

can be due to many factors, including lack of specific nutrients, oxygen level, temperature, pH and osmotic conditions as well as missing growth factors, possibly produced by other organisms in the community (Vannote et al. 2009). Culturing will always favor the organisms that are best at adapting to the conditions applied in the laboratory, and these organisms are not necessarily the most dominant or ecologically important organisms in the environment. Insights into the uncultured fraction have been fueled by sequencing of the 16S rDNA genes of bacteria from environmental samples, and this in turn has resulted in the identification of numerous new bacterial phyla, of which very few are represented by cultivated strains (Aeffmann and Wagner 2008; Stewart 2012).

Several methods that allow exploitation of the vast majority of microorganisms that are difficult to cultivate in the laboratory have been described. The methods can basically be divided into (1) improved cultivation techniques or (2) metagenomic methods. The improved cultivation techniques can be used to establish pure cultures or complex communities available for culture-dependent screenings or metagenomic approaches. The metagenomic methods are either based on sequencing of metagenomes and bioinformatic analysis or functional expression of metagenomic libraries to identify genes or gene clusters of interest.

Bioprospecting in extreme environments with non-standard conditions, such as low temperature, is not without additional challenges. Conventional cultivation may be difficult because of insufficient knowledge on media requirements or very prolonged incubation time, enrichment *in situ* may be problematic if the environment is located in remote areas, metagenomic analyses may be hampered by low amounts of environmental DNA, and heterologous expression of enzymes and other bioactive molecules may be challenging since most host organisms are not developed for extreme conditions. This review will present the methods developed for improved cultivation as well as the metagenomic approaches for bioprospecting with focus on the challenges faced by bioprospecting in cold environments. The methods that have been developed to deal with these problems will be summarized and possible routes to future improvements will be highlighted.

Cultivation-based bioprospecting

A number of techniques have been developed for improved cultivation of natural microorganisms in the laboratory or *in situ* in the environment. Although only a few of these methods have been used specifically to bring cold-adapted microorganisms into culture, they all have the potential to increase the output of cultivation-based bioprospecting projects in cold environments. It is important, however, to

keep in mind that cold-adapted microorganisms are faced with several challenges imposed by the low temperature. These include increased water viscosity, decreased diffusion rates, and not least reduced biochemical reaction rates (Feller 2013). For most biological systems, the activity of a mesophilic enzyme will be 15–80 times lower at 0 °C than at 37 °C (Gierleme et al. 2006). In general, cold-active enzymes maintain a high biochemical reaction rate at low temperature by having a more flexible structure, resulting in a lower substrate affinity and increased heat lability (Feller and Gayday 2003; Feller 2013). Therefore, when designing experiments, care should be taken not to expose enzymes or organisms to elevated temperatures, as this might lead to irreversible inactivation of enzymes.

If communities or pure cultures can be established under laboratory settings, they will in many cases be suitable for bioprospecting efforts. Most techniques have been developed for traditional laboratory conditions, e.g., 20 °C, 1 atm., pH 7, etc., and are often not directly applicable to organisms originating from extreme environments. However, since most laboratories are equipped with facilities that allow incubation at low temperatures, screening of cultivated cold-adapted organisms can be carried out simply using existing assays at low temperature. A classic example is plate-based screening using chromogenic substrates that develop detectable colors upon activity (Faulstich et al. 2012), and by combining a mixture of different insoluble chromogenic substrates, multiple activities can be detected by various color combinations in single plate experiments (Lee et al. 2004, 2005). Subsequent identification and cloning of genes of interest have been aided by the emergence of genomics and access to affordable whole genome sequencing of bacterial isolates.

The cultivation-dependent method of bioprospecting can involve several steps, ranging from traditional culturing to the various versions of optimized culturing conditions discussed below (Fig. 1). The subsequent isolation, screening and purification of microorganisms are typically done by plating on Petri dishes to obtain pure cultures for further analysis. Although improved cultivation methods may increase the proportion of cultivable microorganisms, many of these organisms will not grow as pure cultures in the laboratory. In addition, the specific gene or gene cluster responsible for the trait of interest often has to be identified to facilitate more efficient expression and characterization than possible with the natural isolate. Organisms solely capable of growing as microcolonies or as mixed communities can be analyzed by metagenomic approaches, which may also be applied directly to environmental samples. A useful coupling of culture-dependent and metagenomic methods is to use genomic DNA (gDNA) or rDNA from enrichment cultures or pure natural isolates for metagenomic methods (Hubel et al. 2004).

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Table of Contents Applied Techniques For Cold Environ 2vol

1. Understanding the eBook Applied Techniques For Cold Environ 2vol
 - The Rise of Digital Reading Applied Techniques For Cold Environ 2vol
 - Advantages of eBooks Over Traditional Books
2. Identifying Applied Techniques For Cold Environ 2vol
 - Exploring Different Genres
 - Considering Fiction vs. Non-Fiction
 - Determining Your Reading Goals
3. Choosing the Right eBook Platform
 - Popular eBook Platforms
 - Features to Look for in an Applied Techniques For Cold Environ 2vol
 - User-Friendly Interface
4. Exploring eBook Recommendations from Applied Techniques For Cold Environ 2vol
 - Personalized Recommendations
 - Applied Techniques For Cold Environ 2vol User Reviews and Ratings
 - Applied Techniques For Cold Environ 2vol and Bestseller Lists
5. Accessing Applied Techniques For Cold Environ 2vol Free and Paid eBooks
 - Applied Techniques For Cold Environ 2vol Public Domain eBooks
 - Applied Techniques For Cold Environ 2vol eBook Subscription Services
 - Applied Techniques For Cold Environ 2vol Budget-Friendly Options
6. Navigating Applied Techniques For Cold Environ 2vol eBook Formats

- ePub, PDF, MOBI, and More
- Applied Techniques For Cold Environ 2vol Compatibility with Devices
- Applied Techniques For Cold Environ 2vol Enhanced eBook Features
- 7. Enhancing Your Reading Experience
 - Adjustable Fonts and Text Sizes of Applied Techniques For Cold Environ 2vol
 - Highlighting and Note-Taking Applied Techniques For Cold Environ 2vol
 - Interactive Elements Applied Techniques For Cold Environ 2vol
- 8. Staying Engaged with Applied Techniques For Cold Environ 2vol
 - Joining Online Reading Communities
 - Participating in Virtual Book Clubs
 - Following Authors and Publishers Applied Techniques For Cold Environ 2vol
- 9. Balancing eBooks and Physical Books Applied Techniques For Cold Environ 2vol
 - Benefits of a Digital Library
 - Creating a Diverse Reading Collection Applied Techniques For Cold Environ 2vol
- 10. Overcoming Reading Challenges
 - Dealing with Digital Eye Strain
 - Minimizing Distractions
 - Managing Screen Time
- 11. Cultivating a Reading Routine Applied Techniques For Cold Environ 2vol
 - Setting Reading Goals Applied Techniques For Cold Environ 2vol
 - Carving Out Dedicated Reading Time
- 12. Sourcing Reliable Information of Applied Techniques For Cold Environ 2vol
 - Fact-Checking eBook Content of Applied Techniques For Cold Environ 2vol
 - Distinguishing Credible Sources
- 13. Promoting Lifelong Learning
 - Utilizing eBooks for Skill Development
 - Exploring Educational eBooks
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