Indices for assessing coral reef fish biodiversity: the need for a change in habits

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Abstract

We present the first representative and quantified overview of the indices used worldwide for assessing the biodiversity of coral reef fishes. On this basis, we discuss the suitability and drawbacks of the indices most widely used in the assessment of coral fish biodiversity. An extensive and systematic survey of the literature focused on coral reef fish biodiversity was conducted from 1990 up to the present. We found that the multicomponent aspect of biodiversity, which is considered as a key feature of biodiversity for numerous terrestrial and marine ecosystems, has been poorly taken into account in coral reef fish studies. Species richness is still strongly dominant while other diversity components, such as functional diversity, are underestimated even when functional information is available. We also demonstrate that the reason for choosing particular indices is often unclear, mainly based on empirical rationales and/or the reproduction of widespread habits, but generally with no clear relevance with regard to the aims of the studies. As a result, the most widely used indices (species richness, Shannon, etc.) would appear to be poorly suited to meeting the main challenges facing the monitoring of coral reef fish biodiversity in the future. Our results clearly show that coral reef scientists should rather take advantage of the multicomponent aspect of biodiversity. To facilitate this approach, we propose general guidelines to serve as a basis for the selection of indices that provide complementary and relevant information for monitoring the response of coral reef fish biodiversity in the face of structuring factors (natural or anthropic). The aim of these guidelines was to achieve a better match between the properties of the selected indices and the context of each study (e.g. expected effect of the main structuring factors, nature of data available).

Introduction

Quantifying biodiversity on the basis of diversity indices is essential both for developing successful policies to mitigate biodiversity loss (Perrings et al. 2011) and for addressing ecological issues, such as the relationship between biodiversity and ecosystem functions (Loreau et al. 2001). Diversity now appears as a complex concept in the sense, that is, a multicomponent concept (Purvis and Hector 2000; Magurran and McGill 2011). This means that indices may be related to various diversity components (or facets), such as the number of species in a species assemblage, evenness (the distribution of species abundance within a species assemblage), rarity (e.g., the number of species below a predefined threshold based on their occurrence), taxonomic diversity (the taxonomic breadth of the community with reference to the Linnean classification), functional diversity (the range of traits present in the community), and phylogenetic diversity (the evolutionary breadth of the community). A wide range of indices are available for investigating each of the main diversity components, and some families of indices are related to several components (Magurran and McGill 2011). The multicomponent aspect of biodiversity also means that different diversity components may exhibit different responses in the face of disturbances, and they may also impact key ecosystem functions differently (Wilsey et al. 2005; Mouchet et al. 2010). Consequently, the
selection of the diversity components studied, and of the indices related to these components, may strongly impact our perception of both the biodiversity “patterns” and the role of biodiversity in ecosystem functioning.

This general issue is of particular interest in the context of coral reef fishes. Firstly, coral reefs contain the most diverse fish assemblages to be found anywhere (around 6000–8000 species, Lieske and Myers 2001). Secondly, numerous human populations are highly dependent on the ability of coral reefs to provide ecosystem goods and services (e.g., fisheries, tourism, Bellwood et al. 2004). Thirdly, a serious decline in coral reef fish populations has been observed worldwide due to many factors, such as climate change (Munday et al. 2008; Graham et al. 2013), overfishing (Paddack et al. 2009), invasive species (Kulbicki et al. 2011), and pollution (Adjeroud et al. 2010). For all of these reasons, monitoring coral reef fish structure is considered as a major challenge and diversity indices are widely used for this purpose. In this context, we present a quantified overview of the relative importance of the indices used worldwide in the assessment of coral reef fish biodiversity. On this basis, we discuss the suitability and weakness of the most widely used indices in the assessment of coral fish biodiversity. Finally, we provide guidelines for selecting the diversity metrics best suited, according to the context and available data, to monitoring the response of coral reef fish biodiversity to natural and anthropogenic forcings.

Materials and Methods Used for this Review

In order to obtain a representative sample of the body of work dedicated to assessing coral reef fish biodiversity, an extensive and systematic survey of the literature was conducted. A list of search terms was applied in the widely used database Web of Science® (Falagas et al. 2008) from 1990 up to the present. The 1990s correspond to a period where questions related to biodiversity both increased and diversified (Cousins 1991; Gaston 1994; Humphries et al. 1995). The search keywords were as follows: Topic = ((Diversity OR “species*richness” OR evenness OR equitability OR “species*density” OR rarity OR OR taxonomic OR functional OR phylogenetic) AND (“fish* assemblage*” OR “fish* community*”) AND (coral* OR reef*)) NOT (genetic*)). We carried out a two-step selection procedure. First, the search was limited to scientific journals with an impact factor (ISI) greater than or equal to 1.5. In a second step, we read the abstracts of all papers that emerged from this search (namely 401 papers from 57 journals) and we only selected studies that are focused on coral reef fish biodiversity. Eliminated publications mainly dealt with noncoral reef ecosystems (e.g., Mediterranean artificial reefs). At the end of this process, 205 studies (from 43 journals, see Appendix S1 for the list) were included. Because our study is focused on the relative importance of the main family of indices used for assessing the biodiversity of coral reef fishes, we did not aim to survey exhaustively all the works which have been published in this domain. The selection approach we have adopted should be thus considered as a sampling tool enabling us to sample a broad, representative, and clearly delimited part of the full set of publications assessing coral reef fish biodiversity worldwide during the last two decades. For clarity, in this paper we have used the word biodiversity as an overall generic term, while the term diversity relates to the components or indices.

A Critical Overview of Indices Used in Coral Reef Fish Studies

Our results showed that coral reef fish biodiversity is generally assessed using a small range of families of indices (Figs. 1 and 2), with a high dominance of indices representing the “number of species” component, and to a lesser extent of heterogeneous indices (e.g., Shannon Index, Shannon and Weaver 1949). Indices of this family are commonly called heterogeneous indices (Peet 1974; Williams et al. 2005) because they are not focused on a single component, but take into account both the number of species and the evenness components. Indices allowing the assessment of other diversity components are either under-represented (e.g., functional diversity), or not represented at all (e.g., phylogenetic diversity).

Dominance of species richness: an easy to perform but poorly suited approach

The strong dominance of the use of the number of species component we have recorded for studies dealing with coral reef fishes (92.1%, Fig. 1) is consistent with the situation found in numerous other marine and terrestrial ecosystems (Gotelli and Colwell 2001; Chiarucci et al. 2011; Chao and Jost 2012). The fact that this concept is both easy to understand and based on relatively simple to obtain data (only the identity of the species is needed) broadly explains its wide usage. The basic knowledge required as well as the sampling effort and associated costs are less than those needed for assessing other diversity components (e.g., evenness and functional diversity). Here, the number of species component was mainly assessed through the species richness index (183 publications of the 205 papers, i.e., 89.3%). This result contrasts with the fact that a wide range of indices has been proposed in the literature for estimating the number of species component (e.g., nonparametric estimators of species richness, see Chao 1984; Colwell and Coddington 1994).
In addition, we found that 38.8% of publications focusing on resistance and resilience of coral reef fishes in the face of disturbances (e.g., coral bleaching, human impact, fisheries) used species richness as the sole proxy of biodiversity. However, studying the biodiversity response to disturbances, the number of species is altered only in the last and most serious stages, when the ecosystem has been already strongly impacted (Wilsey and Potvin 2000). In contrast, the effects of a given disturbance on a community firstly impact species abundance (Walker et al. 2006). Altering the relative abundance of species also alters (1) inter- and intraspecific interactions (Robertson 1996; Hillebrand et al. 2008) and (2) the distribution of traits in the community (Petchey and Gaston 2006). Such changes in community structure (not taken into account by estimates of number of species) have strong implications for both the response and the functioning of the coral ecosystem. Thus, focusing biodiversity studies only on the species richness index cannot provide a basis for proper monitoring of the resistance and resilience of a coral fish community in the face of anthropogenic disturbances and/or global change.

**Incorporating species abundance variability: the over-use of heterogeneous indices**

Coral reef fish studies that incorporate species abundance in the computation of diversity indices are mainly based on the use of heterogeneous indices. Indices of this family are found in 54 of the studies analyzed (i.e., 26.3%, Fig. 1) mainly through the use of the Shannon index (Shannon and Weaver 1949). The prevalence of heterogeneous indices in coral reef fish studies is in accordance with the practices found in numerous other marine and terrestrial ecosystems (Jost 2006). However, the use of heterogeneous indices, that mix evenness and species richness in a single value, raises various issues. The degree of association/independence between heterogeneous indices and each of its two basic components (number of species and evenness) is unclear (Beisel et al. 1998) and may vary from one situation to another (see references in Gaertner et al. 2008). Thus, the combination of species richness and evenness in a single value not only leads to loss of information by reducing two dimensions to one (Purvis and Hector 2000), but also provides a descriptor which is of poor value in terms of monitoring and management. Specifically, an increase in the Shannon index (computed in 52 publications, i.e., 25.4%) may have several contrasting meanings. It can be a consequence of an increase (1) in both evenness and species richness, or (2) in species richness while evenness remains stable (or even slowly decreases), or (3) in evenness while species richness remains stable (or even slowly decreases). As a consequence, the use of heterogeneous indices alone does not provide a satisfactory basis for understanding either which of its two basic diversity components vary or to what extent it/they vary. Numerous other problems related to

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**Figure 1.** Assessing coral reef fish diversity. Relative importance of the main diversity components assessed in the set of the 205 papers reviewed in this study. Radar plot shows the percentage of publications assessing each diversity component. The corresponding number of papers is given in brackets. Heterogeneous indices that mix two components (number of species and equitability) are also displayed because of their popularity.
heterogeneous indices have been described in the literature (e.g., May 1975; Stirling and Wilsey 2001; Magurran 2004). In short, the number and variety of drawbacks related to heterogeneous indices should call into question the suitability of their extensive use in the assessment and monitoring of biodiversity in general and in coral fish studies in particular.

An alternative and more relevant suitable way of incorporating abundance variability in biodiversity studies could be based on the use of “pure evenness” indices that are strictly focused on the evenness component. However, studies using “pure evenness” indices are both uncommon (only 19 of 205, i.e., 9.3%) and based on a limited range of indices. We found only three indices of this kind, with a high dominance of the Pielou index (Pielou 1966) (16 studies). Although the use of pure evenness indices should be promoted, the dominant use of the Pielou index raises problems. While this index is supposed to focus exclusively on the variability of evenness, it is, in fact, for purely mathematical reasons, positively correlated with species richness (Ma 2005). Pielou’s index is strongly dependent on sample size and is biased when the number of species is high (Warwick and Clarke 1995). This latter point alone is enough to call into question the suitability of using Pielou’s index in ecosystems such as coral reefs, which are known to support the greatest marine species richness.

**Functional diversity: a need to revisit and enrich the current practices**

Although both richness and distribution of functional traits in coral reef fish communities are assumed to play a key role in the functioning of the whole coral reef ecosystem (Raymundo et al. 2009; Mouillot et al. 2014), only 29.3% of the studies we have reviewed (60 of 205) took into account functional information for investigating the structure of coral reef fish communities. This limited use of functional information might be partly explained by certain difficulties specifically related to coral reef fishes. In particular, incomplete knowledge on the biology and ecology of fishes is a severe limitation on the ability to obtain accurate data on a given functional trait simultaneously for all the fish species belonging to a community (Villéger 2008a). This problem is aggravated for coral reef fish communities, which are characterized by strong richness and a very extensive range of distribution in the tropical belt (Bellwood et al. 2003). Values of traits for a given species may vary from one place to another and from one life stage to another.

In addition, a kind of inertia in the habits and practices of the scientific community working on coral reef fishes and slowness to adopt new concepts and tools, initially developed in other ecosystems, might also contribute to the very poor consideration of functional diversity in coral reef fish studies. Firstly, regarding the availability of functional information, we found that trophic information was strongly dominant in studies incorporating functional aspects (58 of the 60 studies concerned). The dominance of this trait is not surprising. It is considered as a potentially major biological trait for structuring communities (Fox and Bellwood 2014), and the information related to this trait is usually known for all the coral reef fish species, at least roughly, through their belonging to a trophic group (e.g., herbivorous). In this context, what is more surprising is that around 70% of the 205 studies we reviewed did not incorporate functional information while many of them could have included it, at least on the basis of the definition of trophic groups. Secondly, we found that only 21 of the 60 studies taking into account functional information used diversity indices. The 39 other studies were restricted to abundance (or biomass) per functional group (e.g., number of carnivorous individuals) but did not use any diversity indices. Surprisingly, although it was both technically possible and consistent with their aims in many cases, most of the studies dealing with functional information used neither diversity indices nor other tools allowing the explicit assessment of the variety of functional traits in the community under study. Thirdly, regardless of the methods used for incorporating functional information (i.e., using...
diversity indices or not), publications were almost exclusively based on the predefined function of functional groups (59 of 60 studies). This strategy is related to the fact that the decline or loss of important functional groups has the potential to severely compromise ecosystem functions and the resilience of coral reefs (see Bellwood and Hughes 2001). However, approaches based on predefined functional groups suffer from several drawbacks (Petchey et al. 2004, 2009). One of the issues is the exclusion of functional differences that occur between organisms belonging to the same functional group (Petchey and Gaston 2006). All species within a group (e.g., carnivorous species) are assumed to be identical, even though this is rarely the case (e.g., sessile invertebrate feeders vs piscivores).

Assessing “functional diversity indices” that take into account the degree of differences between species in reference to functional variables, could be a solution for bypassing the issues related to the predefined functional groups (Petchey and Gaston 2002; Mason et al. 2003; Mouillot et al. 2005). The use of these tools is increasing for several marine (Villéger et al. 2010; Stuart-Smith et al. 2013) and terrestrial (Conti and Díaz 2013) ecosystems. However, they are still very uncommon for coral reef fish studies (only 1% of publications in our review) even though quantitative information on some functional traits (trophic index, locomotion traits, etc.) could have been used. In addition, the only functional diversity index (FD index, Petchey and Gaston 2002) found in our review (Martins et al. 2012) is based on the presence-absence data. FD index estimates only depend on the value taken by each species for the functional traits studied. The fact that a species with a given functional trait is rare or abundant has no impact on our perception of functional diversity when using functional diversity indices of this kind.

The multicomponent aspect of biodiversity: a major property but still poorly taken into account

Over the last two decades, both theoretical (Cousins 1991; Purvis and Hector 2000) and experimental studies conducted in both marine and terrestrial ecosystems (Wilsey et al. 2005; Mérigot et al. 2007; Wilsey and Stirling 2007; Heino et al. 2008; Chalcraft et al. 2009) have shown that biodiversity is both a complex and multidimensional concept. Surprisingly, although the coral reef is the most diverse and complex ecosystem in the aquatic domain (Lieske and Myers 2001), our study reveals that the multicomponent aspect of coral reef fish biodiversity was, in general, both weakly and poorly taken into account. Almost half of the scientists that we reviewed did not consider the multicomponent aspect of biodiversity at all. For 95 papers analyzed (i.e., 46.3%), variation in biodiversity is only pictured as variation in species richness. According to this rationale, biodiversity is a simple and one-dimensional concept that can be estimated on the basis of species richness alone (Cairns et al. 1993). Moreover, studies taking into account the multicomponent aspect of coral reef fish biodiversity were not always based on relevant methodological approaches. One part of the studies analyzed (24 studies, i.e., 11%) considered the multicomponent aspect of biodiversity only on the basis of heterogeneous indices, which are restricted only to two components and suffer from numerous drawbacks.

An alternative, and more suitable, approach to integrate the multicomponent aspect of biodiversity was based on the simultaneous use of multiple indices related to several diversity components. Recent studies in terrestrial ecosystems, focused on different taxa, such as plants (Wilsey et al. 2005), birds (Devictor et al. 2010), or stream macroinvertebrates (Heino et al. 2008), as well as other studies on marine fishes conducted in temperate and tropical ecosystems (Gaertner et al. 2010; Villéger et al. 2010; Stuart-Smith et al. 2013), have shown the value of such a methodological approach. However, in our review, fewer than a quarter of the studies simultaneously investigated biodiversity through multiple indices related to more than one component and only 18 studies (8.7%) were based on indices related to three diversity components.

In addition, the way by which studies based on multiple indices are carried out raised several problems. In the large majority of cases, the selection of the indices was made regardless of either their properties or their empirical relationships. While taking into account, the multicomponent aspect of biodiversity must be encouraged, the approach consisting in using multiple indices regardless of their complementarity may be counter-productive (Purvis and Hector 2000; Magurran 2004; Mérigot et al. 2007; Gaertner et al. 2010). This situation may lead to working on a set of indices that are “trivially” correlated and may only offer the illusion of taking into account the multicomponent aspect of biodiversity. Ecologists may confuse a biological relationship with a mathematical relationship because of an inadequate selection of the diversity indices examined (see DeBenedictis 1973; for pioneering work on this issue). However, easy-to-use methodological frameworks that have been proposed in other ecosystems for removing trivially correlated indices (e.g., Mérigot et al. 2007 on temperate groundfishes) might be used to overcome this problem in coral reef fish studies. In short, in contrast to the general practice we found in this review, authors should take great care in selecting indices on the basis of their complementarity.
This is a preliminary, but major step, toward properly and efficiently taking into account the multicomponent aspect of biodiversity.

More generally, we also examined whether authors offered a rationale to support the choice of indices and/or components they used. Various types of justification could be expected, such as the aims and the context of each study, and/or the efficiency and the complementarity of indices. However, among the 205 papers reviewed, only 8 publications offered a detailed justification. This means that a very large majority of studies did not provide any information regarding the reasons for which they assessed biodiversity on the basis of one index rather than another. All these observations evidence the fact that the selection of diversity indices is too often mainly driven by empirical criteria, such as the “popularity” of indices and/or the reproduction of widespread habits. We are aware that the nature and accuracy of available data may influence the selection process and restrict the range of diversity indices that can be studied. However, within this framework of constraints, the aims and context of each study should be the most important criteria influencing the index selection process. This is currently far from being the general rule.

Toward Guidelines for Selecting Indices

Our study revealed that choosing a diversity index is often not considered as a key feature in coral reef fish ecology studies. However, the complex and multicomponent aspects of biodiversity clearly imply that using one index rather than another is not meaningless and can strongly alter our perception of biodiversity patterns and responses. Defining which indices should be promoted and which indices should be avoided is a complex issue, notably because no index is drawback free. However, it is possible to propose certain guidelines for helping coral reef fish ecologists in selecting indices. Given that monitoring the response of biodiversity in the face of natural and anthropogenic forcing is currently considered as the major challenge for coral ecosystems (Jones et al. 2004), we here focus our proposal on this issue. Here, we take into account the context and priority of each study according to three yes-no questions (Fig. 3). These three questions are not exclusive and may be simultaneously raised in a single study.

Are the main structuring factor(s) studied assumed to impact the number of species?

The use of species richness, which was strongly dominant in our review, seems to be a relevant index in such a situation (Fig. 3A). However, other approaches, such as nonparametric estimators of true total species richness, could be used for estimating the number of species component (e.g., Chao1, Chao2 see Chao 1984; Gotelli and Colwell 2011; Chao et al. 2013). Indices of this family adjust the observed number of species by the importance of rare species for estimating a “true” total number of species. Rare species can be defined according to the number of individuals in a sample (e.g., using Chao 1) or to the degree of occurrence of species among a set of samples (e.g., Chao 2). The basic hypothesis, which assumes that the number of rare species is positively correlated with the number of non-detected species, seems to be relevant in complex habitats such as coral reefs. As a consequence, this family of indices, surprisingly not used among the 205 studies reviewed, could be promoted for assessing the number of species component of coral reef fish biodiversity. In the same vein, it can be useful to adjust the number of species according to the total number of individuals present in each sample unit to compensate for sampling effects. In such cases, Margalef’s (Margalef 1958) species richness index, which consists in dividing the number of species recorded by the total number of individuals in the sample, can be promoted for its ease of calculation and its widespread use (Magurran 2004), favoring interstudy comparisons.

Are the main structuring factor(s) studied assumed to impact the abundance distribution of species?

When the factors studied are assumed to impact the abundance distribution of species, assessing diversity on the basis of evenness indices is necessary (Fig. 3B). However, choosing a relevant evenness index is not a simple matter. Indices related to the evenness component may focus on different parts of the species abundance variability (Beisel et al. 2003). For instance, some evenness indices are more sensitive to the variation in rare species (e.g., Heip Index, Heip 1974) while others respond better to variation in the most abundant species (e.g., E1/D index, Smith and Wilson 1996). Taking into account, this property might be useful for monitoring purposes because the impact of disturbances on rare versus abundant species may vary according to the context and the structuring factor considered. For instance, some kinds of fisheries are known to threaten rare species more than common or abundant species (Hawkins et al. 2000). In such a context, evenness indices such as the Heip index (Heip 1974), that is, mainly sensitive to the variation of rare species, could be promoted (Fig. 3). In contrast, for fisheries focusing on the most abundant species (e.g., Friedlander and DeMartini 2002), indices such as E1/D...
index (Smith and Wilson 1996), that is, focused on the most abundant species, should be preferred (Fig. 3). In other cases, eutrophication can drive changes in community structure resulting in the domination of a limited number of herbivore fish species (Jones and Sym 1998). Here again, using an evenness index sensitive to the variation of the most dominant species but focusing on the subset of herbivorous species could be a relevant and original way to focus the monitoring effort on the effect of eutrophication. Consequently, selecting evenness indices on the basis of their properties could be a preliminary step toward better adjusting the selection of indices according to the structuring factor, that is, locally considered to be the top monitoring priority.

**Are the main structuring factor(s) studied assumed to impact the distribution of functions?**

Assessing the diversity of functions requires the availability of relevant information (the belonging to a functional group or values on functional traits) for all the species considered (Fig. 3C). As far as possible, in contrast to current practices, functional indices incorporating the degree of difference between species according to functional traits should be preferred to indices based on predefined groups. Among these indices, those taking into account the abundance distribution of traits within the community would be more relevant than those restricted to the presence–absence data (e.g., FD Index, Petchey and Gaston 2002). The Rao Index (Rao 1982) and some of the indices developed within the methodological framework of the “functional space” (e.g., FEve or FDiv, Villéger et al. 2008b; FDIs, Laliberté and Legendre 2010) meet these requirements. In addition, as for the evenness component, several indices related to the functional component can also provide different and sometimes complementary input (Mouchet et al. 2010). Thus, Mouillot et al. (2013) presented a theoretical framework, based on the simultaneous use of indices related to functional richness (FRic index), functional evenness (FEve, Villéger et al. 2008b or Ru, Ricotta et al. 2014), and functional divergence (FDiv, Laliberté and Legendre 2010 or Rao, Rao 1982), as a tool to reveal changes in disturbed communities. Furthermore, incorporating functional diversity in studies focused on the response of communities to disturbance is not only a...
matter of indices. It also calls for the reinforcement of knowledge of which functional traits other than trophic information are the most suitable for characterizing coral reef fish biodiversity. For instance, species mobility might be correlated with both species’ responses to local disturbances, such as habitat destruction from storms or trawling, and species’ ability to recolonize a depleted site from distant sources (Micheli and Halpern 2005).

In conclusion, we have shown that the selection of indices in a major part of coral reef fish studies is driven by an unclear and empirical process. In consequence, the most popular indices (e.g., species richness, Shannon, Pielou) are often not well tailored to the context and the priorities of the corresponding studies. Bellwood et al. (2004) stated that the worldwide decline of coral reefs calls for an urgent reassessment of current management practices. Our work suggests that this reassessment firstly implies urgent and thorough re-examination of biodiversity measurement practices, through a real consideration of the multicomponent aspect of biodiversity. In practice, authors should extend the list of traditionally used diversity indices and take into account the complementarity of the properties of indices (and possibly of their drawbacks) in order to select a set of indices fully tailored to the context and the aims of their study. This approach will involve breaking old habits and adopting new concepts and tools (some of them initially developed for other ecosystems). This will notably require the generalization of multicomponent approaches, while keeping in mind several guidelines for selecting indices according to the aims of the study, the expected impact of the factors studied and the properties and complementarity of the indices. This will also require the reinforcement of the effort dedicated to the collection of functional data as well as the popularization of recent functional diversity indices, such as those recently proposed within the framework of the functional space (see Villéger et al. 2008b; Laliberté and Legendre 2010).

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Conflict of Interest

None declared.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. List of reviewed papers.

Appendix S2. Codes, formula and references of the indices mentioned in figure 3.