{i,poly}))}{\varepsilon 1(EF_{i,poly})}$	$D_{i1a} = \frac{(B_{i,poly} - \varepsilon 1a(B_{i,poly}))}{\varepsilon 1a(B_{i,poly})}$	$D_{i2} = \frac{(EF_{i,poly} - \varepsilon 2(EF_{i,poly}))}{\varepsilon 2(EF_{i,poly})}$
Proportional deviation of total EF of polyculture from the expected total EF of polyculture	$D_T1 = \frac{(EF_{poly} - \varepsilon 1(EF_{poly}))}{\varepsilon 1(EF_{poly})}$	$D_T1a = \frac{(B_{poly} - \varepsilon 1a(B_{poly}))}{\varepsilon 1a(B_{poly})}$	$D_T2 = \frac{(EF_{poly} - \varepsilon 2(EF_{poly}))}{\varepsilon 2(EF_{poly})}$
Deviation from total expected EF of polyculture (net effect of diversity)	$\Delta EF1 = EF_{poly} - \varepsilon 1(EF_{poly})$	$\Delta EF1a = B_{poly} - \varepsilon 1a(B_{poly})$	$\Delta EF2 = EF_{poly} - \varepsilon 2(EF_{poly})$
Relative yield of species i	$RY_i1 = \frac{EF_{i,poly}}{EF_{i,mono,N_{poly}}}$	$RY_i1a = \frac{B_{i,poly}}{B_{i,mono,N_{poly}}}$	$RY_i2 = \frac{EF_{i,poly}}{EF_{i,mono,B_{poly}}}$
Deviation observed relative yield of species i in polyculture from expected relative yield of species i in polyculture	$\Delta RY_i1 = RY_i1 - p_{i,N}$	$\Delta RY_i1a = RY_i1a - p_{i,N}$	$\Delta RY_i2 = RY_i2 - p_{i,B}$
Relative yield total	$RYT1 = \text{sum}(RY_i1)$	$RYT1a = \text{sum}(RY_i1a)$	$RYT2 = \text{sum}(RY_i2)$
Absolute amount of ΔEF caused by the complementarity effect	$\Delta EF_{comp1} = S \times \text{mean}(\Delta RY_i1) \text{mean}(EF_{i,mono,N_{poly}})$	$\Delta B_{comp1a} = S \times \text{mean}(\Delta RY_i1a) \text{mean}(B_{i,mono,N_{poly}})$	$\Delta EF_{comp2} = S \times \text{mean}(\Delta RY_i2) \text{mean}(EF_{i,mono,B_{poly}})$
Absolute amount of ΔEF caused by the selection effect	$\Delta EF_{selec1} = S \times \text{cov}(\Delta RY_i1, EF_{i,mono,N_{poly}})$	$\Delta B_{selec1a} = S \times \text{cov}(\Delta RY_i1a, B_{i,mono,N_{poly}})$	$\Delta EF_{selec2} = S \times \text{cov}(\Delta RY_i2, EF_{i,mono,B_{poly}})$

proportionately between species with high monoculture yields. The partition actually separates two effects, the 'complementarity effect' and the 'selection effect', where mechanisms that result from complementarity, such as resource use differentiation, can influence either. It appears, therefore, that the 'complementarity effect' does not necessarily correspond to the net effect of mechanisms that result from complementarity. Loreau and Hector (2001) acknowledge this when they state that the partitions shares the same strengths and limitations as *RYT*, and as such, ecologists should desist from attributing the 'complementarity effect' to any single mechanism or class of mechanisms.

The different ecological meanings of mathematically identical diagnostics variables

Because the two designs allow different effects of complementarity to influence EF (Fig. 1), the ecological interpretation of the diagnostic variables derived from each differ. Considering design 2 first; the short temporal scale (e.g. every 3 days for 15 days after community assembly, Emmerson et al. 2001) precludes significant changes in standing stock (there was always $\ll 2\%$ mortality of individuals, and often 100% survival, M.C. Emmerson, pers. comm.). Hence, changes in ecosystem functioning cannot be attributed to changes in abundance of particular species, or the presence or absence of species that might come to dominate communities. Here, the effect of complementarity is measured via the net effect of diversity ($\Delta EF2$). It simply measures whether the standing stock of each species contributes additively (i.e. $\Delta EF2 = 0$ because $\sum(EF_{i,mono,B_{i,poly}}) = EF_{poly}$) or not (i.e. $\Delta EF2 \neq 0$ because $\sum(EF_{i,mono,B_{i,poly}}) \neq EF_{poly}$). That is, $\Delta EF2$ measures the net effect of complementarity via mechanisms such as environmental, behavioural, or physiological alteration because the short-term nature of the experiments precludes any change in species' standing stocks. (Note that D_{T2} is a standardized version of $\Delta EF2$.) Using such a short-term experiment, Emmerson et al. (2001) showed that the same total biomass of different benthic invertebrate species causes very different EF (ammonia nitrogen flux) and that the EF was greater than expected from additive effects of biomass ($\Delta EF2 > 0$ because $EF_{poly} > \sum(EF_{i,mono,B_{i,poly}})$). Certain species changed the environment such that other species processed sediment at faster mass specific rates.

In contrast, longer-term experiments (design 1, for example, 2 years after community assembly, Loreau and Hector 2001), allow time for considerable changes in relative abundances (i.e. standing stocks). These can result from complementarity; for example, species that share resource use requirements (i.e. are not complementarity in that respect) will compete, with one proba-

bly increasing in abundance. These changes in abundance can cause one species to dominate mixtures. Here, $\Delta EF1$ measures the effect of complementarity on changes in abundance and other effects of complementarity (e.g. altered environment, behaviour, or physiology). This appeared to motivate methods to separate out the effects of changes in relative abundance (Hector 1998, Loreau 1998, Lepš et al. 2001, Loreau and Hector 2001, Špačková and Lepš 2001), which may make interpreting the experiments difficult (Huston 1997, Tilman et al. 1997). For example, by allowing interpretations that only the initial presence or absence of a dominant species in a mixture matters for levels ecosystem functioning (Wardle 1999). It remains unclear, however, whether changes in relative abundance can be adequately partitioned from other effects of complementarity (see section The 'complementarity effect').

The difference in time scales and EF measured, however, makes designs 1a and 2 complementary. That is, designs 1a and 2, when conducted in concert could provide more information about the processes that determine EF than design 1 can alone. This is because using design 1a and 2 simultaneously divides determination of EF into two steps: a step where standing stock is determined and a step where standing stock determines EF (Fig. 1). This complementarity between designs 1a and 2 provides a sound reason for distinguishing between standing stock (e.g. total above ground biomass) and other EFs. Distinction between standing stock and EF is not necessarily because standing stock is not a valid EF or because standing stock is a poor surrogate of EF. (For example, total above-ground biomass may be a satisfactory surrogate for primary productivity of annuals growing over a single season, Tilman 1996). Making the distinction simply provides more information about the processes that determine EFs (including the rate of biomass accrual) than can be obtained by considering standing stock as a surrogate for EF.

Indeed, design 2 tests whether standing stock is a good surrogate for the EF of interest. Using standing stock as a surrogate of EF implies a proportionality between biomass and EF (i.e. $EF_{poly} \propto B_{poly}$). This proportionality requires that the standing stock of one species equates to the same level of EF as the standing stock of another species (i.e. $EF_{i,mono,B}$ is the same for all i) and that the standing stock of each species contributes independently to total EF (i.e. $\sum(EF_{i,mono,B_{i,poly}}) = EF_{poly}$). These two assumptions are exactly what short term experiments that control standing stock test. Specifically, $\Delta EF2$, the deviation of observed from expected EF, measures if contributions of species' standing stocks are additive ($\Delta EF2 = 0$ if $\sum(EF_{i,mono,B_{i,poly}}) = EF_{poly}$) or not ($\Delta EF2 \neq 0$ if $\sum(EF_{i,mono,B_{i,poly}}) \neq EF_{poly}$). Using such a short-term standing stock control experiment, Cardinale et al. (2002), in a similar result to Emmerson et al. (2001),

showed that the presence of one species of freshwater invertebrate can increase the biomass specific feeding performance of another by decreasing upstream current shading (an altered environment).

An example

To illustrate these points I created data about how species *a*, *b*, *c*, and *d* perform in monoculture and two different polycultures ($\{a,b,c\}$ and $\{a,b,d\}$) for designs 1, 1a, and 2 (Table 2). The two longer term experiments differ because one has standing stock (for the purposes of this example, the measure of standing stock is biomass) as the EF (design 1a) and the other has anything but standing stock as the EF (design 1).

Results of the long-term experiment with standing stock as the EF (Table 2; design 1a) indicate that both polycultures produce greater than expected biomass ($\Delta EF_{1a} > 0$), though the 'complementarity effect' dominates in community $\{a,b,c\}$ ($\Delta EB_{comp} 1a \gg \Delta EB_{selec} 1a$), whereas the 'selection effect' dominates in community $\{a,b,d\}$ ($\Delta EB_{comp} 1a \ll \Delta EB_{selec} 1a$).

Results from the short-term biomass control experiment (Table 2) indicate that biomass acts additively in determining gas flux of polyculture $\{a,b,c\}$ ($\Delta EF_2 = 0$ because the observed = sum(expected)). In contrast, polyculture $\{a,c,d\}$ produces more CO_2 than if biomass determined EF additively ($\Delta EF_2 > 0$). Here, $\Delta EF_2 > 0$ indicates that a polyculture performs better than the sum of its parts in biomass control experiments and a positive net effect of complementarity. Note that the positive 'selection effect' in polyculture $\{a,c,d\}$ occurs because results simulate the effect of disproportionate complementarity between the species *c* and *d*, which have highest gas flux in monoculture.

Total ecosystem functioning is clearly affected by two levels of complementarity in this analytic framework (Fig. 1). First by effects of complementarity that influence the biomass of each species through their effect on patterns of inter-specific coexistence (via resource use partitioning and nitrogen fixation, for example). And second by complementarity that determines how that biomass translates into gas flux (which could be any EF except standing stock). For example, by changes in the local environment, and/or the behaviour and physiolo-

Table 2. Example analyses of the different experiments that can measure complementarity in BD-EF experiments. Designs and statistics correspond with Table 1.

Monoculture			Polyculture					
Species	Factor controlled	Factor measured	Composition	Species	Factor controlled	Factor measured	Statistic and value	
Design 1: Long term abundance control experiment with CO ₂ flux as the measured EF								
	Abundance	CO ₂ flux			density	CO ₂ flux		
a	90	8	{a,b,c}	a	30	3.3	$D_{max} 1$	−0.5
b	90	16		b	30	6.7	$\Delta EF 1$	7.3
c	90	44		c	30	20	$\Delta EF_{comp} 1$	6.5
d	90	56		totals	90	30	$\Delta EF_{selec} 1$	0.8
			{a,b,d}	a	30	0.07	$D_{max} 1$	0.7
				b	30	1.7	$\Delta EF 1$	68.4
				d	30	93.3	$\Delta EF_{comp} 1$	20.8
				totals	90	95.1	$\Delta EF_{selec} 1$	47.6
Design 1a: Long term abundance control experiment with biomass as the measured EF								
	Abundance	biomass			density	biomass		
a	90	12	{a,b,c}	a	30	5	$D_{max} 1a$	−0.3
b	90	24		b	30	10	$\Delta B 2$	7.0
c	90	33		c	30	15	$\Delta B_{comp} 1a$	6.6
d	90	42		totals	90	30	$\Delta B_{selec} 1a$	0.4
			{a,b,d}	a	30	2	$D_{max} 1a$	−0.2
				b	30	5	$\Delta B 2$	9.0
				d	30	28	$\Delta B_{comp} 1a$	1.1
				totals	90	35	$\Delta B_{selec} 1a$	7.9
Design 2: Short term biomass control experiment with CO ₂ flux as the measured EF								
	biomass	CO ₂ flux			biomass	CO ₂ flux		
a	9	6	{a,b,c}	a	3	2	$D_{max} 2$	−0.3
b	9	6		b	3	2	$\Delta EF 2$	0.0
c	9	12		c	3	4	$\Delta EF_{comp} 2$	0.0
d	9	12		totals	9	8	$\Delta EF_{selec} 2$	0.0
			{a,c,d}	a	3	0.1	$D_{max} 2$	−0.1
				c	3	1	$\Delta EF 2$	1.1
				d	3	10	$\Delta EF_{comp} 2$	0.7
				totals	9	11.1	$\Delta EF_{selec} 2$	1.8

ogy of individuals. The long-term experiment can estimate the effect of both levels of complementarity effects simultaneously via $\Delta EF1$. The short term experiment measures the second effect of complementarity with $\Delta EF2$. Both levels of effect of complementarity combine into the overall effect of complementarity that determines how a combination of species influences an ecosystem function in BD-EF experiments.

Interestingly, neither polyculture in the long-term abundance control experiment with biomass as the EF showed evidence of transgressive overyielding (Table 2; all $D_{max1a} < 0$). Neither did the short term experiments (all $D_{max2} < 0$). Polyculture $\{a,b,d\}$ does, however, transgressively overyield in the abundance control experiment with CO_2 production as the EF ($D_{max1} > 0$). This illustrates the notion that the combined effects complementarity on biomass and effects of complementarity on behaviour, environment and/or physiology can cause transgressive overyielding of ecosystem functioning even if there is no overyielding of biomass (standing stock).

The influence of measuring individual species' contributions to EF

Some of the diagnostic statistics require knowledge of contribution to EF of each species in a polyculture ($EF_{i,poly}$, Table 1). This individual contribution of species is measured in some experiments (e.g. the biomass of each species, Tilman 1997, Loreau and Hector 2001, Cardinale et al. 2002) but not in others (e.g. McGrady-Steed et al. 1997, Wardle et al. 1997), where only the total EF of the polyculture (EF_{poly}) is measured. Two circumstances could result in the absence of each species' contribution to EF. Either they could have been measured but were not, or measuring them was not possible. The latter may be true for several EFs; for example, measuring the contribution of individual species to community wide decomposition rate (Wardle et al. 1997) or gas flux (McGrady-Steed et al. 1997) is difficult to imagine.

However, the recommendation in the previous section, of conducting experiments of design 1a and 2 in parallel, largely dispenses with problems associated with not being able to measure contributions of individual species to EF. In design 2, the net effect of complementarity between species' standing stocks is given by $\Delta EF2$, for which the contribution of each species is not required. In design 1a, the EF is standing stock such that the contribution of each species will usually be possible to obtain, allowing calculation of diagnostic variables that may help partition the effects of changes in abundance from other effects of complementarity (Table 1).

Conclusions

Careful definition of complementarity and relating previous methods for analyzing BD-EF experiments provides a number of lessons about investigating how biodiversity can affect EF. First, research programs that treat standing stocks (e.g. total above ground biomass) separately from other EFs will allow a more complete understanding of how complementarity affects EF than otherwise. This lesson is independent of standing stock being a relevant EF or a good surrogate of any EF and independent of measuring the contribution to EF of individual species in a polyculture. Second, the ecological interpretation of mathematically identical statistics depends on the type of BD-EF experiment used (long-term or short-term). For example, ΔEF measures a much wider range of effects of complementarity in designs 1 and 1a than in design 2. Third, total EF may be greater in a polyculture than any monoculture even when the polyculture standing stock is lower than that of the most productive monoculture. That is, an absence of transgressive overyielding of standing stock does not imply the absence of transgressive overyielding in other EFs. Fourth, this review provides a clear direction for new biodiversity–ecosystem functioning experiments in which determination of EF is investigated simultaneously at two levels (determination of standing stock and how standing stock determines EF) and a range of temporal scales.

It is critical to realise, and hopefully quite obvious, however, that none of the diagnostic variables (e.g. RYT or Loreau and Hector's 2001 partition) in any design (1, 1a, or 2), nor any of the experiments discussed, can measure the effect of any one process or mechanism, such as resource use differentiation, facilitation, or allelopathy, changes in behaviour, local environment or physiology. This should be unsurprising, as the experiments were primarily designed to elucidate relationships between biodiversity and ecosystem functioning. These types of experiments can only estimate the net effect of all the processes and mechanisms that result from complementarity (differences) among species. Separating the effects of mechanisms is, however, critical in future experiments (Fridley 2001, Loreau and Hector 2001). Only direct experimental examinations of resource use differentiation (e.g. Stevens and Carson 2001), facilitation, and interference, by manipulating the factors that influence these processes, can estimate their individual importance for EF. For example, estimates of the importance of nitrogen fixers could be obtained by manipulating the nitrogen availability. Direct observations of altered environment and behaviour in polycultures can also shed light on the processes responsible for effects of biodiversity on ecosystem functioning (Hooper and Vitousek 1998, Spehn et al. 2000, Caldeira et al. 2001, Emmerson et al. 2001, Cardinale et al. 2002).

Acknowledgements – Andy Hector, Michael Huston, Cheryl Inglis, Kevin Gaston, Michel Loreau, David Wardle, and Phil Warren made comments that improved previous versions of this article. OLP is a NERC Fellow.

References

- Aarssen, L. W. 1997. High productivity in grassland ecosystems: effected by species diversity or productive species? – *Oikos* 80: 183–184.
- Caldeira, M. C., Ryel, R. J., Lawton, J. H. and Pereira, J. S. 2001. Mechanisms of positive biodiversity-production relationships: insights provided by delta¹³C analysis in experimental Mediterranean grassland plots. – *Ecol. Lett.* 4: 439–443.
- Cardinale, B. J., Palmer, M. A. and Collins, S. L. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. – *Nature* 415: 426–429.
- Chapin, F. S., Zavelata, E. S., Eviner, V. T. et al. 2000. Consequences of changing biodiversity. – *Nature* 405: 234–242.
- Deutschman, D. H. 2001. Design and analysis of biodiversity field experiments. – *Ecol. Res.* 16: 833–843.
- Diemer, M., Joshi, J., Körner, C. et al. 1997. An experimental protocol to assess the effects of plant diversity on ecosystem functioning utilized in a European research network. – *Bull. Geobot. Inst. ETH* 63: 95–107.
- Emmerson, M. C. and Raffaelli, D. G. 2000. Detecting the effects of diversity on measures of ecosystem function: experimental design, null models and empirical observations. – *Oikos* 91: 195–203.
- Emmerson, M. C., Solan, M., Emes, C. et al. 2001. Consistent patterns and the idiosyncratic effects of biodiversity in marine ecosystems. – *Nature* 411: 73–77.
- Fridley, J. D. 2001. The influence of species diversity on ecosystem productivity: how, where, and why? – *Oikos* 93: 514–526.
- Garnier, E., Navas, M.-L., Austin, M. P. et al. 1997. A problem for biodiversity-productivity studies: how to compare the productivity of multispecific plant mixtures to that of monocultures? – *Acta Oecol.* 18: 657–670.
- Harper, J. L. 1977. Population biology of plants. – Academic Press.
- Hector, A. 1998. The effect of diversity on productivity: detecting the role of species complementarity. – *Oikos* 82: 597–599.
- Hector, A., Schmid, B., Beierkuhnlein, C. et al. 1999. Plant diversity and productivity experiments in European grassland. – *Science* 286: 1123–1127.
- Hector, A., Schmid, B., Beierkuhnlein, C. et al. 2000. Response to Huston et al. 2000 *Science* 289: 1255a. – *Science* 289: 1255a.
- Hector, A., Dobson, K., Minns, A. et al. 2001. Community diversity and invasion resistance: an experimental test in a grassland ecosystem and a review of comparable studies. – *Ecol. Res.* 16: 819–831.
- Hooper, D. U. 1998. The role of complementarity and competition in ecosystem responses to variation in plant diversity. – *Ecology* 79: 704–719.
- Hooper, D. U. and Vitousek, P. M. 1998. Effects of plant composition and diversity on nutrient cycling. – *Ecol. Monogr.* 68: 121–149.
- Huston, M. 1979. A general hypothesis of species diversity. – *Am. Nat.* 113: 81–101.
- Huston, M. A. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. – *Oecologia* 110: 449–460.
- Huston, M. A., Aarssen, L. W., Austin, M. P. et al. 2000. No consistent effect of plant diversity on productivity. – *Science* 289: 1255a.
- Jolliffe, P. A. 2000. The replacement series. – *J. Ecol.* 88: 371–385.
- Lepš, J., Brown, V. K., Diaz Len, T. A. et al. 2001. Separating the chance effect from other diversity effects in the functioning of plant communities. – *Oikos* 92: 123–134.
- Loreau, M. 1998. Separating sampling and other effects in biodiversity experiments. – *Oikos* 82: 600–602.
- Loreau, M. 2000. Biodiversity and ecosystem functioning: recent theoretical advances. – *Oikos* 91: 3–17.
- Loreau, M. and Hector, A. 2001. Partitioning selection and complementarity in biodiversity experiments. – *Nature* 412: 72–76.
- Loreau, M., Naeem, S., Inchausti, P. et al. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. – *Science* 294: 804–808.
- McGrady-Steed, J., Harris, P. M. and Morin, P. J. 1997. Biodiversity regulates ecosystem predictability. – *Nature* 390: 162–165.
- Petchey, O. L. 2000. Species diversity, species extinction, and ecosystem function. – *Am. Nat.* 155: 696–702.
- Petchey, O. L. and Gaston, K. J. 2002. Functional diversity (FD), species richness, and community composition. – *Ecol. Lett.* 5: 402–411.
- Ruesink, J. L. and Srivastava, D. S. 2001. Numerical and per capita responses to species loss: mechanisms maintaining ecosystem function in a community of stream insect detritivores. – *Oikos* 93: 221–234.
- Sala, O. E. 2001. Price put on biodiversity. – *Nature* 412: 34–36.
- Schlöpfer, F. and Schmid, B. 1999. Ecosystem effects of biodiversity: a classification of hypotheses and exploration of empirical results. – *Ecol. Appl.* 9: 893–912.
- Schwartz, M. W., Brigham, C. A., Hoeksema, J. D. et al. 2000. Linking biodiversity to ecosystem function: implications for conservation ecology. – *Oecologia* 122: 297–305.
- Špačková, I. and Lepš, J. 2001. Procedure for separating the selection effect from other effects in diversity-productivity relationship. – *Ecol. Lett.* 4: 585–594.
- Spehn, E. M., Joshi, A., Schmid, B. et al. 2000. Above-ground resource use increases with plant species richness in experimental grassland ecosystems. – *Funct. Ecol.* 14: 326–337.
- Stevens, M. H. H. and Carson, W. P. 2001. Phenological complementarity, species diversity, and ecosystem function. – *Oikos* 92: 291–296.
- Tilman, D. 1996. Biodiversity: population versus ecosystem stability. – *Ecology* 77: 350–363.
- Tilman, D. 1997. Distinguishing between the effects of species diversity and species composition. – *Oikos* 80: 185.
- Tilman, D. 2000. Causes, consequences and ethics of biodiversity. – *Nature* 405: 208–211.
- Tilman, D. and Lehman, C. L. 2002. Biodiversity, composition, and ecosystem processes: theory and concepts. – In: Kinzig, A. P., Pacala, S. W. and Tilman, D. (eds), *The functional consequences of biodiversity*. Princeton Univ. Press, pp. 9–41.
- Tilman, D., Lehman, C. L. and Thomson, K. T. 1997. Plant diversity and ecosystem productivity: theoretical considerations. – *Proc. Nat. Acad. Sci. USA* 94: 1857–1861.
- Trenbath, B. R. 1974. Biomass productivity of mixtures. – *Adv. Agron.* 26: 177–210.
- Wardle, D. A. 1999. Is “sampling effect” a problem for experiments investigating biodiversity-ecosystem function relationships? – *Oikos* 87: 403–407.
- Wardle, D. A., Bonner, K. I. and Nicholson, K. S. 1997. Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. – *Oikos* 79: 247–258.
- Williams, A. C. and McCarthy, B. C. 2001. A new index of interspecific competition for replacement and additive designs. – *Ecol. Res.* 16: 29–40.
- Williams, P. H. 2001. Complementarity. – In: Levin, S. A. (ed.), *Encyclopedia of biodiversity*. Academic Press, pp. 813–829.
- Woodhead, T. W. 1906. Ecology of woodland plants in the neighbourhood of Huddersfield. – *J. Linn. Soc. Bot.* 37: 333–406.