

# Measuring conservation outcomes for depleted biological assets

Convergence theory and its applicability to New Zealand

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T.D. Wassenaar and S.M. Ferreira

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# Measuring conservation outcomes for depleted biological assets

## Convergence theory and its applicability to New Zealand

T.D. Wassenaar<sup>1</sup> and S.M. Ferreira<sup>2</sup>

<sup>1</sup> Conservation Ecology Research Unit, Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa

<sup>2</sup>Auckland Conservancy, Department of Conservation, P.O. Box 68-908, Auckland, New Zealand

### ABSTRACT

The single biggest agent of reduced biodiversity values has been the presence of human-induced disturbances, notably through the introduction of alien invasive species. There are very few remaining examples of the pre-human biological condition in New Zealand. Conservation has traditionally involved the management of either single or multiple pest species to achieve objectives such as restoration of viable populations of particularly rare or endangered native species. Recently more emphasis has been laid on the management of whole ecosystems. Both approaches suffer from the lack of reference conditions or benchmarks that can be used to evaluate conservation outcomes. In this report we address the monitoring of ecosystem resilience in terms of the post-disturbance rate and trajectory of change in species composition. We develop a general exponential decay model for biological assemblages that converge on to a regional equilibrium or benchmark after disturbance, where an explicit benchmark target system is present. Such a convergence model will then be used to develop a reciprocal general resilience model that predicts rates and trajectories for development of biological communities in an equilibrium situation, independent of the benchmark. Selection of communities at various trophic levels will reflect stability at an ecosystem level. We suggest collation of time-series data sets worldwide where species compositions of post-disturbance regenerating communities have been recorded with an explicit benchmark. A resilience model that focused on generalities in tangent slopes for various trophic levels and ecosystems would have wide applicability in conservation management of anthropogenically disturbed landscapes with no surviving reference ecosystems.

Keywords: mathematical modelling, convergence model, ecosystem resilience, degraded communities, system recovery, trophic levels, species composition.

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# 1. Introduction

The biological diversity of New Zealand, like that on many other island archipelagos, has been depleted by a variety of human-induced disturbances (Atkinson 1989). Initially, habitat destruction and fragmentation have reduced ranges and/or distributions of species. The greatest remaining threat to surviving habitats or ecosystems is from introduced species (Simberloff 1990). The Department of Conservation (DOC) has a mandate that can be summarised as maximising biological diversity:

To conserve New Zealand's natural and historic heritage for all to enjoy now and in the future (DOC 2001).

An Ecological Management Framework is under development by DOC (Paula Warren, pers. comm.) to address ecosystems, species, biosecurity, and legal land management requirements that will fulfil this mission. Within this context, Ferreira & Towns (unpubl. report 2001) have developed for Auckland Conservancy a theoretically based management framework with an ecosystem approach as the focus.

## 2. Theoretical framework to maximise conservation of biological diversity

Ferreira & Towns (unpubl. report 2001) assumed that limited knowledge of species distributions and life histories is a key constraint for DOC in attaining its objectives. This is a valid assumption as complete inventory data is lacking for all sites and/or taxonomic groups. Furthermore, in most instances taxonomic descriptions are inadequate.

Many types of surrogates have been used (Freitag et al. 1997; Freitag & van Jaarsveld 1997; Leathwick et al. 1998; Erasmus et al. 1999; Fairbanks et al. 2001). Components of these, such as maximising geological diversity (Wessels et al. 1999), have strong theoretical ecological bases and have produced good results. Ferreira & Towns (unpubl. report 2001) argued that a surrogate based on biodiversity theory will be most appropriate if diversity is the key component for DOC. Consequently, their proposed management framework hinges on theoretical predictions of factors affecting  $\alpha$ -,  $\beta$ - and  $\lambda$ -diversity (see Rosenzweig 1995).

In the first instance,  $\lambda$ -diversity, or regional diversity, can be maintained by numerous factors (Rosenzweig 1995), of which three were considered appropriate for Auckland Conservancy (Fig. 1). These can be used as a type of site selection filter. Conservation of maximum  $\lambda$ -diversity is achieved by firstly selecting a suite of sites (SOS) that maximise spatial heterogeneity (Simpson

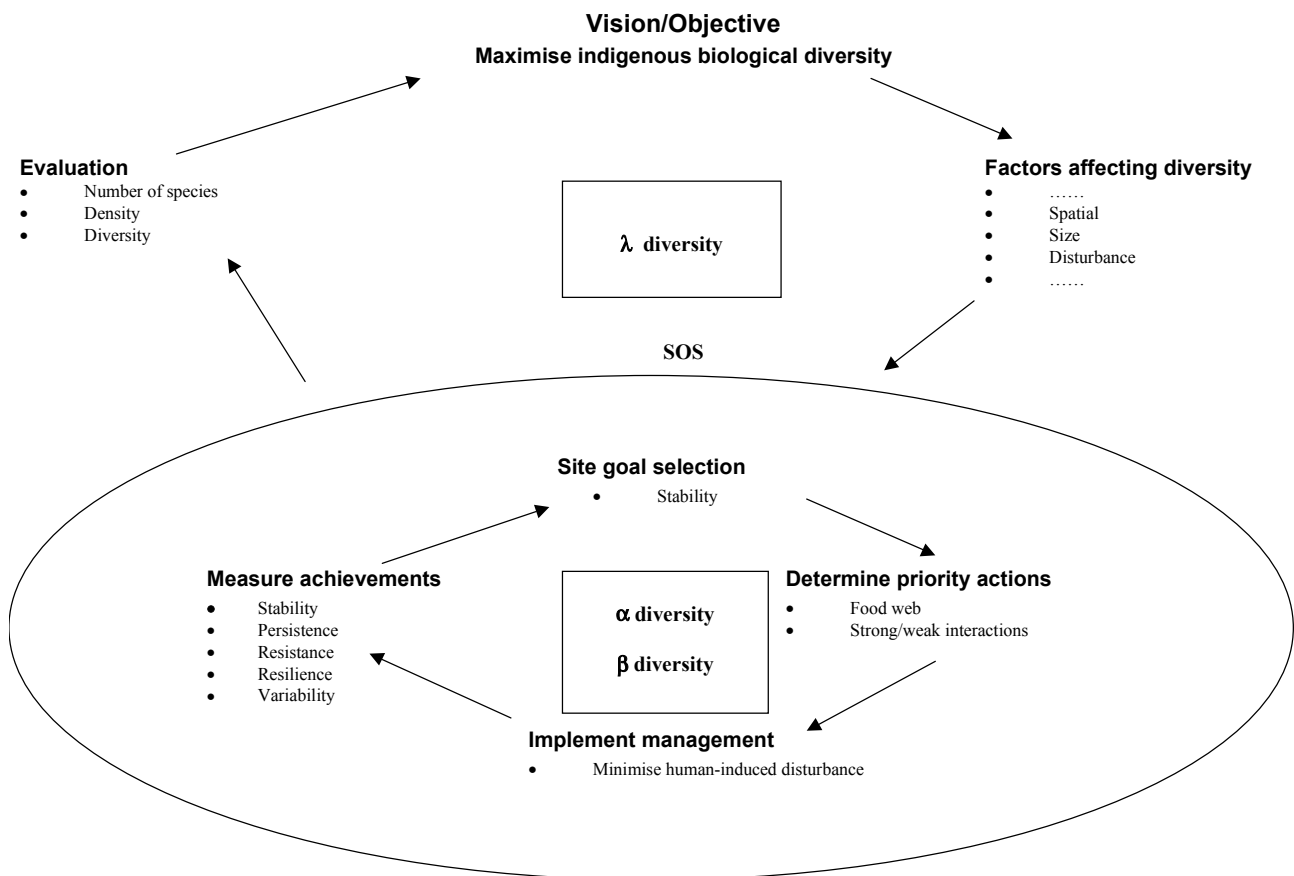


Figure 1. Ferreira & Towns' (unpubl. report 2001) concept of operational ecosystem management in the New Zealand context.

1964; MacArthur 1965, 1969; Richards 1969; Tomoff 1974; Roth 1976; Rosenzweig 1995). In the second instance, sites are selected through optimising species-area relationships (see Preston 1962; Williams 1964; Rosenzweig 1995) and minimising human-induced disturbances, but allowing natural disturbances to take place (under the assumption that intermediate disturbance levels maintain highest diversity - see Connell 1978; Petraitis et al. 1989).

A value judgement needs to be made to define the outcome for a particular site. Ferreira & Towns (unpubl. report 2001) argued that a new species pool exists because of extinction of some native species and the presence of numerous naturalised species, and recovery of any particular ecosystem will take place from this. They suggested that ecosystem stability in the context of these modern species should therefore be a much more attainable and reasonable site outcome than some historic static point that we cannot define other than through some components of macro-vegetation (e.g. McGlone 1983).

Ferreira & Towns (unpubl. report 2001) then use theory behind food web dynamics (Pimm 1984) to identify the key human-induced disturbances that will affect stability and therefore need to be managed. The objective is to attain food webs with many weak and few strong interactions (Cohen & Carlton 1998). Management is then directed at minimising the effect of key human-induced disturbances through integrated pest management. In some circumstances processes such as succession have been severely impeded through, for

example, the presence of dispersal impediments (e.g. skinks on islands, Towns & Ferreira 2001) or other life-history traits (e.g. the stitchbird, Armstrong & Perrot 2000). Economic models are useful at this point, using cost-benefit (Stephens 1999) or scenario selection models (Reagan & Moyle 2001) to identify priorities between management actions.

With this in mind Ferreira & Towns (unpubl. report 2001) suggest that monitoring should logically focus on evaluating outcomes, i.e. ecosystem stability, and give four measures (see Pimm 1991) for this: persistence (measured as the time a system will last) and resistance (change in a particular variable when another variable changes) will be most appropriate for mature, undisturbed ecosystems; the closely associated measures, resilience and variability, should be used for disturbed ecosystems.

Furthermore, Ferreira & Towns (unpubl. report 2001) suggest that the monitoring of species composition, a structural component, at various trophic levels, will adequately evaluate total ecosystem outcomes. This is because functional components will probably be maintained if the full structural component is protected (Hector et al. 2001).

## 3. Measuring ecosystem outcomes

The post-disturbance recovery of a system, or in stability terms, its resilience, can only be evaluated in terms of a reference undisturbed system (Pimm 1991). However, few examples of such reference systems or benchmarks exist for New Zealand's native ecosystems. This is because human-induced disturbance is the most significant factor determining ecosystem characteristics in New Zealand today. The most crucial conservation problem therefore revolves around the definition of these benchmarks in the modern context of naturalised and native species, as this directs objectives and subsequent management actions.

Approaches to overcome this problem range from management for the conservation of single species to the use of predictions from succession theory.

### 3.1 SINGLE-SPECIES PROTECTION

Single-species protection is a fundamental part of conservation (Caughley & Sinclair 1994) and in New Zealand many examples exist of successful species protection projects (Towns & Williams 1993). Measuring single species for ecosystem conservation projects hinges on the validity of concepts such as umbrella species, keystone species, flagship species and indicator species (Power et al. 1996; Towns & Saunders unpubl. report 2000). This approach assumes that protection of one species will have positive consequences for

others in the same system—an assumption that has not yet been tested in New Zealand.

Even if such a benefit-cascade assumption were true, the problem of no benchmark would remain, although in this case it is for a single population and not a complete ecosystem. This often results in conservation objectives of increased densities for the target species with no clear idea of what the target density should be, nor what kind of variation in density would be appropriate. If target population sizes (or equilibrium densities) were known, it would be relatively easy to apply the same kind of stability measures, i.e. persistence, resilience, resistance, and variability to variables of a population of single species (e.g. Ferreira & Smit unpubl. reports 2001a, 2001b). The single-species measurement approach is thus constrained by an incorrect assumption, as well as a lack of benchmark population sizes (Table 1).

### 3.2 MULTIPLE-SPECIES PROTECTION

Multiple-species protection at a single site was a natural progression from single-species management, on offshore islands (Townsend et al. 1997), protected areas on the New Zealand mainland (Saunders & Norton 2001), and marine

TABLE 1. SUMMARY OF POTENTIAL APPROACHES TO MEASURE ECOSYSTEM OUTCOMES IN NEW ZEALAND.

	MEASURE	CONSTRAINT
Single species	Population variable <ul style="list-style-type: none"> <li>• Persistence</li> <li>• Resistance</li> <li>• Resilience</li> <li>• Variability</li> </ul>	<ul style="list-style-type: none"> <li>• Validity of benefit-cascade assumption</li> <li>• Lack of benchmark population variable</li> </ul>
Multiple species	Multiple population variables <ul style="list-style-type: none"> <li>• Persistence</li> <li>• Resistance</li> <li>• Resilience</li> <li>• Variability</li> </ul>	<ul style="list-style-type: none"> <li>• Validity of benefit-cascade assumption</li> <li>• Lack of benchmark population variable</li> </ul>
Ecosystems	Pre-European or pre-human state <ul style="list-style-type: none"> <li>• Resilience</li> <li>• Variability</li> </ul>	<ul style="list-style-type: none"> <li>• Static state in conflict with theoretical and empirical evidence</li> <li>• Species extinction and new naturalised species</li> <li>• Lack of knowledge of pre-European or pre-human state, i.e. static benchmark</li> </ul>
Ecosystems – independent of benchmarks	Succession predictions <ul style="list-style-type: none"> <li>• See Odum 1969</li> </ul> Value criteria (Ewel 1987) <ul style="list-style-type: none"> <li>• Sustainability</li> <li>• Productivity</li> <li>• Nutrient retention</li> <li>• Invasibility</li> <li>• Biotic interaction</li> </ul>	<ul style="list-style-type: none"> <li>• Good promise requiring predictive models</li> <li>• Mostly functional focus</li> <li>• Species redundancy results in functions being maintained even though species are lost</li> </ul>



protected areas (Walls & McAlpine 1993). The measurement of a few 'charismatic' species at a single site is constrained by the same factors as the measurement of a single species, i.e. the benefit-cascade assumption and benchmark population sizes. However, looking at a few species may minimise the potential consequences of the benefit-cascade assumption being wrong (Table 1).

### 3.3 ECOSYSTEM PROTECTION

Ecosystem protection is in its infancy and has only recently been addressed by DOC through the development of an Ecological Management Framework (Paula Warren, pers. comm.). Measuring the outcomes of such projects is a key conceptual difficulty. Ecosystem outcomes have primarily focused on what a particular site would have looked like pre-European or pre-human, based on pollen records, for example (McGlone 1983, 1989).

There are two philosophical constraints to this approach. In the first instance, a pre-European or pre-human condition signifies a static point in time that does not represent the dynamics of ecosystem changes (Pimm 1991), nor does it take into account the current mix of species from which ecosystems must be re-assembled. It is therefore inappropriate to consider a static historical state as a desirable benchmark, as conservation managers will never be able to reach it; ecosystem conservation in this context will always be a failure.

In the second instance, our understanding of what pre-European or pre-human ecosystems looked like is poor and relies on archaeological data (Caughley 1989) and pollen deposits (McGlone 1983, 1989). These types of data often focus on the macro-scale of organisms and almost always reflect only presence/absence of species. In non-terrestrial ecosystems we are even more restricted by a lack of knowledge about these historic systems (Table 1).

An alternative suggestion could be to ignore benchmarks and define ecosystem outcomes in terms of succession predictions. As early as the late sixties, Odum (1969) presented 24 ecosystem traits that could change significantly during succession. Van Aarde et al. (1996) used species richness to evaluate a large ecosystem restoration project. This approach has good potential, but requires a more rigorous theoretical evaluation to create models for predicting the format of change during succession in these traits (Table 1).

Another alternative could be to ignore benchmarks and use value criteria (Ewel 1990) to evaluate outcomes. However, these criteria are often focused on functional aspects, e.g. productivity and nutrient cycling (Ewel 1987), which mask any form of species redundancy (Lawton 1994) that may characterise a particular ecosystem (Table 1).

# 4. Convergence models

## 4.1 CONVERGENCE AS A MEASURE OF RESILIENCE

Under Pimm's (1991) definition, ecosystem resilience should be measured in terms of recovery to some pre-defined state, which could be a set of species that occurred before disturbance, or alternatively a neighbouring site with undisturbed communities.

Wassenaar et al. (unpubl. report 2001) developed a conceptual convergence model for post-disturbance communities regenerating in the presence of a neighbouring benchmark site. Community convergence occurs when one or more communities reach the same state in terms of the identities, as well as absolute and relative abundances, of constituent species (Lawton 1994). This implies convergence to some point equilibrium in a multivariate species-space. However, such a benchmark also has spatial variability in species composition. Consequently Wassenaar et al. (unpubl. report 2001) defined their benchmark in terms of the mean multivariate distance (Fig. 2) between all sampling sites in an undisturbed coastal dune forest ( $D_{bm}$ ), and used  $D_{bm} \pm SD$  to estimate the variability in benchmark species composition. Based on three theoretical assumptions, they proposed a model of age-related negative exponential decay of multivariate distance towards a benchmark, of the form  $y = ae^{-kx} + b$ , where  $y$  is mean multivariate distance between regenerating and benchmark sampling units ( $D$ ),  $x$  is site age,  $a$  is the intercept,  $b$  is the asymptote, and  $k$  is a rate constant (Fig. 3). Under this model  $D$  should decay to the range  $D_{bm} \pm SD$ . The three assumptions that Wassenaar et al. (unpubl. report 2001) made represent the most basic factors that will govern the assembly of a community in the absence of intervening disturbances or stochastic environmental effects:

1. For any particular disturbed but regenerating site there is a limited regional colonist pool of species, i.e. the benchmark community, capable of taking advantage of environmental conditions on the site at each developmental stage (Belyea & Lancaster 1999).

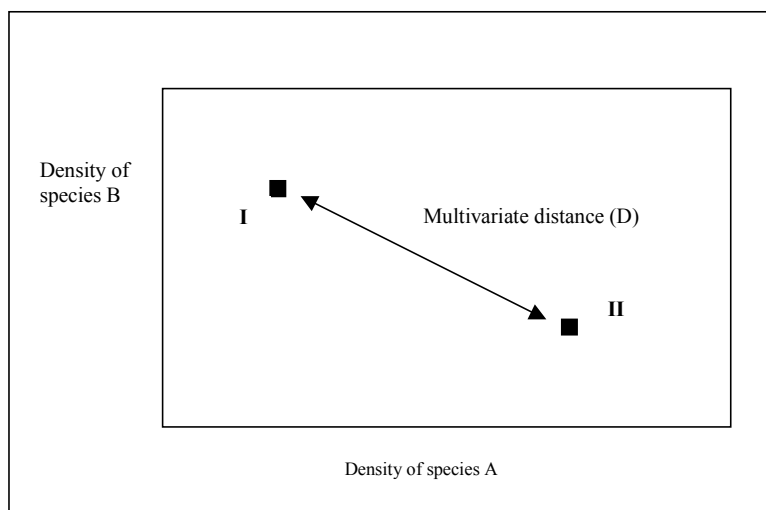
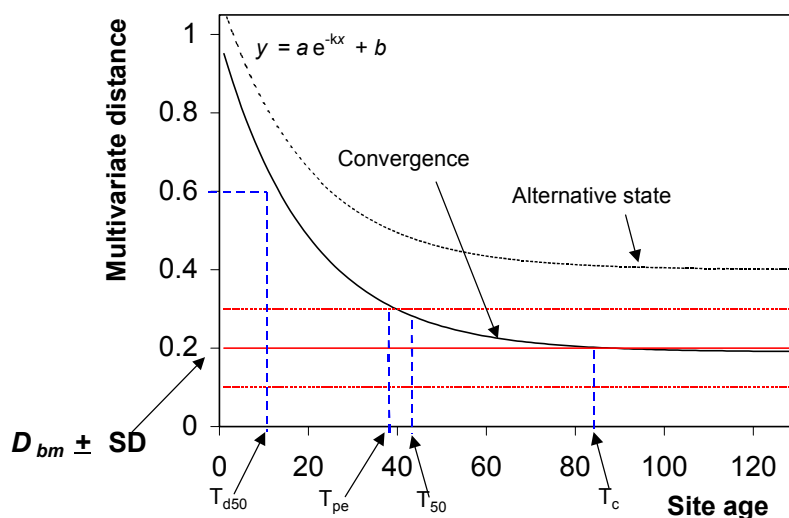


Figure 2. Example of how a multivariate distance between two sites (I and II) containing only two species (A and B) can be calculated. The measure illustrated here is called Euclidean distance, but several types of distance measures are available (see Legendre & Legendre 1998). Euclidean distance can be calculated as  $D = \sqrt{(A_I - A_{II})^2 + (B_I - B_{II})^2}$ . We can expand this to  $n$  dimensions to represent sites containing  $n$  species. We expect  $D$  to decrease if I and II become more similar in species composition.

Figure 3. Conceptual model describing the relationship of stand age and or time with multivariate distance between a biological community/group on a developing site and community/group on a benchmark target site. The lines representing  $D_{bm}$  and  $D_{bm} \pm SD$  are drawn across the figure for illustrative purposes only, and no relationship with site age is implied. Annotations are explained in the text.



2. There is a trade-off in species traits such that species adapted to a certain set of resources (including resources such as habitat) in the initial post-disturbance phase are not adapted to later sets. The corollary of this is that the time since disturbance represents a resource supply gradient for all assemblages (McCook 1994).
3. Invasion resistance increases with diversity/complexity/time since disturbance, with the result that the rate of multivariate distance decay decreases exponentially with age (Lockwood & Pimm 1999).

This model allows the evaluation of convergence (i.e.  $D_{bm} + SD > b > D_{bm} - SD$ ) or non-convergence (i.e.  $b > D_{bm} + SD$ ). Because of the inherent equilibrium nature of the model, non-convergence implies the development of an alternative equilibrium state. Non-equilibrium dynamics can only be evaluated in terms of the dispersion of  $D$  around the fitted model, or in apparently linear trajectories with relatively long predicted return times.

#### 4.2 CONVERGENCE OF COASTAL DUNE FORESTS

The results of Wassenaar et al. (unpubl. report 2001) are summarised in Appendix 1. They tested for the occurrence of convergence or alternative equilibrium states in six different assemblages. Their approach focused on three trophic levels (herbs, and trees; millipedes, and dung beetles; small mammals, and birds) and one abiotic group (soil) on post-mining regenerating coastal dune forest communities by evaluating the asymptote (i.e. the term  $b$  in the model) after fitting the above-mentioned exponential model to their data. They also evaluated the time to convergence for those groups predicted to converge. They used three different distance indices (DI) reflecting multivariate distance between sites in terms of species identity (Ochiai's distance), relative abundance (chord distance), and absolute abundance (Bray-Curtis distance). Five assemblages, i.e. trees (72–75 years), millipedes (46 years), mammals (12–94 years), birds (40 years), and soil (87 years) were predicted to converge in terms of at least one DI. Soils were essentially similar to the benchmark from the very youngest stages, with the consequence that the model was probably not applicable. Birds showed a better fit than any of the other assemblages. Dung

beetles and herbs were predicted to reach alternative equilibrium states. Mammal and millipede communities were the most variable, although this was dependent on DI and probably not the result of the same mechanisms.

The different DI values elucidated finer-scale patterns in community structural development and illustrated the importance of using different indices when evaluating community similarity. For example, the data on dung beetle species identity fitted the model relatively well, but showed a convergence-divergence pattern when taking account of species abundances. Those assemblages that were dominated by one or two species with widely different abundances between the different aged sites tended to show simple patterns in terms of species identity, but not in terms of species abundances. To some extent the results reflect the differences in probable dispersal and establishment rates between assemblages, with trees predicted to take longer to reach an internal alternative state than any of the other convergent assemblages.

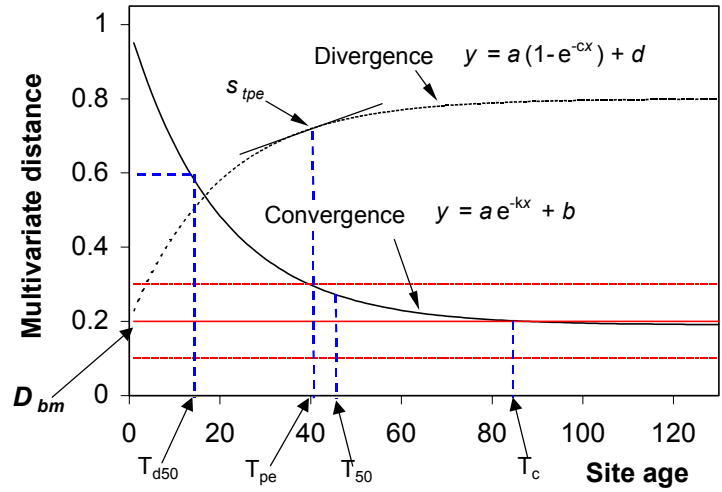
Insofar as colonisation of newly disturbed areas is dependent on species pool effects and species interactions, these results have illustrated the possible existence of a regional equilibrium state in two vertebrate assemblages, one invertebrate assemblage, and one plant assemblage of coastal dune forests. These results have a bearing on the restoration of ecological systems where structural and functional restoration for conservation is an explicit objective.

### 4.3 CONVERGENCE - DIVERGENCE MODEL

Let us consider that a general convergence model exists based on the propositions of Wassenaar et al. (unpubl. report 2001). What does this mean in the New Zealand context? Or, how can we use this information for situations where no explicit benchmark exists? We propose the development of a divergence model for the data sets where we explicitly have convergence, i.e. a benchmark towards which successional stages are developing. Our expectations are that the assumptions of Wassenaar et al. (unpubl. report 2001) should result in a general divergence model with the simplest relationship being that of  $y = a(1 - e^{-cx}) + d$ , the inverse of their convergence model (Fig. 4). In this case the multivariate distance measure is derived from the starting point at age zero relevant to which all other multivariate distance measures at age  $x$  are calculated.

Four points in the convergence model are of interest to us.  $T_c$  is defined when  $\hat{y} = D_{bm}$  and represents the point in time when total convergence has taken place as defined earlier.  $T_{50}$  is half the time to reach full convergence i.e.  $0.5T_c$ . We evaluate the slope of the tangent ( $s_t = dy/dx$ ) at  $\hat{y} = ae^{-kT_{50}} + b$  and expect  $s_t < 0$  for convergence to result. We expect that if  $s_t > 0$ , no convergence will occur, probably as a result of significant influences of environmental conditions during development. Most importantly, a general model predicts that  $s_t$  should be constant irrespective of the value of  $T_{50}$ . The concurrent divergence model should therefore also predict a constant  $s_t$  for  $\hat{y} = a(1 - e^{-cT_{50}}) + d$ , which we designate as  $s_{t50}$ . For data sets lacking a mature benchmark, we expect  $T_{50}$  to have been reached for that system when  $s_{t50}$  has been reached, and we can therefore estimate  $T_c$ .

Figure 4. Divergence model or reciprocal general resilience model independent of a benchmark.



However, because of the non-linear nature of our convergence model we do not expect that convergence would have been half completed at  $T_{50}$ . We consequently also define  $T_{d50}$  which is  $x$  where  $y = (D_0 - D_{bm}) / 2 + D_{bm}$ , with  $D_0$  the multivariate distance at time 0. At  $T_{d50}$  we also evaluate the slope of the tangent and expect  $s_t < 0$  if convergence will result. Similarly if  $s_t > 0$ , no convergence will occur, probably as a result of significant influences of environmental conditions during development. As before, the concurrent divergence model should also predict a constant  $s_t$  for  $\hat{y} = a(1 - e^{-ct_{d50}}) + d$ , which we designate as  $s_{td50}$ . If  $s_{td50}$  has been reached in data sets lacking mature benchmarks we can conclude that the recovering system is half way towards becoming what it eventually will be.

Our final point concerns the potential occurrence of boundary attractors, priority effects or alternative stable states (Grover & Lawton 1994). Here we define a point  $T_{pe}$ , which is  $x$  when  $\hat{y} = D_{bm} + SD$ . Once again convergence is expected if  $s_t < 0$ , with boundary attractors, priority effects, or alternative stable states expected if  $s_t > 0$ . As before, the divergence model is used to predict a constant  $s_t$  at this point, designated  $s_{tpe}$ , and, as before,  $s_{tpe}$  can be used to evaluate the development progress in a system lacking a benchmark state.

The approach suggested here attempts to overcome the problem of defining a benchmark in systems where no examples exist. Our model essentially proposes that a trajectory of change would be the target instead of a particular state.

## 5. Conclusions and recommendations

We have shown that approaches based on convergence theory could be useful in addressing one of the key conservation problems in New Zealand, i.e. what an ecosystem should look like considering past species losses and the abundance of naturalised species. We have proposed a model to employ a

stability criterion on a community level and suggest that selection of communities at various trophic levels will reflect stability at an ecosystem level. However, to date we are aware of only one case study (Wassenaar et al. unpubl. report 2001). We therefore suggest a collation of as many time-series data sets worldwide as possible where species composition of post-disturbance regenerating biological communities have been recorded in the presence of an explicit benchmark. Using the theoretical framework created here, a general convergence model should be developed. Such a general model should focus on finding generalities in tangent slopes for various trophic levels and ecosystems. This could be achieved in the following steps:

1. Develop a general convergence model for various trophic levels and ecosystems
2. Develop a general divergence model directed at evaluating resilience of ecosystems.
3. Evaluate time-series data in New Zealand, focusing on mainland islands and marine reserves.

Such a general model will have wide applicability in conservation management of anthropogenically disturbed landscapes with no surviving reference ecosystems.

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# Appendix 1

## CONVERGENCE OF COASTAL DUNE FORESTS

A summary of results from the Wassenaar et al. (unpubl. report 2001) model describing the exponential decay over time (= site age) of multivariate distance from regenerating coastal dune forest sites of different ages to a benchmark target site, for three distance indices (Legendre & Legendre 1998). Ochiai's distance reflects multivariate distance only in terms of species identity, chord distance reflects distance in terms of species' relative abundances, and Bray-Curtis distance reflects distance in terms of species' absolute abundance. Also included is the site age at which the points  $T_c$  (total convergence),  $T_{d50}$  (half-life),  $T50$  (i.e.  $T_c/2$ ) and  $T_{pe}$  (priority effects) are predicted to occur, with the associated slope of the tangent line at each particular point, for six biological groups and one abiotic resource. Hyphens indicate that a particular point will not be reached, or, as in the case of Ochiai's distance for soil, that the particular analysis was not done. The model was fitted using the program Graphpad Prism (Graphpad Software Inc., San Diego, CA 92121, USA).

**Ochiai's distance**

	SOIL		HERBS		TREES		DUNG BEETLES		MILLIPEDES		SMALL MAMMALS		BIRDS	
Model	-		$y = 0.32e^{-0.01x} + 0.66$		$y = 0.28e^{-0.02x} + 0.70$		$y = 0.22e^{-0.15x} + 0.57$		$y = 0.73e^{-0.29x} + 0.71$		$y = 1.11e^{-0.00x} - 0.38$		$y = 0.55e^{-0.05x} + 0.46$	
R <sup>2</sup>	-		0.51		0.69		0.81		0.44		0.014		0.91	
	<i>Site age</i>	<i>Slope</i>	<i>Site age</i>	<i>Slope</i>	<i>Site age</i>	<i>Slope</i>	<i>Site age</i>	<i>Slope</i>	<i>Site age</i>	<i>Slope</i>	<i>Site age</i>	<i>Slope</i>	<i>Site age</i>	<i>Slope</i>
T <sub>c</sub>	-	-	-	-	-	-	-	-	-	-	12.01	0.0037	36.96	0.0039
T <sub>d50</sub>	-	-	85.51	0.0013	49.01	0.0021	14.71	0.0037	8.08	0.02	5.94	0.0038	11.62	0.015
T <sub>pe</sub>	-	-	408.07	0.000044	72.02	0.0014	-	-	-	-	-22.06	0.0041	27.35	0.0071
T <sub>50</sub>	-	-	-	-	-	-	-	-	-	-	6.01	0.0038	19.85	0.01

**Chord distance**

	SOIL		HERBS		TREES		DUNG BEETLES		MILLIPEDES		SMALL MAMMALS		BIRDS	
Model	$y = -0.25e^{-0.27x} + 0.68$		$y = 0.61e^{-0.003x} + 0.81$		$y = 0.30e^{-0.01x} + 1.12$		$y = 0.46e^{-0.27x} + 0.77$		$y = 0.97e^{-0.31x} + 1.07$		$y = 4.52e^{-0.01x} - 3.25$		$y = 0.69e^{-0.10x} + 0.81$	
R <sup>2</sup>	0.80		0.42		0.61		0.27		0.44		0.17		0.87	
	<i>Site age</i>	<i>Slope</i>	<i>Site age</i>	<i>Slope</i>	<i>Site age</i>	<i>Slope</i>	<i>Site age</i>	<i>Slope</i>	<i>Site age</i>	<i>Slope</i>	<i>Site age</i>	<i>Slope</i>	<i>Site age</i>	<i>Slope</i>
T <sub>c</sub>	-	-	-	-	-	-	-	-	-	-	24.71	0.024	-	-
T <sub>d50</sub>	3.69	-0.025	339.38	0.00066	113.25	0.0009	9.16	0.01	6.54	0.039	11.89	0.026	7.43	0.033
T <sub>pe</sub>	-	-	-	-	74.65	0.0014	-	-	5.97	0.047	12.34	0.026	18.62	0.01
T <sub>50</sub>	-	-	-	-	-	-	-	-	-	-	12.36	0.026	-	-

**Bray-Curtis distance**

	SOIL		HERBS		TREES		DUNG BEETLES		MILLIPEDES		SMALL MAMMALS		BIRDS	
Model	$y = -0.07e^{-0.02x} + 0.64$		$y = 0.28e^{-0.01x} + 0.72$		$y = 0.20e^{-0.01x} + 0.81$		$y = 0.24e^{-0.27x} + 0.73$		$y = 0.36e^{-0.06x} + 0.67$		$y = 0.51e^{-0.01x} + 0.41$		$y = 0.35e^{-0.06x} + 0.67$	
R <sup>2</sup>	0.11		0.42		0.64		0.47		0.40		0.08		0.87	
	<i>Site age</i>	<i>Slope</i>	<i>Site age</i>	<i>Slope</i>	<i>Site age</i>	<i>Slope</i>	<i>Site age</i>	<i>Slope</i>	<i>Site age</i>	<i>Slope</i>	<i>Site age</i>	<i>Slope</i>	<i>Site age</i>	<i>Slope</i>
T <sub>c</sub>	87.11	0.00022	-	-	-	-	-	-	46.92	0.0012	94.28	0.0019	-	-
T <sub>d50</sub>	25.73	0.00081	177.60	0.00058	69.04	0.001	9.20	0.0053	11.58	0.011	37.94	0.0032	11.57	0.01
T <sub>pe</sub>	-	-	-	-	72.46	0.00098	-	-	14.16	0.0093	45.16	0.0030	24.05	0.0048
T <sub>50</sub>	43.56	0.00056	-	-	-	-	-	-	23.46	0.0051	47.14	0.0029	-	-